Landscape scale deer management

Kristin Wäber

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School of Environmental Sciences

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Abstract

This thesis considers responses at landscape scale (450 km^2) to management of a multi-species deer assemblage across a heterogeneous forest and open habitat mosaic in Eastern England. The aims were to explore performance, variation in deer densities, source-sink dynamics and deer impacts on biodiversity across and within different landscapes. The performance of roe deer *Capreolus capreolus* in four contiguous and contrasting landscapes was investigated spanning 1966-2009. Performance differed between landscapes, this is likely to affect deer population dynamics and potentially contribute to source sink dynamics. Fragmented landscapes have been proposed to enhance and increase deer populations in adjacent habitats. However, although body mass of roe deer and Reeve's muntjac *Muntiacus reevesi* in a forested landscape was positively influenced by access to farmland, no positive effect on fertility of either species could be found. Knowledge of deer density is important for evidence based deer control. The performance of distance sampling thermal imaging was tested using three different analysis designs stratifying by block, year or habitat. No difference in deer density estimates across the analysis designs was found confirming the robustness and reliability of this method. Annual changes in deer numbers and estimates of fertility, juvenile survival and mortality were combined to examine potential source- sink dynamics in a forested landscape. Potential net emigration ranged from < 0 to several hundred animals for roe deer and for Reeve's muntjac may total 1200-1500 individuals annually. Large herbivores influence their environment with profound effects on biodiversity. Effects of a mixed species deer assemblage on bird abundance were assessed. Abundance of understorey dependent birds varied more widely among forest blocks than growth stages, but no clear relationship with differing deer species was established. This is one of the first studies investigating deer demography, densities and responses to deer management across large landscapes. Variations of deer performance and deer management strategies across wider scales may lead to source-sink dynamics affecting deer impacts on biodiversity. Therefore, to successfully reduce deer numbers and impacts it is necessary to incorporate an understanding of spatial variation in deer density, population growth and mortality in deer management strategies.

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Chapter One

Introduction

Introduction

Large herbivores are ecological engineers influencing and changing their environment (Danell et al., 2006). Depending on the species composition of herbivore assemblages, habitats differ in structure and diversity (Danell et al., 2006) and therefore herbivores act as keystone species in the landscape (Piraino et al., 2002). Removal of large herbivores from their environment, or conversely their overabundance, can drastically change the structure, ecological functioning and species composition of their ecosystems (McShea et al., 1997, Danell et al., 2006). Deer numbers in Europe and North America have been increased during the 20th century and are still increasing (Ward, 2005). Due to a lack of natural predators (e.g. wolf, lynx) the increasing deer population is mainly managed by culling to meet management objectives in most parts of Europe (Sinclair, 1997).

Almost without exception, forest ecosystems are profoundly influenced by human activity that has altered the presence, species composition and relative abundance of large herbivores and also their potential predators. This can have potentially profound effects on the structure, function and associated biodiversity of forest systems. Understanding the dynamics of natural and un-natural herbivores is key to the management of biodiversity impacts.

Deer impacts in North America and Europe

It is a well-known phenomenon that deer can have pronounced effect on their environment through browsing and grazing (Cooke and Lakhani, 1996), trampling (Cumming and Cumming, 2003), bark stripping and fraying (Gill, 1992) influencing diversity and abundance of plant and animal communities and therefore alter habitat quality (Danell et al., 2006).

The impacts of deer have been investigated in many areas of the world (Barrett and Stiling, 2006, Nomiya et al., 2003, Veblen et al., 1989, Fuller et al., 2005, Gill and Morgan, 2010). Numerous studies in America have addressed the impact of white-tailed deer (Horsley et al., 2003, Royo et al., 2010, Kraft et al., 2004) and black tailed deer (Gonzales and Arcese, 2008) on vegetation. In Europe the influence of herbivores on flora structure and composition has been the object of research in several studies (red deer *Cervus elaphus*: Pepin et al. (2006), Kienast et al. (1999), Palmer et al. (2003); fallow deer: Gill and Morgan (2010), Morecroft et al. (2001); roe deer: Kuiters and Slim (2002), Homolka and Heroldova (2003); moose *Alces alces*: Hegland et al. (2010), Suominen et al. (2008)).

Through preferential grazing of palatable species, and impacts on flower and seed production, deer shift abundance and frequency of plant species (Rooney and Waller, 2003, Tanentzap et al., 2009, Gill and Morgan, 2010, Cote et al., 2004) and affect understorey dependent species such as invertebrates (Feber et al., 2001, Huntzinger et al., 2008, Allombert et al., 2005b), birds (Gill and Fuller, 2007, Holt et al., 2010, McShea and Rappole, 2000) and small mammals (Flowerdew and Ellwood, 2001).

Deer as un-natural keystone species

Hairston et al. (1960) introduced the theory of trophic interactions or "top-down" models stating that herbivores are controlled by predators which limit herbivore population size and limit herbivore impacts on the plant community. Removing carnivores as control element of herbivores should therefore lead to an increase in herbivore density and overexploitation of vegetation. Dynamical interactions between trophic levels including large carnivores preying on herbivores have been part of all habitat types before direct persecution in the 18th and 19th century did lead to the disappearance of large carnivores in Europe (Breitenmoser, 1998). A top-down predator controlled model is widely discussed and has been questioned by for example by Martin et al. (2010) and Murdoch (1966) as evidence of top-down herbivore limitation has only been tested in few studies (e.g. Beschta and Ripple (2009)).

Density dependence occurs in large herbivores, but is generally not strong enough to regulate or limit population growth (Clutton-Brock and Albon, 1989, Sinclair, 1997, Putman et al., 1996). Therefore, in the absence of predators, deer populations may increase to high levels that profoundly alter forest systems. For example, Simard et al. (2008) investigated body mass and reproductive rates of an insular population of white tailed deer *Odocoileus virginianus* on a predator free island in Canada. Despite a decline in body mass they found no change in overall reproductive rates; as a result the deer population continued to increase in the absence of predation.

It has been hypothesised that herbivore-forest systems may exist in alternative states, depending on whether or not herbivores are limited by predators. In the absence of predators, herbivores are predicted to increase to high densities and ultimately to be limited by starvation and disease, but only after imposing substantial impacts on browse and vegetation structure. In the presence of predators, herbivores are predicted to be regulated at lower population density, which moderates their impacts on forest structures. There is increasing evidence in support of this hypothesis of alternative stable states. For example, Ripple and Beschta (2006a) hypothesized that decreasing cougar *Puma concolor* densities led to higher mule deer *Odocoileus hemionus* densities. As a consequence of this deer browsing increased changing species abundances and abiotic environmental processes. In the Zion National Park, USA, comparison of willow (*Salix* spp.) heights before and after reintroduction of gray wolves *Canis lupus* in Yellowstone National Park showed that willow height in valley-bottom riparian sites increased after reintroduction of wolves. They suggested that impacts on vegetation through large herbivores might be controlled by predation risk through carnivores (Ripple and Beschta, 2006b). Throughout Norway Melis et al. (2010) analysed trends in indices of roe deer population abundance incorporating a wide range of landscapes, climatic conditions and varying Eurasian lynx *Lynx lynx* presence over nine years. In areas with lynx presence and harsh climatic conditions roe deer growth rates were lower than in milder climatic conditions with or without lynx presence. This suggests that especially under harsh environmental conditions lynx may negatively affect roe deer density (Melis et al., 2010). Focusing on large scale patterns of roe deer population density in Europe Melis et al. (2009) found only weak effects of large predator on roe density in highly productive environments and in mild climates. This implies even if large carnivores would be present throughout Europe they would not be able to control the deer population and deer numbers would still increase in absence of management.

The Fragmentation nutrition hypothesis

In addition to the removal of predators from the landscape, alteration of habitats by humans has increased the availability of favourable habitat for deer (Alverson et al., 1988). The fragmentation of continuous woodland into smaller patches bordered by nutritious arable farmland has been contributing to an increase in the deer population throughout Europe due to an increase of carrying capacity (Sinclair, 1997). This suggests that if ecological conditions for deer improved there may be also potential for an increase in fertility and survival leading to a further increase of the deer populations. As landscapes are a mosaics of suitable and unsuitable habitats for deer population growth may differ between areas with high carrying capacity and areas with low carrying capacity. As a consequence deer source-sink systems may be created. Smaller woodlands act as refuges for deer during the daytime and offer easy access to the surrounding farmland where food is available at high quantities and qualities (Putman, 1986b). However, being confined within the woodland during the daytime hours to avoid cull pressure and human activities, results in locally high deer densities with potential for major impacts on flora and fauna in such small woodlands. Though, the biological mechanisms underlying the ‘fragmentation nutrition hypothesis’ have not been formally tested previously.

Introduced invasive species

Deer have been widely introduced beyond their native ranges (Dolman and Wäber, 2008). Concerns have been raised that introduced deer species may negatively interact with native deer species due to competition and potential epidemiological effects and may have additive effects on plant dynamics and composition (Dolman and Wäber, 2008, Tanentzap et al., 2009). In Britain the successful introduction of Reeve's muntjac *Muntiacus reevesi* enhanced the pressure on vegetation structure and possibly also on native roe deer *Capreolus capreolus*. Eycott et al. (2007) found that muntjac showed much lower rates of endozoochorous seed dispersal than the native roe deer. The ability of the muntjac to survive and spread in an environment which is completely different from those of its origin in southeastern China has been underestimated. This and its first classification as being not harmful for the environment have lead to explosive population growth and spread throughout England. In some areas muntjac density has been shown to be three times higher than the density of native roe deer (Hemami et al., 2005). Increasing range and density of introduced fallow deer *Dama dama* has been suggested to lead to local decrease in roe deer densities (Delap, 1968). For example in Italy Focardi et al. (2006) reported interspecific competition between roe deer and fallow deer leading to a population decline and poor performance of roe deer.

Exclosure and enclosure experiments versus landscape scale research

Deer impacts have been mainly studied by (1) using fenced areas to exclude deer and (2) studying the impact of deer with varying deer density within enclosures. The alarming effects of heavy grazing and browsing of large herbivores has been repeatedly shown in exclosure research (Holt et al., 2010, Cooke and Farrell, 2001, Morecroft et al., 2001), in which the structure and composition of vegetation in fenced areas is compared to that of the unfenced surroundings. Exclosures show clearly and graphically how deer can affect vegetation structure and composition, but the results can be misleading when the relationship between ungulate density and the dependent variable is non-linear (Rooney and Waller, 2003). Also the recovery of plots from browsing is affected by the existing seed bank (Rooney and Waller, 2003). Seed banks differ between inside and outside the exclosures for example due to long term seed reduction by deer. Consequently, even if vegetation recovery occurs the plant species composition inside and outside the exclosure may be different. Furthermore, exclosure studies are often (though not always) compromised by subjective placement of exclosures and a low level of replication, and are not able to represent vegetation responses to herbivory at a landscape level (Webster et al., 2005). The size of exclosures is generally too small to demonstrate spatial heterogeneity of vegetation (McShea and Rappole, 2000). A key point is that exclosure studies generally contrast complete exclusion of deer, with impacts occurring at a high but unquantified level of deer abundance which does not allow impacts of different levels of herbivory to be understood. The challenge of deer management is to determine what intermediate levels of deer density are optimal or appropriate for biodiversity aims, and this cannot be achieved through the use of exclosure studies.

Another way is to study effects of deer in enclosures with known deer densities. Here, however, it is difficult to achieve enclosures large enough to not interfere with the social and spatial behaviour of deer, and to allow them to interact with the vegetation in ways that reflect natural ranging behaviour (DeCalesta, 1994).

Therefore the impacts of large free ranging herbivores have to be focused at landscape scale (Palmer et al., 2003, Rooney and Waller, 2003). Few studies have examined the impact of varying deer densities at landscape scale (e.g. Martin et al. (2010), Gill and Morgan (2010)). Martin et al. (2010) studied the impact of mule deer *Odocoileus hemionus* on temperate forest community and structure on seven islands of Haida Gwaii in Canada without the presence of significant predation. Islands were colonised by black tailed deer at different times and therefore browse history varies between islands. They found on islands with deer being present for > 50 years a decrease in understorey vegetation and a simplification in plant species community compromising mainly browse tolerant species. This was accompanied by a change in the shrub dependent species communities (Martin et al., 2010). In lowland Britain research by Gill and Morgan (2010) investigating impacts of different deer densities on regeneration of tree seedlings across fifteen sites in woodlands and adjacent fields suggested that regeneration is most likely unsatisfactory when deer densities are above 14 deer km^{-2}.

Deer management in Europe and its effectiveness

Historically deer have been mainly managed for recreational use. Hereby, the main focus is to harvest good deer trophies from males. Little attention has been paid to impacts of overabundant deer. In woodlands and on farmland the emphasis of deer management is to prevent or keep deer damage at low levels. More recently deer management has also been confronted with the issue of deer impacts on biodiversity. The management decisions of how many deer to cull are mainly based on the level of damage occurring (Mayle, 1996). This may be an effective method to prevent deer damage and improve habitat conditions at a local scale. However, it will not be known how the size of the cull relates to the size of the population, the magnitude of productivity or potential for recruitment from neighbouring areas. Therefore, it is necessary to understand deer numbers and the dynamics of cross-boundary recruitment to predict appropriate management targets. Robust methods which are able to evaluate deer densities even in areas with dense undergrowth are needed to establish deer numbers at landscape scale. Neighbouring areas may differ in habitat suitability and for this reason productivity of deer populations may differ between parts of the landscape. Together with different management strategies this may either generate or amplify source sink dynamics.

Deer species in the UK – an unusual multiple species assemblage

In the UK there are six deer species present. Roe deer and red deer are both native to Britain. Non-native Fallow deer is considered as naturalised and three further non-native deer species are also more recently established: Reeve's muntjac, Chinese water deer *Hydropotes inermis* and Sika deer *Cervus nippon* (Ward, 2005). Deer species differ in their feeding ecology, ranging behaviour, height and browse line. Though, it is widely established that deer impact on biodiversity (see above: *Deer impacts in North America and Europe*) research has either concentrated on one species (e.g. Martin et al. (2010)) or the combined impacts of different species (e.g. Gill and Morgan (2010)) although previous studies have shown that browsers and grazers may have different effects on the ground flora (Cooke, 2006).

Roe deer has been native since the last glaciations but was near extinction in the UK in 18th century due to over-hunting and forest clearance. It persisted in Scotland in localised populations and expanded their range since. In Southern England roe deer was reintroduced in the late 18th century and spread subsequently (Ward, 2005, Whitehead, 1964).

Red deer colonised Britain about 11,000 years ago but declined due to hunting and forest loss. In most of England they went extinct in the early 19th century but native populations survived in the Scottish Highlands, Dumfriesshire, Lake District and southwest England. During Victorian times red deer has been reintroduced and escaped from parks in Northern England, Northern Midlands, the New Forest and East Anglia (Clutton-Brock and McIntyre, 1999). Currently populations are increasing and spreading (Ward, 2005).

Although, different sika deer subspecies have been introduced to parks (Formosan, Chinese, Japanese, Manchurian) only Japanese sika deer established in the wild at several sites around Britain (Ratcliffe, 1987).

Chinese water deer has been kept in the London Zoo since 1873. They have been introduced in Britain in the early-mid 20th century. The distribution is localised and currently restricted to Bedfordshire, Cambridgeshire and Norfolk (Corbet and Harris, 1991, Cooke and Farrell, 1998). Nevertheless, the population range is expanding at an annual compound rate of 2.0% in 10 km squares which is similar to the annual range expansion of roe deer (2.3%) (Ward, 2005).

Fallow deer has been introduced by the Normans probably in the 11th century as an ornamental species and for hunting. They have been kept in parks until relatively recently. Since then individuals have escaped from many enclosed park herds throughout England (Chapman and Chapman, 1975). They are now distributed throughout England and Wales. Local populations exist in Scotland and North Ireland (Ward, 2005).

Reeve’s muntjac deer has been first introduced in Woburn Park, Bedfordshire in the early 20th century. Escapes and deliberate releases from parks in Woburn, Northamptonshire, and Warwickshire did lead to the establishment of feral populations throughout eastern England. Since then the muntjac population has expanded their size and range rapidly at an annual rate of 8.2% which is the highest rate of all six deer species in Britain (Ward, 2005).

Research aims

The aims of this thesis are to explore deer performance across and within different landscapes, variation of deer densities at the landscape scale and deer impacts on biodiversity in order to improve the knowledge of landscape-scale deer management.

The main research objectives are to:

- Examine variation in body mass and fertility of roe deer through time and amongst four landscape types: conifer plantation, acid grass heath, cereal farmland and horticultural farmland to explore possible effects on carrying capacity and inter- and intra-specific density-dependent effects (Chapter 2).

- Investigate variation in body mass and fertility of roe deer and Reeve's muntjac within a conifer plantation to explicitly test the importance of the 'fragmentation nutrition hypothesis' to reproductive deer performance (Chapter 3).

- Test the performance of thermal imaging distance sampling as a method to estimate deer densities of roe deer and Reeve's muntjac at the landscape scale (Chapter 4).

- Examine the variation of deer densities, deer cull, population growth and source-sink dynamics at the landscape scale in order to test the effectiveness of deer management (Chapter 5).

- Explore the effect of varying deer density and species composition on vegetation structure and understorey-dependent bird species at the landscape scale (Chapter 6).

References

Allombert, S., Stockton, S. & Martin, J. L. (2005) A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology,* **19,** 1917-1929.

Alverson, W. S., Waller, D. M. & Solheim, S. L. (1988) Forest too deer - edge effects in Northern Wisconsin. *Conservation Biology,* **2,** 348-358.

Barrett, M. A. & Stiling, P. (2006) Effects of Key deer herbivory on forest communities in the lower Florida Keys. *Biological Conservation,* **129,** 100-108.

Beschta, R. L. & Ripple, W. J. (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation,* **142,** 2401-2414.

Breitenmoser, U. (1998) Large predators in the Alps: The fall and rise of man's competitors. *Biological Conservation,* **83,** 279-289.

Chapman, D. I. & Chapman, N. (1975) *Fallow deer: Their History, Distribution and Biology,* Therence Dalton, Lavenham.

Clutton-Brock, T. & Albon, S. (1989) *Red deer in the Highlands,* Blackwell Scientific Publications, Oxford.

Clutton-Brock, T. H. & McIntyre, N. (1999) *Red deer,* Collin Bacter Photography Ltd.

Cooke, A. S. & Farrell, L. (1998) *Chinese Water Deer,* The Mammal Society, London; the British deer Society, Fordingbridge.

Cooke, A. S. & Farrell, L. (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.

Cooke, A. S. C. (2006) Monitoring muntjac deer *Munticacus reevesi* and their impacts in Monks Wood National Nature Reserve. pp. pp. 172. English Nature, Peterborough.

Corbet, G. B. & Harris, S. (1991) *Handbook of British Mammals,* Blackwell Scientific, Oxford, UK.

Cote, 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.

Cumming, D. H. M. & Cumming, G. S. (2003) Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia,* **134,** 560-568.

Danell, K., Bergstrom, R., Duncan, P. & Pastor, J. (2006) Large herbivore ecology, ecosystem dynamics and conservation. *Conservation Biology*. Cambridge University Press, New York.

DeCalesta, D. S. (1994) Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management,* **58,** 711-718.

Delap, P. (1968) Observations on deer in north-west England. *Journal of Zoology,* **156,** 531-&.

Dolman, P. M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research,* **35,** 202-214.

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.

Feber, R. E., Brereton, T. M., Warren, M. S. & Oates, M. (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. *Forestry,* **74,** 271-276.

Flowerdew, J. R. & Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry,* **74,** 277-287.

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.

Fuller, R. J., Noble, D. G., Smith, K. W. & Vanhinshergh, D. (2005) Recent declines in populations of woodland birds in Britain: a review of possible causes. *British Birds,* **98,** 116-143.

Gill, R. M. A. (1992) A review of damage by mammals in north temperate forests: 1. Deer. *Forestry,* **65,** 145-169.

Gill, R. M. A. & Fuller, R. J. (2007) The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis,* **149,** 119-127.

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.

Gonzales, E. K. & Arcese, P. (2008) Herbivory more limiting than competition on early and established native plants in an invaded meadow. *Ecology,* **89,** 3282-3289.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960) Community structure, population control, and competiton. *American Naturalist,* **94,** 421-425.

Hegland, S. J., Jongejans, E. & Rydgren, K. (2010) Investigating the interaction between ungulate grazing and resource effects on Vaccinium myrtillus populations with integral projection models. *Oecologia,* **163,** 695-706.

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.

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.

Homolka, M. & Heroldova, M. (2003) Impact of large herbivores on mountain forest stands in the Beskydy Mountains. *Forest Ecology and Management,* **181,** 119-129.

Horsley, S. B., Stout, S. L. & DeCalesta, D. S. (2003) White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications,* **13,** 98-118.

Huntzinger, M., Karban, R. & Cushman, H. (2008) Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology,* **89,** 1972-1980.

Kienast, F., Fritschi, J., Bissegger, M. & Abderhalden, W. (1999) Modeling successional patterns of high-elevation forests under changing herbivore pressure - responses at the landscape level. *Forest Ecology and Management,* **120,** 35-46.

Kraft, L. S., Crow, T. R., Buckley, D. S., Nauertz, E. A. & Zasada, J. C. (2004) Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. *Forest Ecology and Management,* **199,** 219-230.

Kuiters, A. T. & Slim, P. A. (2002) Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. *Biological Conservation,* **105,** 65-74.

Martin, J. L., Stockton, S. A., Allombert, S. & Gaston, A. J. (2010) Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction. *Biological Invasions,* **12,** 353-371.

Mayle, B. A. (1996) Progress in predictive management of deer populations in British woodlands. *Forest Ecology and Management,* **88,** 187-198.

McShea, W. J. & Rappole, J. H. (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology,* **14,** 1161-1170.

McShea, W. J., Underwood, H. B. & Rappole, J. H. (1997) *The science of overabundance: Deer ecology and population managment,* Smithsonian Institution Press, Washington DC.

Melis, C., Basille, M., Herfindal, I., Linnell, J. D. C., Odden, J., Gaillard, J. M., Hogda, K. A. & Andersen, R. (2010) Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. *Ecoscience,* **17,** 166-174.

Melis, C., Jedrzejewska, B., Apollonio, M., Barton, K. A., Jedrzejewski, W., Linnell, J. D. C., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A., Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovich, V. E., Zawadzka, B. & Zhyla, S. (2009) Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. *Global Ecology and Biogeography,* **18,** 724-734.

Morecroft, M. D., Taylor, M. E., Ellwood, S. A. & Quinn, S. A. (2001) Impacts of deer herbivory on ground vegetation at Wytham Woods, central England. *Forestry,* **74,** 251-257.

Murdoch, W. W. (1966) Community structure population control and competiton - a critique. *American Naturalist,* **100,** 219-&.

Nomiya, H., Suzuki, W., Kanazashi, T., Shibata, M., Tanaka, H. & Nakashizuka, T. (2003) The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. *Plant Ecology,* **164,** 263-276.

Palmer, S. C. F., Hester, A. J., Elston, D. A., Gordon, I. J. & Hartley, S. E. (2003) The perils of having tasty neighbors: Grazing impacts of large herbivores at vegetation boundaries. *Ecology,* **84,** 2877-2890.

Pepin, D., Renaud, P. C., Boscardin, Y., Goulard, A., 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.

Piraino, S., Fanelli, G. & Boero, F. (2002) Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Marine Biology,* **140,** 1067-1074.

Putman, R. J. (1986) Foraging by roe deer in agricultural areas and impact on arable crops. *Journal of Applied Ecology,* **23,** 91-99.

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.

Ratcliffe, P. R. (1987) Distribution and current status of sika deer *Cervus nippon*, in Great Britain. *Mammal Review,* **17,** 39-58.

Ripple, W. J. & Beschta, R. L. (2006a) Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation,* **133,** 397-408.

Ripple, W. J. & Beschta, R. L. (2006b) Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management,* **230,** 96-106.

Rooney, T. P. & Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management,* **181,** 165-176.

Royo, A. A., Stout, S. L., DeCalesta, D. S. & Pierson, T. G. (2010) Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? *Biological Conservation,* **143,** 2425-2434.

Simard, M. A., Côte, S. D., Weladji, R. B. & Huot, L. J. (2008) Feedback effects of chronic browsing on life-history traits of a large herbivore. *Journal of Animal Ecology,* **77,** 678-686.

Sinclair, A. R. E. (1997) Carrying capacity and overabundance of deer. *The science of overabundance: deer ecology and population management* (eds W. J. McShea,

H. B. Underwood & J. H. Rappole). Smithsonian Institution, Washington and London.

Suominen, O., Persson, I. L., Danell, K., Bergstrom, R. & Pastor, J. (2008) Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. *Ecography,* **31,** 636-645.

Tanentzap, A. J., Burrows, L. E., Lee, W. G., Nugent, G., Maxwell, J. M. & Coomes, D. A. (2009) Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. *Journal of Applied Ecology,* **46,** 1064-1072.

Veblen, T. T., Mermoz, M., Martin, C. & Ramilo, E. (1989) Effects of exotic deer on forest regeneration and composition in northern Patagonia. *Journal of Applied Ecology,* **26,** 711-724.

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

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. *Biological Conservation,* **125,** 297-307.

Whitehead, G. K. (1964) *The Deer of Great Britain and Ireland,* Routledge and Kegan Paul, London.

Chapter Two

Long-term temporal trends in body mass and fertility of roe deer *Capreolus capreolus* in relation to inter- and intra-specific competition among contrasting landscapes within Breckland, Eastern England

Abstract

Body mass and fertility are important parameters for demographic performance in many ungulate species and are influenced by environmental and biotic factors. Understanding the variation in body mass and fertility in connected landscapes is therefore important to predictive deer management but is not yet well understood. I use an exceptionally large data set for 3220 culled adult female roe deer, *Capreolus capreolus*, from a 450 km^2 study area in Breckland (Eastern England, UK), comprising contiguous and contrasting landscapes along a gradient of suitability (from pine dominated forest, through extensive grass heath, to productive farmland with patches of deciduous woodland). Cull data span two decades (farmland and grass heath landscapes) up to more than four decades (conifer forest). I use these data to examine spatial heterogeneity and dynamic temporal variation in female body mass and fertility. Body mass and fertility differed significantly among the contiguous landscapes: culled adult female roe deer in the cereal farmland were 1.2 kg heavier (8 %) and their fertility was 0.2 foetus/female higher (11 %), than those culled in the conifer dominated landscape (with other landscapes intermediate), despite current comparable or higher densities in the farmland and forest. No temporal trend in body mass or fertility was found in the cereal farmland (over 18 years) or in the grass heath landscape (over 23 years) from the late 1980s to 2009. In contrast, performance decreased significantly in the forest landscape over the period 1966-2009. As data from the forest landscape are from four discrete time periods (totalling 20 years, but spanning the four decades) rather than a continuous annual record, they were also reanalysed considering period as a categorical fixed factor. Both body mass and fertility declined significantly across four discrete time periods (totalling 20 years) from 1966-2009. Between the low density (colonisation phase) of 1966-69, and the period of maximal density, body mass declined about 5 kg (25 %) and fertility about 0.4 foetus (25 %) per pregnant female suggesting that the forest population were subject to intra-specific density dependence. This decline may also include some additive effect of inter-specific competition with increasing numbers of Chinese muntjac (*Muntiacus reevesi*) and fallow deer (*Dama dama*) and a stable or fluctuating population of red deer (*Cervus elaphus*). The subsequent recovery of both body condition and fertility following a decline in roe density achieved through increased cull intensity, occurred despite continued high numbers of both muntjac and fallow. This suggests that interspecific competition is outweighed by intra-specific density dependence. Differences in landscape productivity and the additive effects of a multispecies assemblage on body mass and fertility of roe deer are likely to affect deer population dynamics amongst contiguous subpopulations,

potentially contributing to source-sink systems if cull pressure differs among landscape elements. However, results of this study suggest that effects of density were greater than contrasts among landscapes of differing intrinsic productivity.

Introduction

Predictive management of deer populations requires knowledge of demographic performance (Radeloff et al., 1999). It is, therefore, important to understand how both spatial heterogeneity and temporal variation in environmental and biotic factors, affect fertility (Hamel et al., 2009, Pettorelli et al., 2005, Gaillard et al., 2000). Both body mass and fertility of deer have been shown to vary with intra-specific density (Bonenfant et al., 2009, Gaillard et al., 1993, Albon et al., 1983, Kjellander et al., 2006), with stochastic weather or environmental effects (Toigo et al., 2006, Putman et al., 1996, Clutton-Brock and Albon, 1989, Hamel et al., 2009) and across broad geographical gradients (Kjellander et al., 2006, Andersen and Linnell, 2000, Herfindal et al., 2006). For the latter, it is not easy to separate effects of climate from habitat productivity. Wild deer populations often inhabit complex landscapes, with consequences for local performance. However, the extent to which condition and fertility vary among large scale contiguous landscapes that differ in habitat composition and intrinsic productivity, has not been examined previously. In addition, most European habitats are shared by multi-species assemblages of deer and other ungulates, such that inter-specific competition may occur in addition to intra-specific density dependence. However, although numerous authors have speculated on the potential or action of inter-specific competition among deer (Focardi et al., 2006, Mysterud, 2000, Latham, 1999, Hemami et al., 2004, Dolman and Wäber, 2008, Putman, 1986a), no previous study has examined potential evidence of a mechanism for such effects, in terms of maternal condition or fertility. In this study, I examine variation in body weight and reproductive potential of a spatially structured roe deer population across contrasting but contiguous landscapes within Eastern England. These landscapes differ in habitat composition, productivity and their intrinsic suitability for roe deer. Furthermore, I use long term data spanning 1966-2009 to examine temporal variation in these parameters within each landscape, in relation to changes in both the density of roe deer, and that of other potentially competing deer species.

Differences in deer condition amongst diverse landscapes and geographic regions have been reported throughout Europe (Sand, 1996, Kjellander et al., 2006, Hewison and Gaillard, 2001). However, the complex interaction of climate, habitat composition and deer species assemblage make it difficult to understand such broad-scale geographical variation in deer body mass and fertility. Fecundity is not only related to body weight but also to environmental condition as shown in Sweden (Sand, 1996) where fecundity of female moose (*Alces alces*) was positively related to body mass and the relationship between body mass and fecundity varied amongst geographically separated populations in contrasting environments. Female moose in a harsher more seasonal environment had to accumulate 22% higher body mass to achieve the same fecundity as females in a milder, less seasonal environment (Sand, 1996). Across the UK fecundity (carcass material) varied by a factor of 2.35 amongst roe deer populations covering the geographic range from latitude 50° to 57°30, from Scotland to Southern England (Hewison, 1996). Across populations both the proportion of females ovulating and the average number of embryos per female were significantly positively related to the body weight of adult female roe deer. However, the proportion of pregnant adult female roe (logistic linear models) and the average number of foetuses per adult female (sample size weighted ANOVA) (females grouped into four groups of equal size according to body mass) differed among study sites with higher fecundity populations mainly in the South and lower fecundity populations mainly in the North of the UK suggesting that these variations may be due to environmental conditions (Hewison, 1996). Very few studies have examined the extent to which population performance may be affected by differences in the suitability of habitats within or among contiguous landscapes within a single region, and how such effects compare to those found for larger scale geographic gradients examined in such studies. A long term study of roe deer in France (in an enclosed forest of 26 km^2) showed that body mass is affected by population density, by stochastic events such as drought (Toigo et al., 2006) and differences in habitat quality, with higher body mass in oak than in beech forest (Pettorelli et al., 2005, Pettorelli et al., 2002, Pettorelli et al., 2003). This habitat effect was interpreted in terms of greater availability of principal food plants, and higher forage nitrogen content, in the ‘richer’ oak forest. Such density-dependent and environmental effects on maternal body weight may have consequences for fertility, as found in radio-telemetry studies of roe deer in both Norway (Andersen and Linnell, 2000) and Italy (Focardi et al., 2002b). Research in Norway suggests that landscapes with low / medium productivity lead to negative population growth with low adult survival due to high predation and harvest; whereas island population (high productivity) showed positive population growth under favourable conditions with the ability to recolonise areas (Nilsen et al., 2009). These differences in landscape productivity may result in source-sink systems amongst landscapes which affect emigration and immigration.

Increasing deer population densities intensify intra-specific competition reducing both body weight (Kjellander et al., 2006, Pettorelli et al., 2002, Gaillard et al., 2000) and fertility (Andersen and Linnell, 2000, Vincent et al., 1995, Putman et al., 1996). Reviewing intra-specific variation in body mass and demographic parameters of many ungulate species (Bonenfant et al., 2009) found density dependent variation in reproductive rates from the Arctic to the subtropical zone.

It has been frequently suggested that roe deer may be susceptible to interference competition with other deer species, including native red deer (*Cervus elaphus*), introduced fallow deer (*Dama dama*) and invasive Reeve's muntjac (*Muntiacus reevesi*) (Dolman and Wäber, 2008, Hemami et al., 2004, Chapman et al., 1993). A number of studies have demonstrated possible habitat or spatial displacement of roe deer by sympatric deer species (Dolman and Wäber, 2008). For example, in Scotland (Latham et al., 1996) examined cull records and standing-crop dung-group counts and showed that roe deer densities were lower in areas with greater densities of red deer. Similarly, in Italy the spatial distribution of roe deer was influenced by the local abundance of fallow deer in addition to effects of habitat (Focardi et al., 2006). Although, higher deer densities may lead to behavioural interactions and interference competition, as observed between roe and fallow deer in pastures in Italy (Ferretti et al., 2008) where roe deer moved further away from fallow deer or left the feeding ground, intra-specific competition among ungulates is most commonly expected to occur via exploitation competition for limiting forage resources (Dolman and Wäber, 2008). High overlap in diet has been demonstrated between roe deer and other species including muntjac and red deer (reviewed by Dolman and Wäber, 2008). Hemami et al. (2004) studied habitat usage by roe deer and introduced Reeve's muntjac using pellet-group clearance transects in a conifer forest in England. They showed substantial overlap in use of habitat and key forage resources, especially in winter when food is limited. Hemami et al. (2005) and K. Wäber, unpublished, found that the introduced species outnumbers the native roe two- to three-fold across 195 km^{-2}, and key forage resources are depleted (Hemami, 2003) providing a situation in which inter-specific competition may affect demographic performance. In northeast France Richard et al. (2009) investigated the sex-specific responses of roe deer juvenile body mass to changes in red deer density (abundance index method) in a 27 km^2 unfenced forest. They found an increase of female and male juvenile body mass of 8% in both sexes in the same year and the following year when red deer abundance index changed from high density (0.8 deer/km) to low density (0.4 deer/km). However, despite the various strands of evidence suggestive of potential inter-specific competition, changes in the reproductive performance of roe deer in multi-species deer assemblages have not previously been examined.

Reviewing inter-specific interactions of ungulates Latham (1999) stated that it has been argued that in natural systems inter-specific interactions might be slight through co-evolution of sympatric herbivores. Nevertheless, niche overlap of introduced deer species and livestock, with that of indigenous species might result in competition (Latham, 1999).

I examine long term data for adult female fertility and body weight of roe deer sub-populations from three contiguous landscapes covering more than 430 km^2 of Eastern England. Data were available from one landscape spanning the period 1966-2009, and for the other three landscapes spanning the last two decades. Landscapes differ in habitat composition and thus their intrinsic favourability for roe deer, but are physically contiguous, experiencing the same climatic and weather conditions. The regional population derives from a single source population introduced in 1884 (Chapman and Whitta, 1996), with adjacent sub-populations linked by dispersal. I use these data to 1) compare overall performance among the contrasting landscapes (horizontal comparison); 2) examine whether changes in the performance of sub-populations have occurred within each landscape (longitudinal comparison), and 3) relate these changes to trends in the relative density of both roe deer and three other competing deer species.

Methods

(a) Study area

The study was conducted in Breckland, a biogeographic region comprising approximately 1,000 km^2 of Eastern England, UK, and characterised by sandy soils and semi-continental climate (Dolman and Sutherland, 1992). Demographic data used in this study were obtained from four different landscapes types that together extend over 430 km^2: a pine dominated forest landscape managed by rotational clear-felling, an extensive area of grass-heath with scattered patches of woodland, and two farmland estates, one comprising mixed horticulture (including nutritious irrigated root crops) and cereal agriculture with scattered coniferous and mixed woodlands, the second dominated by cereals with scattered deciduous woodland (Table 2.1).

A large data set providing information about adult female roe body mass was collated from each of the four landscapes, with fertility data available from three of these landscapes. I analysed temporal variation in adult female body mass and fertility within each landscape, over periods spanning from two decades (three landscapes) to four decades (one landscape: 1966-2009). I examined spatial variation of body mass and fertility amongst the landscape types pooling recent data from the consistent period 2000-09, during which a large sample of adults were obtained within each landscape.

Thetford Forest (195 km^2) is the largest lowland conifer dominated plantation forest in the UK, and covers approximately one quarter of Breckland. The forest consists of a mosaic of growth stages with Corsican pine (*Pinus nigra*) (59 %) and Scots pine (*Pinus sylvestris*) (15 %) the dominant tree species, other conifers comprising 5 % and deciduous tree species 10 % of the area. More details such as crops species, planting year, area and soil type of each management sub-compartment (part of a single even aged planted coupe separated by trackways) are available from a GIS database managed by Forestry Commission (FC).The forest is managed by rotational clearfelling and replanting of even aged stands (Eycott et al., 2006) and therefore comprises a mosaic of growth stages (Figure 2.1). Stanford Practical Training Area is a military training area extending over 102 km^2, and is contiguous with the north-eastern margin of Thetford Forest. It comprises extensive areas of sheep-grazed acidic grassland and grass heath, limited areas of calcareous grass heath, arable land, deciduous woodland and conifer plantations (Sheail, 1979). Details about the landscape composition were available from a GIS database managed by Ministry of Defence (MoD). The Euston Estate (43 km^2), is a private farmland estate located in the South eastern part of the study area that is dominated by arable cereal agriculture with areas of deciduous woodland and permanent grassland together comprising 35 % (Euston Estate land use database). The Elveden estate (91 km^2) is a private farmland estate located in the south-western part of the study area and partly contiguous with Thetford Forest, and is dominated by a mixture of horticulture (particularly carrots, parsnips and onions), cereal agriculture and with coniferous and deciduous woodlands (http://www.bbc.co.uk/suffolk/nature/elveden_estate/index.shtml).

Table 2.1. Summary of the four contrasting contiguous landscapes within the study area, detailing landscape composition (based on average configuration within the last 10 years) and availability of roe deer cull data providing adult female body weight, age and fertility for differing year periods N/A = not available for that period.

Landscape	**Area** (km^2)	**Landscape composition** (%)						**Period**	**Sample size [number of females]**		**Aging**
		Conifer	Deciduous	Heath	Open / intensive grassed pasture	Croplands	Other		**Body weight**	**Fertility** (embryos per doe)	
Forest landscape	195	79	10	7	2	0	4	1966-1969	557	117	N/A
								1979-1983	292	153	incremental analysis
								1989-1990	50	27	incremental analysis
								2001-2003	325	120	incremental analysis
								2004-2009	880	270	N/A
Grass heath with scattered woodland	102	3	13	38	22	18	6	1986-2009	292	111	tooth eruption
Horticulture farmland with scattered woodland	91	22	8	16	0	52	2	1998-2009	343	-	N/A
Cereal farmland with scattered woodland	43	0	16	0	19	57	8	1988-2002	258	137	tooth eruption
								2006-2009	223	124	N/A

From 1968/69s as the first rotation tree crop matured, the Forestry Commission greatly increased felling and planting within the forest which increased the age structure complexity forest (Figures 2.1 and 2.2).

Farmland management altered on the cereal farmland estate in 2006/07 (J. Broatch, pers comm.). Before 2006/07 cereal crops (40%), grassland / set-aside (17%), semi-natural grass heath (26%), oil fruits (8%), vegetables (8%) were covered over 90 % of the farmland area. After 2006/07 the area of vegetables increased to 30% and that of cereal corps decreased to 30%. There was also a decrease of 8% in the area covered by grassland / set-aside. The area covered by semi-natural grass heath did not change.

During the study period some detailed aspects of management changed including the ride and spray management within the forest, cropland management, particularly the introduction of set-aside in 1992, conservation areas and the increase of game cover crops (especially maize) during the 1970s as game shooting came more available. However, the broad habitat composition remained similar and major contrasts between landscapes were maintained.

(b) Deer species assemblage

Four species of deer occur in the study area, including re-established native red deer, long-established introduced fallow deer and recently introduced Chinese muntjac, in addition to roe deer. Although consistent and accurate population assessments are not available, temporal trends in the relative density of each species are known as Forestry Commission deer managers have been active throughout the study period. From 1970 to 1990 annual censuses were carried out to estimate numbers of roe, red and fallow deer within the forest, by visual counts and expert assessment by deer managers (Chapman and Whitta, 1996, Ratcliffe, 1996). Although these estimates do not reliably quantify density, methodology was consistent across years, thus these counts provide an index of relative abundance through time.

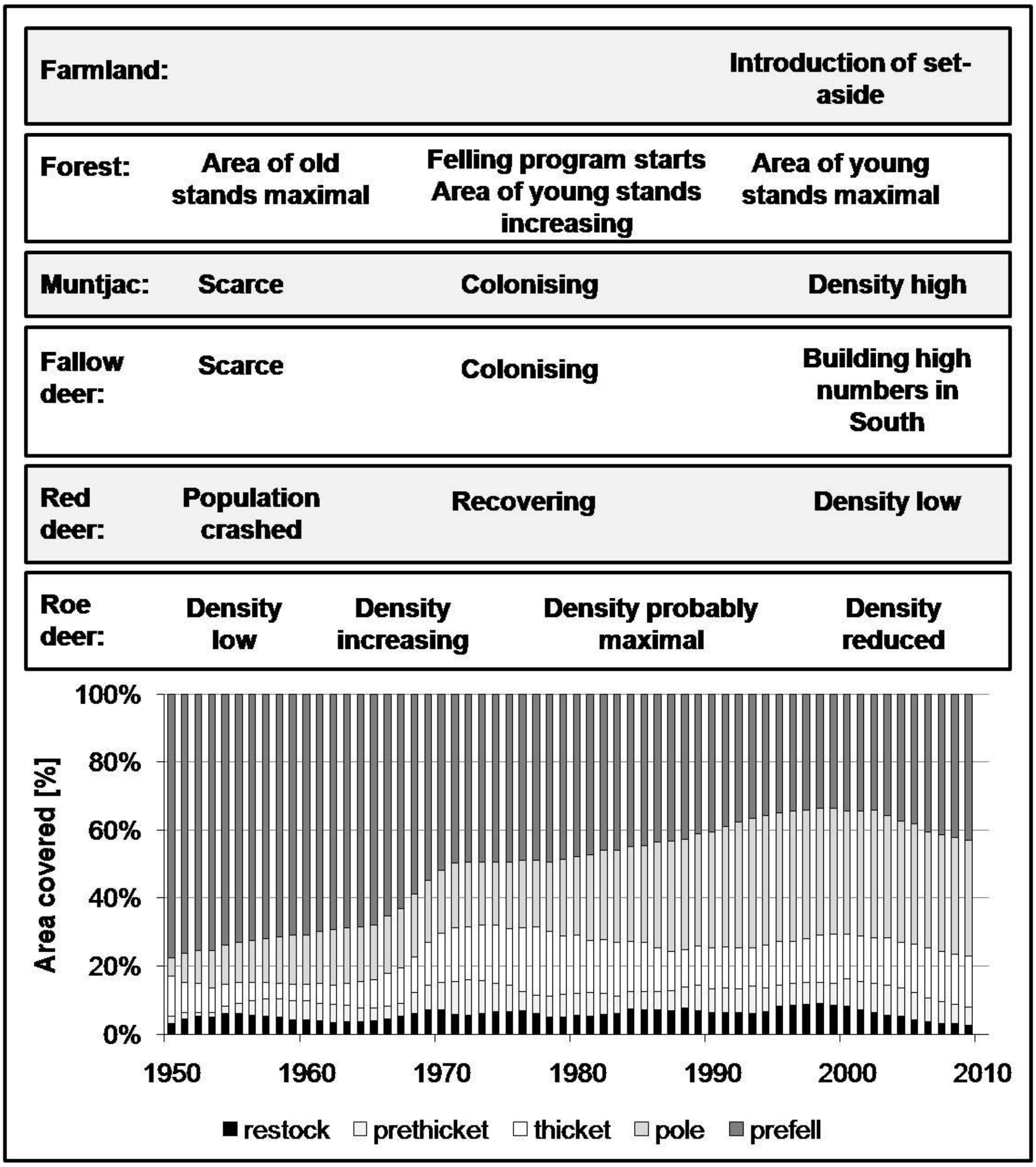

Figure 2.1. Changes (a) in farmland management, timber management, deer density and (b) age structure composition of Thetford Forest (restock, 1-5 years; pre-thicket, 6-10 years; thicket, 11-20 years; pole, 21-45 years; prefell > 45 years) over the period 1950-2009.

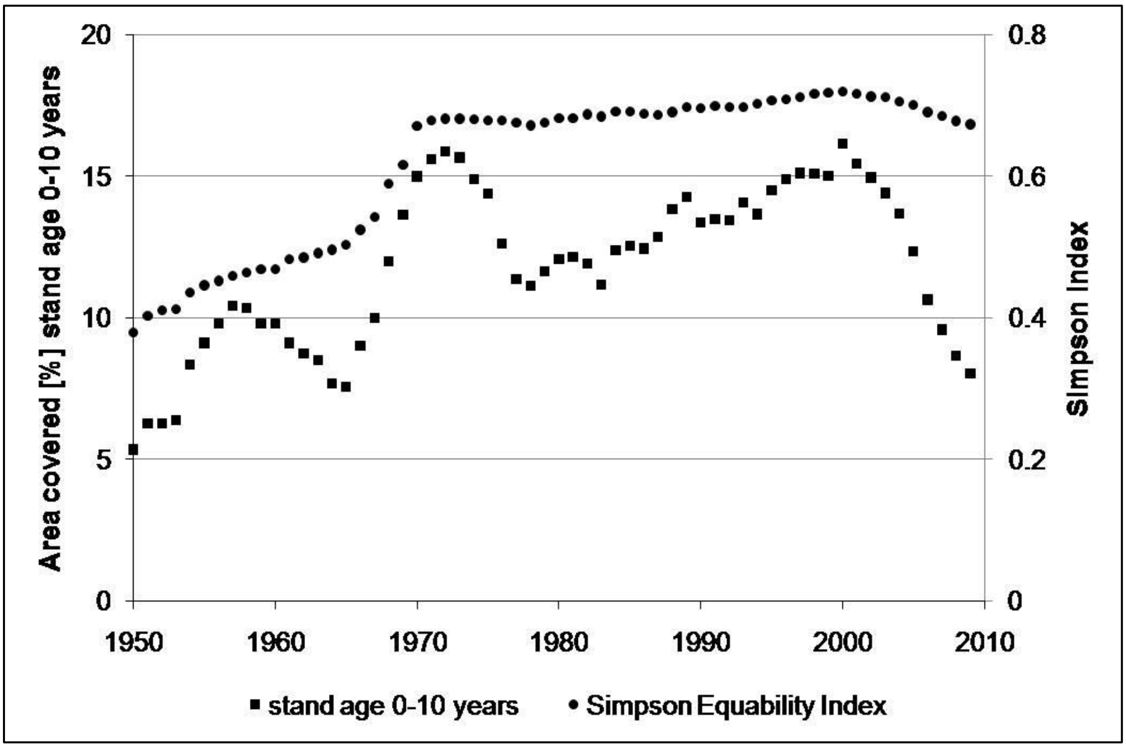

Figure 2.2. Growth stage composition of Thetford Forest 1950-2009 showing (a) suitable roe deer habitat [%] (unplanted areas, restock and pre-thicket aged 0-10 years) and (b) forest age structure equability (Simpson Equitability Index) considering the total area planted with conifers as well as the area of each stand (classed in stand age groups: unplanted (0 years), restock (1-5 years), pre-thicket (6-10 years), thicket (11-20 years), pole (21-45 years) and pre-fell (> 45 years) (Hemami et al., 2004)):

$$1\text{-}D = \frac{\sum ijni(ni-1)}{Nj(Nj-1)}$$

where D is the Simpson Equitability Index, N is the total area of all stands in year j, n_i is the total area of a particular stand in year j.

Roe deer population trends

Roe deer were re-established in the study region in 1884 (Chapman and Whitta, 1996) prior to the start of planting of Thetford Forest from the 1930s. By the 1960s roe deer were widely but thinly spread throughout the forest remaining scarce or absent in the wider Breckland landscape. Few deer were culled in the forest during this period and roe deer were not observed in surrounding farmland until the 1970's (Banham unpublished data; Whitta pers. comm.; Natural England Breckland SSSI scientific files). During the 1970s and 1980s roe deer numbers progressively increased (Figure 2.3) (Chapman and Whitta, 1996, Ratcliffe, 1996) probably due to underestimation of the true numbers by visual count methods and a low culling rate. The census index show that roe deer were fast increasing in the forest from the 1970s. At this time they started to occur in farmland in the southern part of the study area, reflecting increasing numbers within the forest landscape, although they did not appear on farmland in the northern part of the study area until the 1980s. During the 1980s roe deer numbers reach a maximum in the forest (T. Banham pers. comm.).

From the mid-1990s cull pressure on all deer species increased checking population increase so that numbers remained stable or slowly decreased (for roe deer see Figure 2.3) (T. Banham, unpublished observations).

Estimates of roe deer population density in each of three winters 2007-09, obtained by nocturnal distance sampling using thermal imaging equipment (total length of transect driven, about 1400 km) range from about < 10 roe km^{-2} in south-eastern blocks of Thetford Forest to about > 30 km^{-2} in the north-west (K. Wäber, unpublished data). Thermal imaging estimates in STANTA (total length of transect driven, 250 km) showed that roe deer are present in low numbers (< 10 km^{-2}) in 2009 (K. Wäber, unpublished data). Less intensive thermal imaging counts from the cereal farmland estate provided estimates of 12 roe deer km^{-2} in 2002/03. Cull pressure on this estate increased after a change in deer management policy from 2005/06. Thermal imaging counts were repeated in 2008/09, by which time the farmland roe deer density in this estate had decreased by around 50 %, to approximately 6 roe km^{-2} (J. Broatch, pers. comm.). Roe deer remain widespread within the horticultural farmland estate with no change in cull pressure.

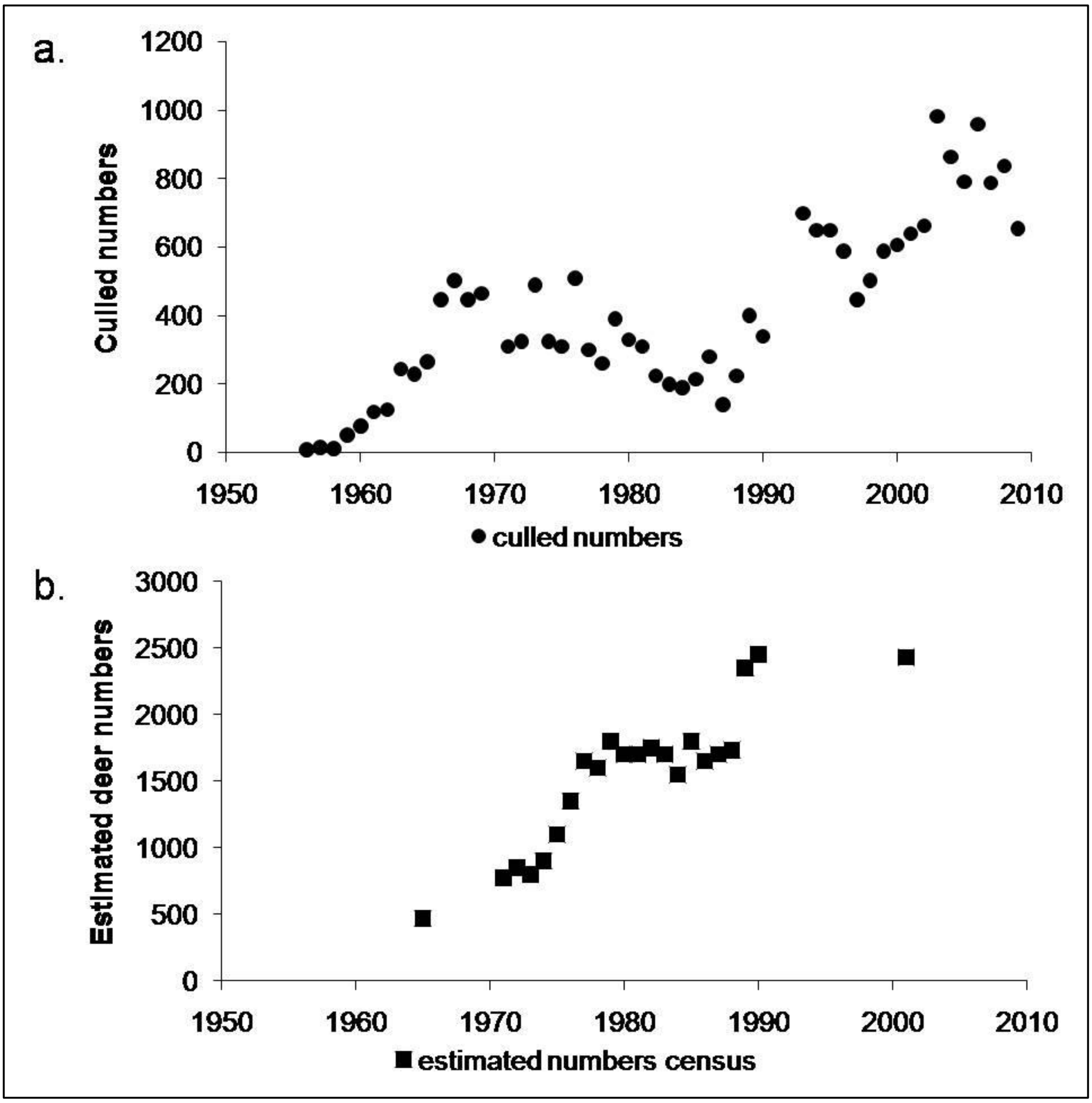

Figure 2.3. Thetford Forest roe deer population, showing (a) numbers culled annually, obtained from cull records 1956-1969 (FC database), 1970-90 (Ratcliffe 1996) and 1993-2009 (FC database) (cull has been continuous since 1956; but numbers culled are only available for the time periods shown); and (b) population estimates from 1965 (Chapman 1993), annual visual census of forest roe deer 1970-90 (Chapman and Whitta 1996; Ratcliffe 1996) and population estimates from 2001 (Hemami (2003): T. Banham speculative estimate, unpublished data).

Thus, in summary, roe numbers were low but increasing in the 1970s, reached a peak within Thetford Forest in the late 1980s, and were subsequently progressively reduced from the mid 1990s to their current lower density. Current density within Thetford forest, ranging 4-41 km^{-2} is low to high relative to other UK populations (Mayle, 1996).

Other potential competitor species: red deer, fallow deer and Reeve's muntjac

During the 1950s and 1960s red deer, fallow deer and muntjac were also present in the forest and surroundings, but at low densities (Chapman and Whitta, 1996). Muntjac and fallow deer were initially restricted to the most southern parts of the study area but densities increased from the 1970s, and both species began to spread into more northerly parts of the study area. Fallow deer occurred only occasionally in the North during the 1980s and 1990s and numbers are still low in the North. Muntjac were established throughout the forest around 1975 and numbers increased rapidly during the end of the 1970s. In the early 1980 muntjac were identified as problem species and the cull management started. Red deer are widespread throughout the study area at low densities (T. Banham, unpublished observations). All deer species reached their highest densities in the study region in the end of the 1980s and beginning of the 1990s (T. Banham, pers. obs.).

The thermal imaging distance sampling transects driven during the winters of 2007-2009 (Wäber, unpublished) provided mean estimates of muntjac density ranging from 10 km^{-2} in the South West to 47 km^{-2} in the North and 71 km^{-2} in the South East parts of Thetford Forest and between 4 km^{-2} and 20 km^{-2} in STANTA in 2009. Muntjac are widespread throughout all small woodlands in the study area. Red deer are widespread, mobile and freely ranging over the research area, and are generally evenly distributed at a density of around 5 animals km^{-2} (see Chapter 4). Fallow deer have higher densities in the southern half of the study area (approximately 7 deer km^{-2} within southern blocks of Thetford Forest) but remain much scarcer (approximately 1 deer km^{-2}) in the northern Thetford Forest, north of the Little Ouse River (see Chapter 4), reflecting their gradual colonisation from areas to the south of the study area. In the horticultural farmland estate fallow deer numbers are similar to those in the adjoining southern parts of the forest landscape. On the cereal farmland estate in the east of the study area (C. Rogers pers. comm.) and on grass heath in the north-east of the study area (B. Monckton pers. comm.) fallow deer are still only transient and at low numbers. Densities of potential competitors, particularly muntjac and fallow progressively increased from the 1980s and remain high to the present, with fallow particularly prevalent in southern blocks and muntjac throughout.

Similarly, the density of competing muntjac has progressively increased in both STANTA and the cereal estate, however in contrast to Thetford Forest, fallow deer are virtually absent.

Hypotheses tested

Although the situation is complex, the gradual changes in deer density and contrasting spatial and temporal trends for competing species, provide opportunities to compare the effects of landscape suitability, intra-specific density dependence and inter-specific competition. For roe deer in the forest landscape, the late 1980s represent a period when potential intra-specific competition would have been substantially greater than at present; in contrast, the potential influence of competing deer species is now much greater than it was at that time. I therefore sought to test the following hypotheses.

(1a) Due to intra-specific density dependence, I predict that both body condition and fertility of roe deer in the forest landscape will have been significantly lower during the time period of peak density (1980s-1990s) than during the preceding (lowest density) and current (intermediated density) periods.
(1b) Similarly, I predict that in the forest landscape, body condition and fertility are expected to have at least partly recovered (2000-09) following the reduction of roe density since the mid-1990s, due to intra-specific density dependent release.
(2a) Due to intra-specific density dependence I predict that roe condition and reproductive performance will have progressively declined in both the cereal farmland, and the grass heath and horticultural landscapes over the period 1980-present, although some recent recovery of condition in the cereal farmland may have occurred (2b, below).
(2b) Due to intra-specific density dependence I predict that, following a circa 50% reduction in density from 2002/03 to 2008/09 (6 years), condition and fertility of roe deer in the cereal farmland estate will have recently increased.
(3) If inter-specific competition with muntjac and or fallow deer are of importance, this may steepen any density dependent reduction in the forest landscape roe condition during the period from the1970s, through the 1980s to the early 1990s – however, this effect cannot be distinguished from prediction (1a).

(4) If inter-specific competition is stronger than density dependence then the continued high numbers of fallow and muntjac during the recent period of reduced roe density may offset, or even overwhelm, any density dependent recovery of roe condition within the forested landscape predicted from (1b).

(5) I predict a gradient of roe deer condition and fertility, which I expect to be lowest in the low productivity pine forest landscape and highest in the farmland with scattered deciduous woodland and the farmland with coniferous woodland. The grass heath landscape with scattered forest blocks is expected to be intermediate in productivity.

(6) The relative magnitude of any temporal trends in condition and productivity attributable to density dependence, compared to the magnitude of any additive variation among differing landscapes, may provide information on the relative importance of local environmental effects relative to inter-specific competition. However, if density dependent emigration among landscapes is considerable, this may mask such effects.

(7) I predict that any temporal trends in condition and fertility attributable to competition will be of greater amplitude in the lower productivity pine forest landscape, but lower amplitude in the cereal and grass heath landscapes, due to moderating effects of landscape quality on food limitation. However, I am unable to accurately quantify the magnitude of density variation within the different landscapes.

(c) Cull data: sources and time periods

Roe deer cull data were collected by Forestry Commission (FC) (forest landscape), Ministry of Defence (MoD) (grass heath), Elveden Estate (horticultural farmland) and Euston Estate (cereal farmland) (Table 2.1). For each deer culled, the date shot, sex, age, body mass, reproductive productivity of females (presence and number of embryos, not recorded in Elveden Estate) and remarks (e.g. if shot damage affected body weight) were recorded. Females are culled during winter, from November to February/March.

Carcass mass is defined as total body mass minus head, lower legs, blood and viscera. Throughout the paper carcass mass is referred to as body mass and is measured to the nearest 0.1 kg. I included only adult female roe deer excluding juveniles and yearlings in our analyses.

The cereal farmland estate’s cull records have been collected for 18 years from 1988-2009. The horticultural farmland estate provided cull data without reproductive data for

11 years from 1998-2009. The grass heath MoD cull records were available for 23 years from 1986-2009. All MoD stalkers have been trained to age deer by year based on tooth eruption and tooth wear, and to record embryos. From 1986-2009 cull data were checked with the head of local MoD Deer Management Group (Hemami, 2003) and B. Monckton. Data from less reliable sources were excluded and only those from known expert stalkers retained.

FC cull records were available provided for a total of 20 years, comprising a number of distinct periods spanning 1966-2009. Before 2000, standard cull records did not contain reliable aging or fertility data. Exceptionally, body mass and fertility of culled females determined by examination of the removed uterus and ovaries, were recorded during three discrete periods: 1966-1969 (n = 662: Banham unpublished); 1979-83 (n = 582; Mayle, unpublished; Hewison (1993)) and 1989-90 (n = 210; Mayle, unpublished; Hewison (1993)). Since 2001 fertility data are collected routinely in addition to carcass mass data.

(d) Aging of culled females

In the grass heath landscape deer have been aged from dentition criteria as well as tooth eruption and tooth wear. In the cereal farmland tooth eruption and tooth wear have been used in 1988-2002 and after 2005 as dentition criteria to determine age. In the forest landscape, deer were aged by incremental analysis of sectioned teeth for animals culled during 1979-83, 1989-90 and 2001-03, following Aitken (1975), Ratcliffe and Mayle (1992) and Hewison (1993), and by dentition criteria in 2004-09. Dentition criteria can reliably separate kids (juveniles from the date of birth till the following April), yearlings and adults as in juveniles the third premolar is still tricuspid and the third molar is lacking. All permanent teeth are erupted by 10 to 15 month in roe deer (Ratcliffe and Mayle, 1992).

Changes in culling intensity may alter the relative age structure among landscapes or among time periods with a reduction in the proportion of older individuals when cull intensity is higher. Therefore, any substantial declines in body weight and or fertility of older adults have the potential to confound analyses of temporal and horizontal (among landscapes) effects. It was not possible to consistently control for age in analyses, as only a subset of forest deer were analysed by incremental sectioning to determine age (number of years), while a subset from the cereal landscape were aged by tooth eruption and wear. Aging deer by using tooth eruption and wear is not as reliable as aging by incremental sectioning. Therefore, to compare the age structure in the forest landscape and the cereal landscape female adult deer were grouped in two age classes: 2-6 year old and over 6 year old animals following Gaillard et al. (2000). Therefore, I first explored whether body weight or fertility were related to age, for these subsets of the data. I also examined whether age structure is similar between the cereal and forest landscapes, and whether it had changed through time within either of these.

(e) Treatment of fertility data

Due to delayed implantation (Aitken, 1974, Sempéré et al., 1998) fertilised blastocysts develop very slowly in the uterus until late December or early January. Afterwards implantation of the fertilised blastocyst should be complete and embryos should be visible on opening the uterus (Ratcliffe and Mayle, 1992). Previous studies of reproductive output of roe deer in Britain considered data of females culled from the first of January (Hewison, 1996, Ratcliffe and Mayle, 1992). However, Hemami (2003) investigated Breckland roe deer subpopulations in early days after implantation of fertilised blastocysts and showed that there is a risk of overlooking embryos in their first state of foetal development as fertilised blastocysts which were not yet implanted or too small to recognise in 21% of roe females shot in early to mid January (Hemami, 2003). In his study he included only females shot from the 25th of January to the end of the cull season (end of February/March) in analysis of fertility. I investigated the frequency of pregnant and non-pregnant adult females from 1st of January to the end of February in the forest landscape in 1966-2009 using General Linear Model with negative binomial error. There was a significant difference in probability of a female being pregnant between 1st of January and 24th of January (64%) versus 25th of January and until the end of February (92%) ($n = 745$, $\chi^2_{(1)} = 24.4$, $p < 0.001$, early period: $B = -0.25 \pm 0.05$ *SE*).

Within the forest landscape, the proportion of pregnant versus not pregnant females was significantly lower in one forest block where deer are culled and data recorded by a private stalking club, than in the eleven other forest blocks managed by the professional Forestry Commission ranger team ($\chi^2_{(1)} = 42.41$, $p < 0.001$). Fertility data from this block were therefore excluded in all analyses of fertility (Table 2.2).

Table 2.2. Numbers of Thetford Forest adult female roe deer recorded as pregnant or not pregnant contrasting eleven Deer Management Units pooled, versus a single Management Unit at Mundford in 2001-09.

DMU	pregnant	Not pregnant	not pregnant [%]
DMU’s pooled	384	37	10
Mundford	270	96	36

Previous studies have found that only a very low frequency of adult female roe deer fail to conceive. For example Gaillard et al. (1992) investigated the reproductive status of 140 female roe deer and found a high conception rate (98%) of females older than 20 month. Comparison between roe deer populations across the UK showed that more than 98% of female adult roe deer carried at least one *corpora luteum* and found that 67%-91% of adult females were pregnant (Hewison, 1996). Thus a non-trivial frequency of zero foetus records among the cull data may represent errors in larder and data protocols, rather than actual lack of pregnancy. To investigate whether larder protocols appear to be consistant I compared the frequency of non-pregnant adult females among time periods. I examined whether recording protocols for logging fertility have been consistent among differing time periods. Within the forest landscape, the probability of an adult female roe deer being recorded as pregnant differed significantly between 1979-1983 and 2001-2009 ($\chi^2_{(1)} = 4.2$, $p = 0.04$), with the odds ratio of pregnancy, 2.5 times higher in 1979-1987 than in 2001-2009. Furthermore, the proportion of all culled females that were recorded as pregnant was significantly higher in the period 2006-09 (5.5% not pregnant) after revision of data logging protocols, than in the period 2001-05 (11.7% not pregnant) ($\chi^2_{(1)} = 5.00$, $p = 0.03$). Based on the odds ratio the chance of an adult female roe being not pregnant is 1.3 times higher in the earlier period.

Ovulation rate and number of foetuses carried by adult female roe deer are positively related to body mass (Hewison, 1996, Hewison and Gaillard, 2001). To verify that low frequency of zero foetus records is due to errors in the larder and data protocols and not connected to expetional low body mass I compared body weights of non-pregnant adult females with adult females carrying one foetus. I found no significant difference in body mass in adult female roe carrying no foetus or one foetus in the forest landscape (no foetus n = 48, one foetus n = 641) ($F_{1,685} = 2.05$, $p = 0.15$, $R^2 = 0.24$, $B = -0.40 \pm 0.28$ *SE*) whilst controlling for time period ($F_{3,685} = 89.74$, $p < 0.001$). These finding suggests that, either not every female was checked for foetuses thoroughly in 2001-05, or an external effect that changed over time.

Similarly, I detected no significant differences in body mass between female adult roe deer carrying no or one foetus in the grass heath (no foetus n = 18, one foetus n = 33) ($F_{1,48}$ = 0.66, p = 0.25, R^2 = 0.01, B = -0.24 ± 0.48 SE) whilst controlling for annual effects (cull year, continuous) ($F_{1,48}$ = 0.91, p = 0.34). Although, in the cereal farmland there was a difference close to significance in body mass between adult female roe carrying no or one foetus (no foetus n = 18, one foetus n = 51) ($F_{1,66}$ = 3.70, p = 0.06, R^2 = 0.06, B = -0.79 ± 0.41 SE) whilst controlling for cull year (continuous) ($F_{1,66}$ = 2.31, p = 0.13).

Our findings suggest that the non-trivial frequency of zero foetus records among the cull data are more likely due to errors in larder and data protocols. Therefore, I excluded non-pregnant females from analyses of fertility, which is analysed as the number of foetuses present in females recorded as pregnant. Thus our measure of fertility is conservative and may underestimate the full response of fertility of density or competition and also affect the proportion of females that are pregnant.

(f) Analysis

General Linear Models were used to analyse effects of spatial heterogeneity and dynamic temporal variation on body mass (with normal error term) and fertility (number of foetuses per pregnant female culled after 24th January taking the values 1-4). Models of fertility on density with poisson error gave lower Akaike Information Criterion (AIC) values than those with negative binomial error.

I explored variation in body mass through time within each landscape, with cull year as a continuous variable in the farmland and the grass heath landscapes, or as fixed categorical effects (time periods) in the forest landscape, fitting GLM's with normal error term using data from 1966-2009. For the period 2000-2009 for which I have a large volume of data from all landscapes, differences in body mass among landscapes were examined using GLM's controlling for year (categorical) and Post-hoc analyses (Games-Howell tests).

Changes through time, from 1966-2009, in the fertility of pregnant females within each landscape were analysed using GLM's with Poisson error, with cull year as a continuous factor (cereal farmland and grass heath) or time periods as fixed categorical effects (forest landscape). Further GLMs were used to compare fertility of pregnant adult female roe amongst three connected landscapes, using pooled data for each landscape from 2000-2009 whilst controlling for year (categorical). As each female has been checked for foetuses consistently and reliably recorded in the cereal farmland and the forest landscape from 2006-09 I investigate differences in fertility of non-pregnant and pregnant females in these two landscapes. Pairwise comparisons were conducted using Sequential Sidak test.

All statistical analyses were conducted in SPSS 16.0.

Results

Potential of age structure effects

The population in the forested landscape is now heavily hunted. In 2000-2009 the main cull of adult female roe deer compromised about 60% of females aged ≥ 2 years. Adult female roe deer aged between 2-6 years accounted for 77% and femeles older than 6 years for 23% of the cull in the forest landscape.

Potentially confounding effects of a change in age structure within the forest landscape are unlikely, as age (in years; dependent variable) did not differ between two discrete time periods (fixed categorical effects) 1979-1983 (n = 292) and 2001-2002 (n = 125) ($F_{(1, 415)}$ = 1.26, p = 0.26). Amongst landscapes no significant differences in age classes (class 1 = 2-6 years, class 2 ≥ 7 years) were found between the cereal farmland (1997-2002, n = 75) (class 1 = 88%, class 2 = 12%) and forest landscape (2001-02, n = 125) (class 1 = 86%, class 2 = 14%) ($\chi^2_{(1)}$ = 0.12, p = 0.73).

In the forest landscape, body mass did not vary with age for females aged from two to thirteen years when considering the pooled data from 1979-2003 (n = 628; model 1: R^2 = 0.01; age $F_{(1,625)}$ = 1.27, p = 0.26; age squared $F_{(1,625)}$ = 2.66, p = 0.10; model 2: R^2 = 0.02; age $F_{(11,616)}$ = 4.00, p = 0.43; Tukey test n.s.). Body mass was not affected by female age when controlling for time period (age $F_{(1,624)}$ = 1.61, p = 0.21, B = 0.18 kg/year ± 0.14 SE; age squared $F_{(1,624)}$ = 2.91, p = 0.08, B = -0.02 kg/year^2 ± 0.01 SE)

but differed among time periods (1979-83 and 1989-90 pooled n = 322 and 2001-02 n = 306: $F_{(1,624)}$ = 9.37, $p < 0.01$; 1979-83 and 1989-90: B = 0.48 kg ± 0.16 SE).

No significant difference of body mass was found between prime-aged (2-6 years, n = 533) versus older (>6 years, n = 95) females in a model that controlled for significant effects of year periods (period $F_{(2,624)}$ = 16.89, $p < 0.001$; age class $F_{(1,624)}$ = 2.31, p = 0.13).

Examining fertility (i.e. number of foetuses: 1,2,3 or 4) within pregnant females in the forest only, no relationship was found with age for females between two and thirteen years old, either for all years pooled (n = 288: age $\chi^2_{(1)}$ = 1.04, p = 0.31; age quadratic term $\chi^2_{(1)}$ = 0.67, p = 0.42), or when controlling for significant effects of time period (1979-83 and 1989-90 pooled n = 171, 2001-02 n = 117: model 1: period $\chi^2_{(1)}$ = 32.97, $p < 0.001$; age (continuous) $\chi^2_{(1)}$ = 0.84, p = 0.36; age quadratic term $\chi^2_{(1)}$ = 0.71, p = 0.40; model 2: period $\chi^2_{(1)}$ = 47.53, $p < 0.001$; age (categorical) $\chi^2_{(11)}$ = 15.22, p = 0.17, Sequential Sidak n.s.)

Simplifying to compare the fertility of females using prime-aged (n = 281) to older females (n = 48) as classified by other studies, no difference in age classes was found either for fertility alone (age: $\chi^2_{(1)}$ = 0.05, p = 0.83) or when controlling for significant differences among time periods (period $\chi^2_{(1)}$ = 33.76, $p < 0.001$; age $\chi^2_{(1)}$ = 0.02, p = 0.97).

As I could not detect any differences in female fertility and only small percentage of older females exists in the population I did not distinguish between age classes.

Body mass through time

No significant change in body mass of adult female roe was found in the cereal farmland over the entire period from 1988 to 2009 (18 years; $F_{(1,479)}$ = 1.09, p = 0.297) (Table. 2.3). However, within the cereal farmland body mass decreased significantly from 1988 to 2002 (14 years; $F_{(1,256)}$ = 34.58, $p < 0.001$, B = -0.12 kg/yr ± 0.02), during the period of increasing densities, prior to the imposition of greater cull intensity. I tested if the reduction of roe deer numbers in the cereal landscape positively affected body mass by comparing five years before cull pressure increased as body mass was lowest in this period (1997-2002) with the period with increased cull (2006-09). Following imposition of greater cull there was a recovery in body mass of about 5%

(period as categorical: 1997-2002 (n = 131) versus 2006-09 (n = 223); $R^2 = 0.03$, $F_{(1, 352)} = 17.50$, $p < 0.001$, $B = 0.63$ kg ± 0.15 *SE*) (year as continuous: 1997-2009 (n = 354): $F_{(1, 352)} = 12.29$, $p = 0.001$, $R^2 = 0.03$, $B = 0.06$ kg/yr ± 0.02 *SE*) (Fig. 2.4).

In the forest landscape adult female body mass declined from 1966-2009 by approximately 19% (3.1 kg) ($F_{(1, 2102)} = 815.70$, $p < 0.001$, $B = -0.07$ kg/yr ± 0.003 *SE*). Considering the discrete time periods for which cull data were obtained, body mass was highest in the 1960s, and lowest in the late 1980s, with a recovery to intermediate levels in the latest period (1966-69^a > 1979-83^b > 2000-09^c > 1989-90^d; shared superscripts do not differ; Games-Howell test $p < 0.001$) (Table. 3). The difference in body mass between the periods of minimal (1960's) and maximal (1989-90) density was 4.9 kg ± 0.23 *SE*; the subsequent recovery following increased cull effort was of the order of 1.8 kg ± 0.22 *SE*.

Table 2.3. Generalised Linear Models of adult female roe deer body weight [kg] through time analysed separately within each of four contiguous landscapes. Data (n = 3220) are collected from 1966-2009 amongst four connected landscapes.

Model description	n	$\bar{x}$ ± SD [kg]	B ± se [kg/year]	F	p	R^2	df
a. cereal farmland [1988-2009]	481					0.002	1
Cull year		16.0 ± 1.8	-0.01 ± 0.01	1.09	0.30		
b. horticultural farmland [1998-2009]	343					0.01	1
Cull year		14.2 ± 1.6	0.06 ± 0.03	4.83	0.03		
c. grass heath [1986-2009]	292					0.003	1
Cull year		14.9 ± 2.0	-0.01 ± 0.01	0.83	0.36		
			B ± se [kg]				
d. forest landscape [1]	2104			390.54	< 0.001	0.36	3
1966-69	557	16.8 ± 2.2^{a}	3.10 ± 0.10				
1979-83	292	14.4 ± 2.0^{b}	0.70 ± 0.12				
1989-90	50	11.8 ± 2.4^{c}	-1.82 ± 0.27				
2001-09	1205	13.7 ± 1.6^{d}	-				

[1] Body weight Games-Howell test comparing four distinct periods (1966-69; 1979-83; 1989-90; 2000-09) are shown with superscripts, periods that do not share the same superscript differ significantly ($p < 0.001$).

The influence of body mass on fertility

I examined if adult female roe deer fertility was related to body mass (as a continuous independent variable) whilst controlling for landscape (as a fixed factor) and testing for a possible interaction between body mass and landscape. Considering cull data from across all three landscapes, and pooling all years (1966-2009, n = 1024), fertility of pregnant adult female roe was significantly related to body mass (Wald $\chi^2_{(1)} = 4.76$, p = 0.03) (model log-likelihood (LL) = -1.302E3, AIC = 2.616E3), with an additive effect of landscape type on fertility (Wald $\chi^2_{(1)} = 8.82$, p = 0.01; foetuses per female grass heath: B = 0.13 ± 0.32 *SE*; foetuses per female cereal farmland: B = 0.70 ± 0.24 *SE*). The interaction between landscape and body weight was close to significance (Wald $\chi^2_{(1)} = 5.04$, p = 0.08) suggesting that the influence of body mass on the fertility of pregnant adult females is higher in the forest landscape and the grass heath with lower habitat quality and generally lower body mass than in the cereal landscape with higher habitat quality and generally higher body mass (grass heath: Wald $\chi^2_{(2)} < 0.001$, $p = 0.99$, $B = 0.0003$ foetuses/kg ± 0.02 *SE;* cereal farmland: Wald $\chi^2_{(2)} = 4.98$, $p < 0.001$, $B = -0.04$ foetuses/kg ± 0.02 *SE*) as the body mass is highest in the cereal farmland.

Changes in fertility through time

For animals culled during 1988-1999, there was no significant difference between the cereal farmland (84%), grass heath (88%) and forest landscape (82%) in whether or not an adult female roe deer would be pregnant (Fisher's Exact test $\chi^2_{(2)} = 1.99$, $p = 0.39$). However, in 2001-2009 a significant difference was found in the probability of a female being preganant among the cereal farmland, grass heath and forest landscapes ($\chi^2_{(2)} = 19.51$, $p < 0.001$). The chance of a roe female being pregnant was higher in the cereal farmland (99%) than in the grass heath (77%) ($\chi^2_{(1)} = 21.86$, $p < 0.001$), and higher than in the forest landscape (91%) ($\chi^2_{(1)} = 10.02$, $p = 0.002$), and higher in the forest landscape (91%) than in the grass heath (77%) ($\chi^2_{(1)} = 5.68$, $p = 0.02$). As recorder error may contribute to these differences, I analysed the change through time, and differences among landscapes of fertility expressed as the number of foetuses found per doe in those females recorded as pregnant.

No significant temporal trend in the number of foetuses carried by pregnant adult female roe was dectected within the grass heath (23 years; Wald $\chi^2_{(1)} = 1.10$, $p = 0.30$) or within the cereal farmland (18 years; Wald $\chi^2_{(1)} = 0.16$, $p = 0.69$) (Table 4). For the cereal farmland landscape, no significant change in fertility was found during 1988-2002 (14 years (continuous variable); $\chi^2_{(1)} = 0.23$, $p = 0.64$, $n = 137$). In comparison to body mass no difference in fertility in the period of increasing densities (1997-02; $n = 64$) prior to the imposition of greater cull intensity from 2006 onwards was detected (2006-09; $n = 124$) (period as categorical variable: Wald $\chi^2_{(1)} = 0.08$, $p = 0.78$, 1997-02: $B = 0.01 \pm 0.04$ *SE* foetuses per female, Pearson $\chi^2/df = 0.13$) (Table 2.4).

In contrast fertility of female roe in the forest landscape (estimates for a total of 20 years, spanning 43 years from 1966-2009:) differed significantly among periods (Wald $\chi^2_{(3)} = 101.82$, $p < 0.001$, Table 4) [1966-69^a > 1979-83^b > 1989-90^c ≈ 2001-09^c; shared superscripts do not differ, Games-Howell test $p < 0.001$]. As with body weight, changes in fertility were consistent with changes in the relative density of roe deer within this landscape.

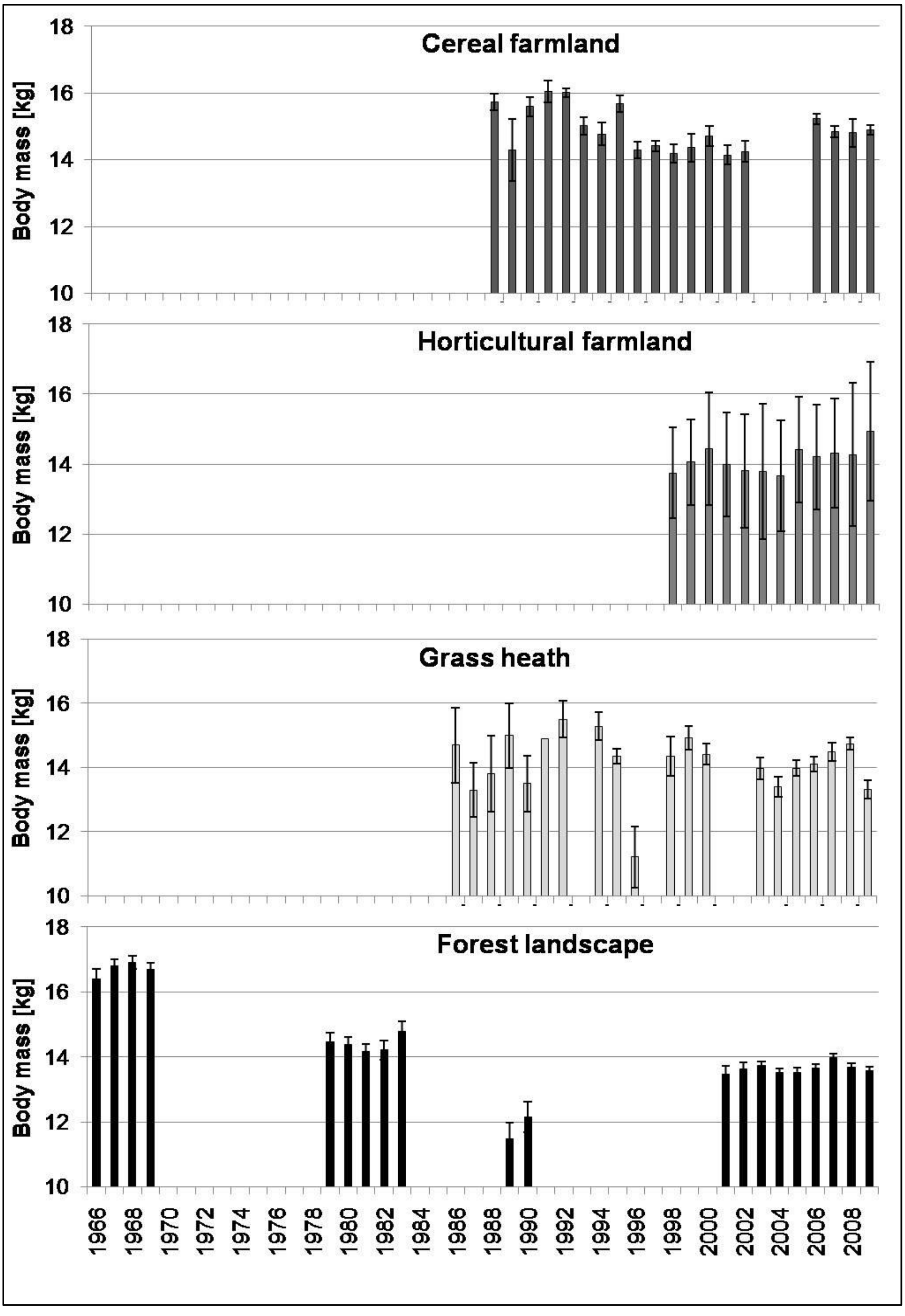

Figure 2.4. Mean ± *SE* adult female roe deer body mass [kg] in relation to year (1966-2009) in four different landscapes (cereal farmland (*n* = 481 animals; *n* = 19 years); horticultural farmland (*n* = 343; 12); grass heath (*n* = 292; 20); conifer plantation (*n* = 2104; 20).

Table 2.4. Generalised Linear Models of pregnant adult female roe deer fertility through time; foetuses per female is considered as count data analysed with Poisson error. Data (total *n* = 1059) are analysed separately within each of three connected landscapes from 1966-2009.

Model description	n	$\bar{x}$ ± SD [foetuses per female]	B ± se	Wald χ^2	p	Model		Goodness of fit criteria			
						Wald χ^2	p	Log-likelihood	Deviance	Dev/df	df
a. Cereal farmland [1988-2009]	261	1.9 ± 0.5	-0.002 ± 0.002	0.48	0.489			-344.23	33.53	0.13	1
b. Grass heath [1986-2009]	111	1.7 ± 0.5	-0.004 ± 0.004	1.10	0.296			-143.52	16.41	0.15	1
c. Conifer forest [2]	687			101.82	<0.001	107.14	< 0.001	-851.48	110.01	0.16	3
1966-69	117	1.8 ± 0.6^{a}	0.10 ± 0.03	10.33	0.001						
1979-83	153	1.2 ± 0.4^{b}	-0.29 ± 0.03	72.62	<0.001						
1989-90	27	1.5 ± 0.5^{b}	-0.04 ± 0.07	0.47	0.494						
2001-09	390	1.6 ± 0.5^{c}	-	-							

[2] Sequential Sidak comparing fertility in four distinct periods (1966-69; 1979-83; 1989-90; 2001-09) are shown with superscripts, periods that do not share a superscript differ significantly (*p* < 0.01) if not shown otherwise (1966-69 vs. 1989-90 p = 0.047; 1989-90 vs. 2001-09 p = 0.49).

Influence of winter temperature on body mass and fertility

Changes of body mass and fertility through time may have been influenced by winter weather conditions. Therefore I tested if body mass (n = 1307) and fertility (n = 1074) of animals shot after the 25th January in 1966-2008 were affected by the pooled mean temperature [°C] from November to February in each year across three landscapes (cereal farmland, grass heath and forest landscape). For body mass and for fertility I found no effect of winter temperature (body mass: $F_{(1, 1302)} = 0.08$, $p = 0.78$; fertility: Wald $\chi^2_{(1)} = 2.09$, $p = 0.15$) whilst controlling for landscape (body mass: $F_{(2, 1302)} = 124.16$, $p < 0.001$, grass heath: $B = 0.35$ kg ± 0.18 *SE*, cereal farmland: $B = 1.14$ kg ± 0.13 *SE*; fertility: Wald $\chi^2_{(2)} = 12.79$, $p = 0.002$, foetuses per female grass heath: $B = 0.05$ ± 0.08 *SE*; foetuses per female cereal farmland: $B = 0.21$ ± 0.06 *SE*) and cull year (body mass: $F_{(1, 1302)} = 177.16$, $p < 0.001$; fertility: Wald $\chi^2_{(1)} = 1.17$, $p = 0.28$).

Body mass and fertility amongst connected landscapes

Amongst the four connected landscape there was a gradient in adult female roe deer body mass, that was highest in the cereal farmland and lowest in the forest landscape (cereal farmland^a > horticultural farmland^b ≈ grass heath^b > forest landscape^c; shared superscripts do not differ, Games-Howell test $p < 0.001$) in 2000-2009 (Table 2.5). The comparison of adult female roe fertility (foetuses per pregnant doe) showed significant differences among landscapes, with a similar gradient as found in body mass. Here, fertility was significantly lower in both the forest landscape and grass heath than in the cereal farmland (cereal farmland^a > grass heath^b ≈ forest landscape^b; shared superscripts do not differ, Sequential Sidak $p < 0.001$) (Table 5). In the cereal farmland female adult roe deer were mainly pregnant with two embryos ($\bar{x} = 1.9$ ± 0.04 *SE* foetuses per doe) whereas in the grass heath ($\bar{x} = 1.7$ ± 0.06 *SE* foetuses per doe) and forest landscape ($\bar{x} = 1.6$ ± 0.03 *SE* foetuses per doe) the proportion of females being pregnant with one or two embryos was similar.

During the period 2006-09 each female checked for foetuses has been consistently and reliably recorded in both the cereal farmland and the forest landscapes. For this period, a GLM with Poisson error examining the fertility of all adult female roe deer (dependent) showed a significant difference between the cereal farmland (n = 124; $\bar{x} = 1.84$ ± 0.06 *SE* foetuses per doe) and the forest landscape (n = 199; $\bar{x} = 1.59$ ± 0.04 *SE*) (Wald $\chi^2_{(1)} = 11.80$, $p < 0.001$). Thus during this period, when density of roe deer was broadly similar between the cereal and forest landscape, the mean difference in fertility of adult female roe deer between the farmland and the forest landscape was $\bar{x}$ = 0.25 ± 0.07 *SE* (14%).

Table 2.5. General Linear Models comparing female roe deer (a) body mass [kg] (*n* = 2005) and (b) fertility (pregnant females) (*n* = 612) amongst landscapes from deer culled 2001-2009.

Model description	n	$\bar{x}$ ± SD [kg]	F	p	R^2	df
a. *Body mass*			13.62	< 0.001	0.076	12
Landscape [2]			35.85	< 0.001		3
Cereal farmland	280	14.9 ± 1.4^a				
Horticultural farmland	310	14.2 ± 1.6^b				
Grass heath	210	14.1 ± 1.4^b				
Forest landscape	1205	13.7 ± 1.6^c				
Cull year			2.31	0.01		10

Model description	n	$\bar{x}$ ± SD [foetuses per female]	Wald χ^2	p	Goodness of fit assessment criteria			
					Log-likelihood	Deviance	Dev/df	df
b. *Fertility*			57.39	< 0.001	-780.95	92.42	0.15	11
Landscape [3]			11.27	0.004				2
Cereal farmland	156	1.8 ± 0.5^a						
Grass heath	66	1.7 ± 0.5^b						
Forest landscape	390	1.6 ± 0.5^b						
Cull year			29.34	0.001				10

[2] Body mass Games-Howell test comparing four landscape types are shown with superscripts, periods that do not share a superscript differ significantly (*p* < 0.001) (horticultural farmland vs. grass heath *p* = 0.83).

[3] Fertility Sequential Sidak Significance comparing three landscape types are shown with superscripts, periods that do not share a superscript differ significantly (*p* < 0.001) (grass heath vs. forest landscape *p* = 41).

Discussion

Evidence was found for effects of both intra-specific population density, and differences in the quality of neighbouring landscapes, on both the body weight and fertility of adult female roe deer. Generally, differences among landscapes had effects that were smaller than the largest effects of density within a landscape.

Age structure effects

In several studies roe deer females aged between two and six years are classified as prime-aged adults (Loison et al., 1999, Gaillard et al., 2000) and are reported to have higher fertility than adult female roe older than six years (Gaillard et al., 2000). Although no difference in body mass and fertility between prime-aged and older adult female roe deer was found in this study. Similarly, McIntosh et al. (1995) found no relationship between age (age classes from 0-11 month to 11-13 years), body mass and number of *corpora lutea* in a roe deer population under heavy hunting pressure in Northern England, UK. However, the small sample size of older females in the forest landscape may confound the effect of age structure on body mass and fertility. This may lead to underestimating of age affects.

Contrasting performance among landscapes

Habitat composition and quality varied markedly amongst contrasting but contiguous landscapes (450 km^2) in Breckland. This was reflected in differences in body mass and fertility of adult female roe deer. Average differences in body mass and fertility between the most productive (cereal farmland) and least productive (forest landscape) landscape were 1.5 kg (10%) and 0.2 foetuses (11%) respectively in 2001-09. Similar differences in body mass due to differences in habitat quality have been found on smaller spatial scales than investigated in this study. Within one enclosed landscape (26 km^2) variations in habitat quality also influenced juvenile roe deer body mass in Chizé, France (Kjellander et al., 2006, Pettorelli et al., 2003) with an average difference of 0.6 kg and 1.1 kg respectively between rich oak stands and poor beech stands. Likewise, Pettorelli et al. (2002) showed that the living weight of adult female roe differed about 0.5 kg between rich and poor habitats within Chizé, France. In Norway female roe deer inhabiting high quality home-ranges during the winter produced more often litter sizes of 2 and 3 juveniles than females in low quality-home ranges within one landscape (7.8 km^2) (Nilsen et al., 2004). The influence of environmental conditions on body mass and fertility has also been suggested in female moose; fecundity differed with body mass and population location significantly between not connected landscapes in Sweden (Sand, 1996).

Intra-specific density dependence

In the forest landscape (poor landscape productivity) body mass and fertility varied among four periods (20 years) with increasing deer density from the colonisation phase (1966-69) to the most recent period (2000-09) where roe density is not increasing anymore. Time periods explained 36% of the total variation in body mass amongst individuals. Changes in density and body mass among periods were consistent with changes in relative density, from colonisation, through lower body mass at peak densities in 1980s, with some density-dependent recovery in recent years following an increase in cull pressure. However, in North England after introducing a new heavy hunting pressure following a period of lower hunting pressure no changes in roe deer body mass and the average number of *corpora lutea* were observed within five years in a spruce plantation (McIntosh et al., 1995). In contrast to the forest landscape no change in condition could be detected in the grass heath throughout 23 years or in the cereal farmland throughout 18 years. Density dependence has also been reported in Chizé, France, where body weight of adult females increased by 4.7 kg over a period from 13 years due to delayed density-dependence following a reduction of about 60% in deer numbers (Pettorelli et al., 2002). Similarly, Pettorelli et al. (2002) showed that juveniles born in years with high population density weighed approximately 2 kg less than juveniles born under more favourable conditions. These cohort effects led to lower weights throughout adulthood and are therefore long term detectable. Density dependence in juvenile roe deer has also been reported by Toigo et al. (2006) in France (Chizé) and by Kjellander et al. (2006) in France (Chizé) and Sweden (Bogesund).

Evidence of inter-specific competition

I predicted that if inter-specific competition is stronger than intra-specific density-dependence there would be no recovery in roe condition in the recent period following elevated cull levels. However, roe deer body mass and fertility did increase in the most recent period 2000-09 following higher cull management, despite muntjac and fallow deer density remaining high in the forest landscape. Similarly, in the cereal landscape adult female roe deer body mass did increase after reduction of roe deer density despite frequent muntjac. This leads to the suggestion that the influence of intra-specific density-dependent effects on body mass and fertility are stronger than inter-specific competition. However, due to the overall reduction of deer densities, density-dependent impacts on roe condition are possibly compounded by competition with other deer species. Reeve's muntjac have been previously identified as possible competitors of roe deer (Hemami et al., 2005, Chapman et al., 1993) suggesting that high numbers of muntjac may reduce phenotypic and reproductive performance of roe deer (Hemami, 2003). Hemami et al. (2004) found substantial niche overlap for both species in particular in winter when both species used bramble as food source in East England, UK. Effects of winter weather may therefore explain the lower body mass and fertility found in the study of Hemami (2003). Roe deer has also been reported to be susceptible to competition with fallow deer in Italy (Focardi et al., 2006) and red deer in France (Richard et al., 2009).

No clear trend in body mass or fertility could be detected in the grass heath suggesting that roe population densities as found in thermal imaging distance sampling in 2009 may be lower than in the forest landscape or less effect of competitors due to absence / lower density. In the horticultural farmland female adult roe deer body mass increased throughout 11 years (1998-2009) despite an increase in red deer, fallow deer and muntjac highlighting the importance of environmental conditions for deer performance.

Temporal trends in condition and fertility and additive effects

In Breckland environmental conditions changed from 1966 to 2009 including the timber management, farmland management and the establishment of invasive deer species. In the 1960s, the colonisation phase, the performance of female adult roe deer was high within the forest landscape. Also effects of intra- or interspecific competition were negligible at this time. The new felling regime introduced in 1968/69 was expected to enhance population density and food availability from the 1970s and particularly during the late 1980s and 1990s, when the extent of early successional forest was greater than at the present time (Figure 2.4). Several studies have shown that early stages of forest succession improve habitat availability for roe deer through increase of high-quality food (Fuller and Gill, 2001, Kramer et al., 2006, Said and Servanty, 2005). However, roe deer body mass decreased by more than $\bar{x}$ = 4.9 kg ± 0.27 *SE* from the colonization phase to the late 1980s suggesting that density dependent effects and inter-specific competition due to increasing deer density of all species overwhelmed any benefits of improved quality of within-forest habitat on body mass at this time. However, fertility of pregnant adult females did increase significantly from the late 1970s to the late 1980s / early 1990s (about $\bar{x}$ = 0.3 foetuses ± 0.10 *SE*) and stayed stable during the most recent period. This implies that even though intra- and interspecific competition increased from the 1960s to 1990s fertility did increase with habitat quality.

In 1986-2009 (23 years) adult female roe body mass declined about 2% (0.3 kg) in the grass heath (23 years). However, body mass decreased from 1997-2002 and increased in 2006-09 ($\bar{x}$ = 0.6 ± 0.15 *SE*) following a circa 50% decline in roe deer density in the cereal farmland. Though, at the same time there was an increase of vegetable crop (about 20%) which did lead to higher quality food availability. Therefore, a combination of lower roe deer density and higher quality food may have contributed to the higher roe deer body mass. Similarly, adult female roe deer body mass increased about 5% (0.7 kg) in the horticulture farmland estate (11 years) 1998-2009 (Table 2.3). The increase in body mass may be also due to an increase in root crops in the horticulture farmland estate. In contrast fertility in the cereal farmland was not influenced by a change in deer density or food availability despite the body mass effect suggesting that a threshold for fertility exist within the cereal landscape. McIntosh et al. (1995), who did not find an improvement in average body mass and fertility after a reduction of deer density, suggested habitat quality rather than population density influenced fertility in his study. Amongst populations in the UK Hewison (1996) showed that the average number of foetuses per adult female varied from about 1.1 to 1.9 and body mass varied from 12.1 kg to 18.7 kg. This variation in fertility is similar to the variation between the year period with the lowest fertility in the forest landscape in 1979-83 (1.2 foetuses per pregnant female) and the average fertility in the cereal farmland (1.9 foetuses per pregnant female) in this study. However, the difference in body mass was stronger within the forest landscape. Our results suggest in landscapes with low habitat quality and lower productivity increase of habitat quality may positively affect fertility while intra- and interspecific competition may negatively affect body mass in adult female roe deer. On the contrary, an increase in habitat quality in landscapes with already high productivity may not further improve fertility while reduction of intra- and interspecific competition still may improve body mass.

Weather conditions may influence body mass and fertility (Bonenfant et al., 2009, Hewison and Gaillard, 2001). In this study no effect of winter weather condition (pooled mean temperature from November to January) on body mass and fertility was found.

Habitat quality, density-dependence and competition

The maximum effect of density dependent change in body weight found in this study, within the forest landscape (which is least buffered by habitat quality, but which also provided the longest year span of data), is considerably greater than the differences among landscapes during a period of low to moderate deer density (4.9 kg versus 1.5 kg). The positive effect of high quality food availability on both body mass (Pettorelli et al., 2002) and fertility (Hamel et al., 2009) in the cereal farmland suggests that the performance of roe deer subpopulations may be affected by landscape productivity although landscape type explained only a small amount (about 7 %) of the total variation in body mass among individuals in 2000-09.

Woodland habitats are favoured by deer which might lead to higher population density in the pine forest than in the surrounding landscapes suggesting that intra- and interspecific interactions might first occur in forests (Nilsen et al., 2004).

The knowledge of demographic performance at landscape scale will help us to understand the interactions of deer between landscapes. However, further long-term landscape scale research is necessary to understand the complex interactions of landscape habitat quality, intra- and interspecific competition and management within and amongst landscapes and their significance for predictive deer management. Also less is known about source-sink dynamics within and amongst landscapes and how deer density, deer condition and habitat quality influence these dynamics and impact on biodiversity.

References

Aitken, R. J. (1974) Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility,* **39,** 225-233.

Aitken, R. J. (1975) Cementum layers and tooth wear as criteria for aging deer. *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. & Linnell, J. D. C. (2000) Irruptive potential in roe deer: Density-dependent effects on body mass and fertility. *Journal of Wildlife Management,* **64,** 698-706.

Bonenfant, C., Gaillard, J. M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L. E., Blanchard, P., Pettorelli, N., Owen-Smith, N., Du Toit, J. & Duncan, P. (2009) Empirical Evidence of Density-Dependence in Populations of Large Herbivores. *Advances in Ecological Research, Vol 41*, pp. 313-357. Elsevier Academic Press Inc, San Diego.

Chapman, N. & Whitta, R. (1996) The history of the deer of Thetford Forest. *Thetford Forest Park - The ecology of a pine forest* (eds P. R. Ratcliffe & J. Claridge), pp. 141-149. Forestry Commission, Thetford.

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. & Albon, S. (1989) *Red deer in the Highlands,* Blackwell Scientific Publications, Oxford.

Dolman, P. M. & Sutherland, W. J. (1992) The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* **29,** 402-413.

Dolman, P. M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research,* **35,** 202-214.

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.

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

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.

Focardi, S., Pelliccioni, E. R., 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.

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., Delorme, D., Boutin, J.-M., van Laere, G., Boisaubert, B. & Pradel, R. (1993) Roe deer survival patterns: a comparative analysis of contrasting populations. *Journal of Animal Ecology,* **62,** 778-791.

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

Gaillard, J.-M., Sempéré, A. J., van Laere, G., Boutin, J.-M. & Boisaubert, B. (1992) Effects of age and body mass on the proportion of females breeding in a population of roe deer. *Canadian Journal of Zoology,* **70,** 1541-1545.

Hamel, S., Gaillard, J. M., Festa-Bianchet, M. & Cote, S. D. (2009) Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology,* **90,** 1981-1995.

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, Norwich.

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.

Herfindal, I., Solberg, E. J., Saether, B. E., Hogda, K. A. & Andersen, R. (2006) Environmental phenology and geographical gradients in moose body mass. *Oecologia,* **150,** 213-224.

Hewison, A. J. M. (1993) The reproductive performance of roe deer in relation to environmental and genetic factors. University of Southampton, Southampton.

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.

Kjellander, P., Gaillard, J. M. & Hewison, A. J. M. (2006) Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia,* **146,** 521-530.

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.

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

Latham, J., Staines, B. W. & Gorman, M. L. (1996) The relative densities of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer and their relationship in Scottish plantation forests. *Journal of Zoology,* **240,** 285-299.

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J. & Jullien, J. M. (1999) Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology,* **80,** 2539-54.

Mayle, B. A. (1996) Progress in predictive management of deer populations in British woodlands. *Forest Ecology and Management,* **88,** 187-198.

McIntosh, R., Burlton, F. W. E. & McReddie, G. (1995) Monitoring the density of a roe deer *Capreolus capreolus* population subjected to heavy hunting pressure. *Forest Ecology and Management,* **79,** 99-106.

Mysterud, A. (2000) Diet overlap among ruminants in Fennoscandia. *Oecologia,* **124,** 130-137.

Nilsen, E. B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., van Laere, G. & Linnell, J. D. C. (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology,* **78,** 585-594.

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.

Pettorelli, N., Dray, S., Gaillard, J. M., Chessel, D., Duncan, P., Illius, A., Guillon, N., Klein, F. & Van Laere, G. (2003) Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia,* **137,** 363-369.

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

Pettorelli, N., Gaillard, J.-M., Yoccoz, N. G., Duncan, P., Maillard, D., Delorme, D., van Laere, G. & Toigo, C. (2005) The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. *Journal of Animal Ecology,* **74,** 972-981.

Putman, R. J. (1986) Competition and coexistence in a multispecies grazing system. *Acta Theriologica,* **31,** 271-291.

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.

Radeloff, V. C., Pidgeon, A. M. & Hostert, P. (1999) Habitat and population modelling of roe deer using an interactive geographic information system. *Ecological Modelling,* **114,** 287-304.

Ratcliffe, P. R. (1996) The performance of roe and red deer at Thetford Forest. *Thetford Forest Park - The ecology of a pine forest* (eds P. R. Ratcliffe & J. Claridge), pp. 150-156. Forestry commission, Thetford.

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

Richard, E., Gaillard, J.-M., Said, S., Hamann, J.-L. & Klein, F. (2009) High red deer density depresses body mass of roe deer fawns. *Oecologia,* **163,** 91-7.

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

Sand, H. (1996) Life history patterns in female moose (*Alces alces*): The relationship between age, body size, fecundity and environmental conditions. *Oecologia,* **106,** 212-220.

Sempéré, A. J., Mauget, R. & Mauget, C. (1998) Reproductive physiology of roe deer. *The European roe deer: the biology of success* (eds R. Andersen, P. Duncan & J. D. C. Linnell), pp. 161-188. Scandinavian University Press, Oslo.

Sheail, J. (1979) Documentary evidence of the changes in the use, management and appreciation of the grass-heath of Breckland. *Journal of Biogeography,* **6,** 277-292.

Toigo, C., Gaillard, J.-M., van Laere, G., Hewison, A. J. M. & Morellet, N. (2006) How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography,* **29,** 301-308.

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.

Chapter Three

A test of the fragmentation-nutrition hypothesis: Is deer performance in woodland affected by forest configuration and access to farmland?

Abstract

Fragmented landscapes, comprising small woodlands set in a farmland matrix have been proposed to enhance the expansion and increase of deer populations in adjacent habitats. In this study I assessed whether landscape structure and configuration of forest blocks affect body mass and fertility in adult roe deer (*n* = 1132) and female Reeve's muntjac (*n* = 808) in a 195 km^2 pine forest in East England in 2001-09. Deer density and habitat quality effects were considered at the scale of *n* = 22 forest beats. Body mass in both species was positively affected by access to farmland: adult female roe deer within a 1000m-buffer from farmland were 4% heavier and female muntjac 3% heavier than those in the forest core. I also found effects of year on female muntjac body mass and fertility with body mass and fertility being 4% and 14% higher in 2006 than 2009 suggesting that annual weather changes may be important to Reeve's muntjac performance. High roe deer densities negatively impacted on roe deer body mass. In roe deer individuals were 0.5 kg lighter in areas with high roe deer densities (> 20 deer km^{-2}) than in areas with low densities (< 10 km^{-2}). Fertility of neither species was significantly affected by access to farmland. For roe deer I found a positive significant effect of habitat quality within forest beat (higher proportions of calcareous soil) on fertility.

Although landscape structure may affect deer quality, I found no evidence that configuration would alter fertility. Thus, landscape structure is unlikely to amplify source-sink dynamics within and amongst landscapes and therefore will affect impacts on biodiversity.

Introduction

It is important to understand the influence that landscape composition and configuration have on local deer performance in order to advance both conservation management in forested landscapes and predictive deer management. Deer numbers and range are still increasing in Europe and North America (Ward, 2005, Dolman and Wäber, 2008, Cote et al., 2004). Changes in vegetation composition and structure due to increasing numbers of deer affect composition and abundance of bird communities (Gill and Fuller, 2007, Fuller, 2001); invertebrates (Allombert et al., 2005b, Feber et al., 2001); and small mammals (Flowerdew and Ellwood, 2001, McShea, 2000). It has been proposed that fragmentation of continuous forests into small woodlands bordered by nutritious farmland has contributed to deer population expansion due to higher quality food supply (Putman and Moore, 1998, Alverson et al., 1988, Sinclair, 1997). In a study using pellet group transects, Hemami et al. (2005) found a positive relationship between the density of Reeve’s muntjac *Muntiacus reevesi* (controlling for forest growth stage) and the ratio of open habitat to forest area perimeter, but not for roe deer *Capreolus capreolus*.

Landscape mosaics can provide patches of high and low quality habitats for herbivores. Deer populations show gradients in distribution along these structural features influencing local population densities (Hemami et al., 2005), home range sizes (Said et al., 2009), body size (Hewison et al., 2009), performance (Nilsen et al., 2004) and habitat exploitation (Hemami et al., 2004, Gordon, 2003). For example, Said and Servanty (2005) examined whether fragmentation of the landscape caused by hurricane Lothar and massive tree felling in an enclosed forest at Chizé, France, affected home range size of roe deer. They found home range size following the hurricane decreased with increasing edge density. For female mule deer *Odocoileus hemionus* in California, USA, 57% of the variation in home range size was explained by landscapes structure including patch density per 100 ha, mean nearest neighbour (spatial arrangement of patches), mean shape index (patch shape) and mean edge contrast index (structural contrast between neighbouring patches) (Kie et al., 2002). Although, previous studies have considered the effects of landscape configuration on home-range size and deer density, few have examined effects on performance (body size and fertility). On a peninsula in central Japan Miyashita et al. (2008) showed that the length of forest edge (total length of forest perimeter abutting open habitats and roads > 2m) in a 200 m buffer around the location where individual deer were caught had a positive effect on pregnancy rate of sika deer *Cervus nippon* (*n* = 61).

In this study I examine the effects of landscape structure on fertility and body mass of adult female roe deer and female Reeve's muntjac in a 195 km^2 conifer plantation in Eastern England, UK. Data have been collected during 2001-09. I treated each culled animal as an observation. I controlled for effects of forest block and year, and tested whether body mass or fertility were higher for those animals culled close to the forest/farm boundary versus those culled deep inside the forest core. I also examined important ecological elements to deer such as: 1.) availability of nutritious food within the forest (assessed using soil type as a proximate soil composition), 2.) habitat suitability (percentage of preferred habitat) and 3.) for Reeve's muntjac access to roads (the wide cut verge of major roads ('A'-roads) may offer nutritious food).

Our main hypothesis is that deer performance (fertility and body mass) of both species will be positively influenced by access to farmland that provides a source of highly nutritious forage and for Reeve's muntjac by access to roads as additional feeding sources. I also hypothesised that within the forest (a) habitat suitability (Hemami et al., 2004, Hemami et al., 2005) and (b) the availability of nutritious food positively affect deer performance whereas (c) high deer densities have negative impacts.

Methods

(a) Study area

The study was carried out in Thetford Forest, the largest lowland conifer forest in England (Eycott et al., 2006) (latitude: 52°30’, longitude: 0°38’). Thetford Forest occupies 195 km^2 of Breckland, a biogeographic region in eastern England characterised by semi-continental climate and sandy, nutrient-poor soils (Dolman and Sutherland, 1992).

Four deer species occur in Thetford Forest: native roe deer and red deer *Cervus elaphus* as well as introduced Reeve’s muntjac and fallow deer *Dama dama*. Both roe deer and Reeve’s muntjac are widespread and abundant throughout the forest. Red deer are evenly distributed throughout the forest in low numbers and fallow deer are abundant in the Southern blocks of the forest but are scarce in the North.

The forest comprises a mosaic of growth stages with Corsican pine (*Pinus nigra* var. *maritima*) (59%) and Scots pine (*Pinus sylvestris*) (15%) the dominant tree species, other conifers comprise 5% and deciduous species 10% of the area. The forest landscape is surrounded by areas of grass-heath, farmland and scattered coniferous and mixed woodlands, with urban settlement abutting a small proportion of the forest perimeter.

The forest is divided into twelve deer management units (DMU), separated by roads. Eleven DMU’s are managed by the Forestry Commission (FC) but one unit is leased to a private stalking club. Due to the large variation in the area of individual DMU’s (mean area = 15.6 km^2 ± 10.2 SD, range 4.5 km^2 to 34.7 km^2) these were further divided into smaller units hereafter referred to as beats. Beats (n = 22, mean area = 8.5 km^2 ± 4.0 *SD*, range 2.0 km^2 to 16.5 km^2) were demarcated by major roads within individual DMU’s, and were defined on the basis of access to farmland and soil characteristics within the extent of each beat. Details (crops species, planting year, area and soil type) of each management sub-compartment (part of a single even aged planted coupe subdivided by trackways, mean area = 3.1 ± 3.1 ha *SD*) are available from a GIS database managed by FC.

(b) Cull data

Roe deer and Reeve's muntjac cull data were collected by the FC from 2001-2009, recording the date shot, location (compartment number or from Global Positioning System (GPS)), sex, age, body mass, reproductive status of females (presence and number of embryos, *corpora lutea*, milk) and remarks (e.g. if shot damage affected body weight). In 2001-03 culled roe deer were aged (Hemami, 2003) by incremental analysis of sectioned teeth following Aitken (1975), Ratcliffe and Mayle (1992) and Hewison (1993); and by tooth wear and tooth eruption criteria in 2004-09 reliably separating kids (juveniles from the date of birth till the following April), yearlings (from April in the year after their birth, until the subsequent spring) and adults. Female roe deer are culled during winter, from November to February/March whereas female Reeve's muntjac are culled all year round. Throughout the paper carcass mass following the removal of head, lower legs, blood and viscera is referred to as body mass and is measured to the nearest 0.1 kg for both species.

(c) Roe deer

In roe deer fertilised blastocysts are not implanted until December due to delayed implantation (Aitken, 1974, Sempéré et al., 1998). Embryos are therefore not visible before January on opening the uterus (Ratcliffe and Mayle, 1992). Although, previous studies on reproductive output of roe deer in Britain considered data of females culled from the first of January (Hewison, 1996, Ratcliffe and Mayle, 1992) there is a risk of missing embryos in the early stages of development (Hemami, 2003). Cold weather in November/December can also influence the detectability of embryos in the uterus in early January (P. Mason, pers. comm.). In our study 28% of adult roe deer females ($n = 207$) shot from early January to 24th of January lacked any foetuses whereby only 7% of females ($n = 538$) shot from 25th of January appeared to lack any foetus ($n = 614$, $\chi^2_{(1)} = 27.67$, $p < 0.001$, early January: $B = -0.28 \pm 0.05$ SE). Therefore, in analyses of roe deer fertility I only considered females shot from the 25th of January to the end of the cull season in March.

Analysis of fertility was restricted to cull data, recorded by FC rangers, data from one DMU managed by a private stalking club were excluded as the proportion of females recorded as pregnant was significantly lower than in forest blocks managed by the FC ($\chi^2_{(1)} = 64.62$, $p < 0.001$).

The proportion of culled females recorded as non-pregnant was significantly different in the time period 2001-05 (11.7% not pregnant, $n = 26$) versus the time period 2006-09 (5.5% not pregnant, $n = 11$) (GLM with Poisson errror: $\chi^2_{(1)} = 5.00$, $p = 0.03$) after the introduction of improved data management protocols from 2006 that distinguished from a record of zero foetus in a checked uterus, versus unchecked. Either not every female was checked for foetuses thoroughly in 2001-05, or an external effect has changed over time. Therefore I conduct two seperate analyses of fertility. First considering data from the entire period 2001-09, whilst incorporating a categorical variable for time periods (2001-05 versus 2006-09) for over-representation of zeros in the period 2001-05; and second restricting data to animals culled during 2006-09.

Body mass and fertility of deer can be affected by age (Pettorelli et al., 2002, Pettorelli et al., 2001, Andersen and Linnell, 2000, Focardi et al., 2002b). Prime aged roe deer (2-6 years) have been found to have higher body mass and fertility than senescent animals (> 6 years) (Gaillard et al., 2000). Accurate determination of age by cementum annuli technique was available for individuals culled in 2001-03. I tested whether body mass of $n = 306$ individuals from 2001-03 and fertility of $n = 137$ individuals from 2001-03 was affected by adult female age (between 2-13 years). Using a General Linear Model with normal error for body mass and a General Linear Model with poisson error for fertility I explored the effects of age on deer condition, including age (years, continuous) and additional quadratic terms. For body mass I found a marginally significant quadratic increase and subsequent decline of body mass with age (age $F_{(1,303)} = 3.40$, $p = 0.07$, $B = 0.32$ kg/year ± 0.18 SE; age squared $F_{(1,303)} = 4.47$, $p = 0.04$, $B = -0.03$ kg/year^2 ± 0.01 SE). However, body mass was not affected by age in females aged from two to ten years ($n = 298$: age $F_{(1,295)} = 1.40$, $p = 0.24$, $B = 0.26$ kg/year ± 0.22 SE; age squared $F_{(1,295)} = 1.41$, $p = 0.24$, $B = -0.02$ kg/year^2 ± 0.02 SE). Thus, in 97.7% of the aged animals no effect of age structure on body mass was found. The significant age effect on body mass related just to a small handful of exceptionally old (> 10 years) individuals ($n = 7$) mean = 12.2 kg ± 0.5 SE compared to the overall mean = 13.7 kg ± 0.1 SE ($n = 298$) found in 2001-03. Fertility of female roe deer was not affected by age structure ($n = 137$: age $\chi^2_{(1)} = 0.36$, $p = 0.55$, $B = 0.06 \pm 0.09$ SE; age quadratic term $\chi^2_{(1)} = 0.17$, $p = 0.69$, $B = -0.003 \pm 0.007$ SE).

Cull pressure has been consistent over the last ten years and it is highly unlikely that age structure of the roe population has altered. Combined with the minimal effect of age on body mass I am confident that age will not bias or confound my test of fragmentation effects.

(d) Reeve's muntjac

As in roe deer, considering FC data Reeve's muntjac fertility (*n* = 3510) (here females recorded with foetuses, *corpora lutea* and/or milk) was significant lower in 2001-05 (fertility: mean = 0.4 ± 0.01 *SE*) than 2006-09 (mean = 0.5 ± 0.01 *SE*) (Wald $\chi^2_{(1)}$ = 35.25, $p < 0.001$; 2001-05: $B = -0.15 \pm 0.03$ *SE*) and significant lower in the leased deer block (fertility: mean = 0.2 ± 0.01 *SE*) than in the FC deer management blocks (fertility: mean = 0.8 ± 0.01 *SE)* (Wald $\chi^2_{(1)}$ = 555.39, $p < 0.001$, FC DMU's: $B = 1.29 \pm 0.06$ *SE*). Consequently, I restricted the analyses to Reeve's muntjac culled during 2006-09 and excluded the leased block in all analyses. Cull year was included as a categorical variable in further analyses to control for variations in body mass and fertility between years.

Unlike roe deer, introduced Reeve's muntjac are originally a sub-tropical species and do not show a seasonal reproductive cycle (Chapman et al., 1997) with births are distributed throughout the year. Female Reeve's muntjac are classified as adults when they reach a live weight of 10 kg (around 8 months) at which stage they are capable of breeding (Chapman, 1991). In Southern England the mean live weight of females over 2 years is 12 kg (range 9.0-15.8 kg, *n* = 124) (Chapman, 1991).

There were no distinctions of sub-adult and adult animals within the data logging protocols. As blocks with higher fertility and higher proportion of young animals may have lower mean body masses I assessed the influence of body mass classes here (carcass weight: class 1: < 5 kg; 2: 5 - 6 kg; 3: 6 - 7 kg; 4: 7 - 8 kg; 5: 8 - 9 kg; 6: > 9 kg; table 1 and 2) on Reeve's muntjac fertility (foetuses per female: *n* = 1381, mean = 0.7 ± 0.1, range: 0-2) and fertility status (whether or not female is reproducing (0/1) whereas 0 = no signs of reproduction; 1 = pregnant females (foetuses, *corpora lutea*) and/or females with kid (milk)) (Table 3.1). Using GLM's with poisson error Reeve's muntjac fertility and fertility status differed significantly among body mass classes (fertility: *n* = 1172, Wald $\chi^2_{(5)}$ = 123.80, $p < 0.001$) [$6^a \approx 5^a \approx 4^a > 3^b > 2^c > 1^d$; shared superscripts do not differ, Sequential Sidak test $p < 0.001$]; fertility status: *n* = 1177, Wald $\chi^2_{(5)}$ = 284.74, $p < 0.001$) [$6^a \approx 5^a \approx 4^a > 3^b > 2^c > 1^d$). Therefore, I restrict analyses to reproductively mature adult Reeve's muntjac (≥ 7 kg).

Table 3.1. Reeve's muntjac mean fertility ± *SE* (foetuses per female) and mean fertility status ± *SE* (mean proportion of females (0/1) showing either milk, *corpora lutea* or foetuses) (n = 1177) in each body mass class in 2006-09 (n = 1172).

Body mass class	Mean fertility (foetuses per female) ± *SE* (n)	Mean fertility status (0/1) ± *SE* (n)
1 (< 5 kg)	0.2 ± 0.03 (90)	0.3 ± 0.02 (91)
2 (5-6 kg)	0.5 ± 0.04 (102)	0.6 ± 0.03 (103)
3 (6-7 kg)	0.6 ± 0.04 (172)	0.8 ± 0.03 (173)
4 (7-8 kg)	0.8 ± 0.03 (380)	1.0 ± 0.02 (381)
5 (8-9 kg)	0.9 ± 0.03 (304)	1.0 ± 0.02 (305)
6 (> 9 kg)	0.9 ± 0.05 (124)	1.0 ± 0.04 (124)

Reeve's muntjac are culled all year round therefore I tested if body mass and fertility of adult female muntjac (≥ 7 kg) are affected by month. Whilst controlling for cull year body mass was affected by month (n = 810, month: $F_{(11,795)} = 2.26$, $p = 0.01$, $R^2 = 0.08$, cull year: $F_{(3,795)} = 11.41$, $p < 0.001$) but fertility differed significantly between months (AICc = 1607.10, n = 808, month: Wald $\chi^2_{(11)} = 24.05$, $p = 0.01$, cull year: Wald $\chi^2_{(3)} = 3.10$, $p = 0.08$) (Table 3.2).

To further explore seasonal differences in fertility I pooled the data in 2-month-periods (Table 3.2) and accessed the influence of these periods on fertility whilst controlling for cull year. Fertility differed significantly among 2-month periods (AICc = 1596.28, Wald $\chi^2_{(5)} = 19.16$, $p = 0.002$; cull year: Wald $\chi^2_{(3)} = 9.85$, $p = 0.02$) (Table 3.2) and was generally higher during January-June, March-April, May-June and September-October than July-August and November-December. Model fit was further improved by pooling January-June (n = 525) versus July-December (n = 283) (AICc = 1588.93, Wald $\chi^2_{(1)} = 17.66$, $p < 0.001$; $B = 0.20 \pm 0.05$ *SE* in foetuses per month in January-June) whilst controlling for cull year (Wald $\chi^2_{(3)} = 10.97$, $p = 0.01$).

Table 3.2. Effect of month on body mass [kg] (n = 810) and fertility (foetuses per female) (n = 808) of female Reeve’s muntjac in 2006-09. Sequential Sidak[1] significance comparing muntjac fertility in 2-month-periods and 6-month-periods are shown with superscripts, periods that do not share a superscript differ significantly ($p < 0.05$).

Month	Body mass Mean ± *SE*	Fertility Mean ± *SE*	Fertility[1] Mean ± *SE*	Fertility[1] Mean ± *SE*
January	8.2 ± 0.07 (129)	0.84 ± 0.05 (129)	0.87 ± 0.03^{a} (274)	0.88 ± 0.02^{a} (525)
February	8.1 ± 0.07 (145)	0.90 ± 0.05 (145)		
March	8.1 ± 0.13 (6)	1.0 ± 0.23 (6)	$0.87 \pm 0.05^{a,b}$ (124)	
April	7.9 ± 0.06 (118)	0.87 ± 0.05 (118)		
May	8.2 ± 0.07 (105)	0.88 ± 0.05 (105)	0.87 ± 0.05^{a} (127)	
June	8.0 ± 0.09 (22)	0.84 ± 0.11 (22)		
July	8.3 ± 0.13 (40)	0.58 ± 0.07 (40)	0.67 ± 0.05^{c} (84)	0.72 ± 0.03^{b} (283)
August	8.1 ± 0.12 (44)	0.75 ± 0.07 (44)		
September	8.1 ± 0.13 (43)	0.84 ± 0.08 (42)	$0.79 \pm 0.06^{a,b,c}$ (69)	
October	8.3 ± 0.17 (28)	0.71 ± 0.09 (27)		
November	8.4 ± 0.11 (68)	0.77 ± 0.06 (68)	$0.71 \pm 0.04^{b,c}$ (130)	
December	8.3 ± 0.11 (62)	0.64 ± 0.06 (62)		

(e) Analysis

Each culled individual was treated as an observation. I investigated whether body mass using General Linear Models with normal error or fertility using General Linear Models with poisson error were higher for those animals close to the forest/farm boundary versus those culled in the forest core areas (Table 3.3). For Reeve’s muntjac I also tested whether body mass and fertility were higher for animals shoot close to major road verges (‘A’-roads) versus those culled in some distance away from major roads (‘A’-roads). I controlled for annually changing events such as weather effects by inserting cull year as categorical variable in the model, and to take account of the complex structure of ecological factors within the location the deer was shoot in I inserted beat as categorical variable. For Reeve’s muntjac analysis of fertility I also added the season (month) the deer was shoot in as categorical variable as fertility varied throughout the year. The proportion of culled roe females recorded as pregnant differed between the periods 2001-05 versus 2006-09 therefore I controlled for these periods in analysis of fertility in 2001-09 (Table 3.4).

Table 3.3. Description of the explanatory variables used to analyse the effect of landscape configuration on body mass and fertility of adult female roe deer and female Reeve's muntjac.

Name	Definition	Mean ± SD (n)	Individuals within buffer [%]	Buffer area [%] of study area
Habitat suitability roe	Proportion of preferred forest GS (open, restock, pre-thicket, mature pine) in each beat in each year (range: 0-1)	0.43 ± 0.12 (198)	-	-
Habitat suitability muntjac	Proportion of preferred forest GS (pre-thicket, mature pine, broadleaf) in each beat in each year (range: 0-1)	0.44 ± 0.13 (198)	-	-
Access to farmland 100m	Whether (0/1) compartment in which individual was culled, intersects by > 50% a buffer (radius defined by approximate home range) from the beat perimeter to farmland or major ('A') road. Buffers of 100m, 500m, 1000m	0.13 ± 0.10 [1] (22)	muntjac: 54	12
Access to farmland 500m		0.55 ± 0.32 [1] (22)	muntjac: 73 Roe: 66	49
Access to farmland 1000m		0.75 ± 0.30 [1] (22)	Roe: 85	70
Access to farmland and ('A') roads 100m		0.16 ± 0.11 [1] (22)	muntjac: 59	14
Access to farmland and ('A') roads 500m		0.64 ± 0.31 [1] (22)	muntjac: 81	57
Calcareous soil	Proportion of calcareous soil in each beat (range: 0-1)	0.42 ± 0.22 (22)	-	-

[1] mean ± SD of buffer as proportion of beat area

I defined buffer areas with three different widths from the forest edge into the forest. Animals culled within the buffer where close to the forest/farm boundary whereas animals outside the buffer area where culled in the forest core. Deer performance may also be influenced by the availability of preferred growth stages (habitat suitability) and the proportion of calcareous soil (habitat quality), and deer density. The percentage of preferred growth stages and the proportion of calcareous soil were calculated for each individual beat. Deer density was estimated at DMU level.

Access to farmland and ‘A’-roads

Whether (0/1) an individual had access to farmland or ‘A’-roads depended on the location at which the animal was culled (compartment: mean = 11.1 ha ± 3.81 *SD*, *n* = 1737). Individuals were able to access farmland and roads when the cull location was situated within defined buffer zones from farmland or major ‘A’-roads into the forest. Buffer zone width was based on a study of the ranging behaviour of Reeve’s muntjac and roe deer by radio-tracking techniques in the southern part of Thetford Forest (Chapman et al., 1993). Minimum convex polygons were calculated at bimonthly periods. Largest home range sizes for adult female Reeve’s muntjac were found in March-April (mean = 14.5 ha ± 1.9 SE, *n* = 36) and for adult female roe deer in January-February (mean = 114.1 ha ± 23.0 SE, *n* = 7) (Chapman et al., 1993). No seasonal change of core areas for adult female Reeve’s muntjac or roe deer was detected (Chapman et al., 1993). I therefore assume that the annual home range was stable in location though varying in overall area throughout the year. Two buffer zones were created. The first buffer zone width was defined by the approximate radius of home range size. A second buffer zone width was then set closer to the periphery of the forest as the first buffer zone, to test if the possible effect of farmland or major roads on deer performance was stable or increased. An increase of the effect of farmland or major roads within the second buffer zone compared to the first zone may suggest a possible overlap with animals living in the forest core. Consequently, two buffer zones for roe deer (1000 m and 500 m) and for Reeve’s muntjac (500 m and 100 m) were established. The definition of these buffer zones was also emphasised by the maximum mean distance adult female roe deer (mean = 1856.2 m ± 245.9; *n* = 17, January-February) and adult female Reeve’s muntjac (mean = 961.9 m ± 81.0; *n* = 44, September-October) daily travelled (Chapman et al., 1993).

Farmland areas had been marked on maps during field surveys and transferred in ArcGIS 9.3 (ESRI Co. Ltd) using Ordnance Survey data (scale 1:25 000, colour raster file) for Breckland and a GIS database managed by FC. The same Ordnance Survey data were also used to identify and map ‘A’-roads. Then, perimeter farmland and ‘A’-roads were buffered into the forest using Arc toolbox. Animals where cull location (forest compartment) lay within the buffer or where more than 50% of the compartment area was located within the buffer were considered to have access to farmland or ‘A’-roads.

Availability of nutritious food within the forest

Soil types were classified as acidic (podsols, acidic brown earth), calcareous (rendzinas and calcareous brown earth), or others (mainly ground water influenced gleys) following Eycott (2005) and Corbett (1973).

Calcareous soil supports greater plant species diversity (Eycott et al., 2006) offering a greater diversity of food than found on more acid soil. Thus, food quality within the forest was defined as the proportion of calcareous soil in each beat (*n* = 22) ranging between 1% and 86% (mean = 42% ± 22% SD).

Habitat suitability

Body mass and fertility of deer are influenced by habitat (Kjellander et al., 2006, Pettorelli et al., 2002, Nilsen et al., 2004). Following (2005) and Hemami et al. (2004) I distinguish five growth stages within the coniferous forest: restock (1-5 years); pre-thicket (6-10 years); thicket (11-20 years); pole stage (21-45 years) and mature (> 45 years) and additionally mature broadleaf (> 45 years). For each deer species I pooled the proportion of the most preferred habitat (Hemami et al., 2004, Hemami et al., 2005): for muntjac pre-thicket, mature pine and broadleaf; and for roe deer open, restock, pre-thicket and mature pine.

Roe deer and Reeve’s muntjac densities

Roe deer body mass and fertility have been suggested to be negatively impacted by intra-specific competition with Reeve’s muntjac (Hemami et al., 2004, Chapman et al., 1993, Dolman and Wäber, 2008). Deer densities in the twelve DMU’s in Thetford Forest have been estimated using intensive thermal imaging distance sampling counts in 2007-2010 (K. Wäber, unpublished; T. Banham, unpublished). Roe deer and Reeve’s muntjac densities ranged from low (< 10 deer km^{-2}) or moderate (10-30 km^{-2}) to high (> 30 km^{-2}) following the classification from (Mayle, 1996) for roe deer. As distribution of deer densities throughout the forest did not change during the period 2007-2010 I assume that density classifications in 2007-2010 are broadly representative of those of 2001-06. Therefore I assess the effect of roe and Reeve’s muntjac density on adult female roe deer body mass and fertility in 2001-2009 using the density classification from 2007-10.

Inter-correlations of predictors roe deer

I tested whether my predictors are related to investigate whether changes in one variable are met with similar changes in the other by using correlations. Correlations are tested across all forest beats (n = 22) in 2001-09. Access to farmland (variable: 0/1; 1000m buffer) was not related to proportion of calcareous soil (n = 22) in each beat (n = 198, ρ = 0.03, p = 0.71) and to the proportion of preferred growth stage (n = 198) in each beat (n = 22) in each year (n = 9) (n = 198, ρ = 0.10, p = 0.16). There was a significant relationship between access to farmland (variable: 0/1; 500m buffer) and the proportion of calcareous soil (n = 22) in each beat (n = 198, ρ = 0.23, p = 0.001). No significant relationship was found between access to farmland (500m buffer) and proportion of preferred growth stage (n = 198) in each beat (n = 22) in each year (n = 9) (n = 198, ρ = 0.01, p = 0.85). The proportion of preferred growth stage (n = 198) was significantly negative related to the proportion of calcareous soil (n = 22) (n = 198, r = -0.14, p = 0.04). All correlations have a small to medium effect.

Inter-correlations of predictors Reeve's muntjac

Correlations are tested across all forest beats (n = 22) in 2001-09 (n = 9). Access to farmland (variable: 0/1, 500m buffer and 100m) was significantly related to proportion of calcareous soil (n = 22) (500m: n = 198, ρ = 0.23, p = 0.001 and 100m: n = 198, ρ = 0.20, p = 0.005) in each beat (n = 22) and proportion of preferred growth stage (n = 198) (500m: n = 198, ρ = 0.18, p = 0.01 and 100m: n = 198, ρ = 0.20, p = 0.005) in each beat (n = 22) in each year (n = 9).

Access to farmland and 'A'-road (500m and 100m) were significantly related to preferred growth stage (n = 198) in each beat (n = 22) in each year (n = 9) (500m: n = 198, ρ = 0.17, p = 0.02 and 100m: n = 198, ρ = 0.21, p = 0.003) and to proportion of calcareous soil (n = 22) (500m: n = 198, ρ = 0.18, p = 0.01 and 100m: n = 198, ρ = 0.17, p = 0.02) in each beat. No significant relationship was found between proportion of preferred growth stage (n = 198) and proportion of calcareous soil (n = 22) (r = -0.06, p = 0.37).

Table 3.4. Summary of models tested for Reeve’s muntjac and roe deer examining the effect of landscape fragmentation, forest beat configuration and composition on body mass and fertility in Thetford Forest in 2001-09.

Model	Model configuration	
a) Reeve’s muntjac: body mass and fertility 2006-09		
1	Buffer farmland 500m Beat Month	Buffer farmland 500m Beat Month Year
2	Buffer farmland/roads 500m Beat Month	Buffer farmland/roads 500m Beat Month Year
3	Buffer farmland 100m Beat Month	Buffer farmland 100m Beat Month Year
4	Buffer farmland/roads 100m Beat Month	Buffer farmland/roads 100m Beat Month Year
5	Best model plus as replacement for beat:	a) Habitat quality b) Habitat suitability c) Muntjac density
b) Roe deer: body mass 2001-09 and fertility 2006-09		
1	Buffer farmland 1000m Beat	Buffer farmland 1000m Beat Year
2	Buffer farmland 500m Beat	Buffer farmland 500m Beat Year
3	Best model plus as replacement for beat:	a) Habitat quality b) Habitat suitability c) Muntjac density d) Roe density
c) Roe deer: fertility 2001-09		
4	Buffer farmland 1000m Beat Year period	Buffer farmland 1000m Beat Year
5	Buffer farmland 500m Beat Year period	Buffer farmland 500m Beat Year
6	Best model plus as replacement for beat:	a) Habitat quality b) Habitat suitability c) Muntjac density d) Roe density

Results

The effect of landscape structure on body mass

Reeve's muntjac

Female muntjac body mass was significantly positively affected by access to farmland in 500m- and 100m-buffer zone (Table 3.5, Table A3.1). Although both buffer zones showed significant effects of access to farmland on body mass, the best model fit (500m: AIC = 1859.89 vs. 100m: AIC = 1853.68) and the strongest body mass effect (500m: *B* = 0.18 kg ± 0.08 *SE* vs.100m *B* = 0.21 kg ± 0.06 *SE*) were found within the 100m-buffer zone (Table 3.5, Table A3.1). Females within the 100m-buffer zone were about 3% heavier than females in the core of the forest. For buffers of both 500m and 100m models considering solely the access to farmland provided a better fit to the data than models that pooled access to farmland and access to 'A'-road (best model farmland 100m-buffer vs. farmland and road 100m-buffer ΔAIC = 3.94) (Table 3.5, Table A3.1).

Body mass was also weakly affected by beat configuration (Wald $\chi^2_{(20)}$ = 29.05, p = 0.05) (Table 3.5). However, no significant differences between beats were found (Sequential Sidak n.s.). Cull year also negatively impacted on female muntjac body mass (Wald $\chi^2_{(3)}$ = 29.80, $p < 0.001$; 2006: *B* = 0.33 kg ± 0.08 *SE*; 2007: *B* = 0.29 kg ± 0.08 *SE*; 2008: *B* = 0.03 kg ± 0.07 *SE*) having a stronger effect than access to farmland (Table 3.5). This may suggest that muntjac body mass is more affected by weather effects e.g. cold winter temperature than landscape structure. Reeve's muntjac female body mass was 4% higher in 2006 than in 2009 (mean difference = 0.33 kg ± 0.08 *SE*).

Table 3.5. Best model overview (General Linear Models with normal error) showing the effect of landscape structure and forest beat configuration on (a) female Reeve's muntjac body mass [kg] (*n* = 808) in 2006-09 and (b) adult female roe deer body mass [kg] (*n* = 1125) in 2001-09.

No.	Model predictors	*n*	B ± SE	Wald χ^2	p	ΔAIC	Log-likelihood	Dev/df	df
(a) Reeve's muntjac body mass									
1	Model			89.21	< 0.001	-	-901.84	0.56	784
	Access farmland 100m			12.30	< 0.001				1
	Yes	439	0.21 ± 0.06						
	No	369	-						
	Beat			29.05	0.05				18
	Year^1			29.80	< 0.001				3
	2006^a	160	0.33 ± 0.08						
	2007^a	206	0.29 ± 0.08						
	2008^b	218	0.03 ± 0.07						
	2009^b	224	-						
	Month			16.23	< 0.001				1
11	Model			57.55	< 0.001	11.49	-917.67	0.57	800
	Access farmland 100m No		369	12.65	< 0.001				1
	Yes		439						
	Year			37.16	< 0.001				
	Month			3.15	0.08				3
	Muntjac density^2			6.59	0.04				2
	High^a	413	-0.15 ± 0.09						
	Moderate^a	270	-0.01 ± 0.08						
	Low^a	125	-						
(b) Roe deer body mass									
1	Model			153.97	< 0.001	-	-2064.94	2.30	1109
	Access farmland 1000m			9.28	0.002				
	Yes	972	0.49 ± 0.16						
	No	160	-						
	Beat			124.02	< 0.001				
5	Model			49.81	< 0.001	66.16	-2117.02	2.47	1128
	Access farmland 1000m No	160		22.19	< 0.001				1
	Yes	972	0.69 ± 0.15						
	Muntjac density^3			13.62	8				2
	High^a	568	0.64 ± 0.17						
	Moderate^a	461	0.52 ± 0.17						
	Low^b	103	-						

[1] Body mass Reeve's muntjac Sequential Sidak test comparing cull year 2006-09 are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.05$).

[2] Body mass Reeve's muntjac Sequential Sidak test comparing Reeve's muntjac density classes (low / medium / high) are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.05$).

[3] Body mass roe deer Sequential Sidak test comparing Reeve's muntjac density classes (low / medium / high) are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.05$).

Roe deer

In adult roe deer females greater body mass was associated with access to farmland in both buffer zones (500m- and 1000m-buffer) (Table 3.5, Table A3.1). The model with the best fit (1000m-buffer) included access to farmland (Wald $\chi^2_{(1)}$ = 9.28, *p* = 0.002; *B* = 0.49 kg ± 0.16 *SE*) and forest beats (Wald $\chi^2_{(21)}$ = 124.02, *p* < 0.001) (Table 3.5). Females which had access to farmland in the 1000m-buffer zone were generally 4% heavier than females in the forest core. The maximal mean difference in body mass between beats was mean = 2.4 kg ± 0.44 *SE* (13%). Overall, higher body mass was found in beats with small area sizes (< 15 km^2) surrounded by farmland (AIC = 4220.28; access to farmland: Wald $\chi^2_{(1)}$ = 17.76, *p* = < 0.001; *B* = 0.58 kg ± 0.14 *SE*; island beat vs. core beat Wald $\chi^2_{(1)}$ = 35.85, *p* = < 0.001; *B* = 0.61 kg ± 0.10 *SE*).

Table 3.6a. Best model overview (General Linear Models with poisson error) showing the effect of landscape structure and forest beat configuration on (a) female Reeve’s muntjac fertility (foetuses per female) (*n* = 806) in 2006-09.

Model	Model predictors	*n*	B ± SE	Wald χ^2	*p*	ΔAIC	Log-likelihood	Dev/df	df
1	Model				0.90	-	-784.27	0.32	23
	Access farmland and (‘A’)-roads 100m No	332		0.30	0.58				1
	Yes	474							
	Month			5.22	0.02				1
	Beat			5.17	0.99				18
	Year			4.26	0.24				3
2	Model				0.90	0.09	-784.31	0.32	23
	Access farmland 100m No	369		0.22	0.64				1
	Yes	437							
	Month			5.23	0.02				1
	Beat			5.08	0.99				18
	Year			4.23	0.24				3

The effect of landscape structure on fertility

Fertility of adult female roe deer and female Reeve’s muntjac was not significantly affected by access to farmland (Table 3.6a and b, Table A3.2) in 2001-09 or 2006-09. In both species no significant effect of beat configuration on fertility was found in 2006-09 (Table 3.6a and b, Table A3.2).

Model fit of female muntjac fertility for buffers of both 500m and 100m comparing access to farmland versus access to farmland and ‘A’-roads whilst controlling for forest beat, cull year (some models) and monthly differences in fertility had similar AIC (Table 3.6a, Table A3.2).

Forest beats significantly affected roe deer fertility (1000m-buffer: Wald $\chi^2_{(18)} = 32.22$, $p = 0.02$; 500m-buffer: Wald $\chi^2_{(18)} = 32.62$, $p = 0.02$) in 2001-09 (Table 3.6b). No significant differences between beats were found (Sequential Sidak n.s.) and only a weak gradient in fertility differences between island beats versus core beats could be detected (farmland 1000m-buffer: AIC = 1078.80; fertility access to farmland: Wald $\chi^2_{(1)} = 0.55$, $p = 0.46$; $B = -0.05 \pm 0.07$ *SE*; fertility island beat Wald $\chi^2_{(1)} = 3.27$, $p = 0.07$; $B = -0.10 \pm 0.06$ *SE*). However, maximum mean difference in fertility between beats was mean fertility = 0.7 ± 0.26 *SE* (37%).

The effect of habitat quality within forest beats on body mass and fertility

Forest beats did significantly affect body mass in adult female roe deer (2001-09) and female Reeve’s muntjac (2006-09) (Table 3.5, Table A3.1) whereas no significant effect was found in fertility of both species in 2006-09. Only adult female roe deer in 2001-09 was significantly affected by forest beat (Table 3.6b). I replaced beat in the models with the best fit with ecological factors characterising the beat habitat quality: habitat suitability, proportion of calcareous soil, muntjac density and roe density (only in roe deer). Overall, model fit did improve when forest beat was replaced in analyses of female muntjac body mass, female muntjac fertility and adult female roe fertility in 2006-09 and in 2001-09 but not in analyses of adult female roe deer body mass (Table A3.1).

The effect of access to farmland (best model fit 100m-buffer) on female Reeve’s muntjac body mass showed a weak decrease in the model containing beat characteristics (beat: $B = 0.21$ kg ± 0.06 *SE* vs. beat replaced: $B = 0.15$ kg ± 0.05 *SE*) (Table 4) whereas the effect of cull year showed a weak increase (beat: 2006: $B = 0.33$ kg ± 0.08 *SE* vs. beat replaced: $B = 0.34$ kg ± 0.08 *SE*; 2007: $B = 0.29$ kg ± 0.08 *SE* vs. beat replaced: $B = 0.33$ kg ± 0.07 *SE*; 2008: $B = 0.03$ kg ± 0.07 *SE* vs. beat replaced: $B = 0.05$ kg ± 0.07 *SE*). In contrast to our predictions I did not find any significant effect of habitat suitability (Wald $\chi^2_{(1)} = 0.01$, $p = 0.92$), proportion of calcareous soil (Wald $\chi^2_{(1)} = 0.23$, $p = 0.63$) and only a weak effect of muntjac density (Wald $\chi^2_{(2)} = 6.59$, $p = 0.04$) on muntjac body mass (Table 3.5, Table A3.1). Habitat suitability showed a positive impact on body mass while proportion of calcareous soil and muntjac density did show a weak negative effect on body mass (Table 3.5, Table A3.1).

In adult female roe deer the effect of access to farmland (best model fit 1000m-buffer) increased body mass when replacing forest beats (Table, 3.4Table A3.1). No effect of roe deer density (Wald $\chi^2_{(1)}$ = 2.26, p = 0.13), calcareous soil (Wald $\chi^2_{(1)}$ = 0.08, p =0.78) and habitat suitability (Wald $\chi^2_{(1)}$ = 2.27, p =0.13) on roe deer body mass was found. Surprisingly, roe deer body mass was significant higher in areas with high Reeve's muntjac density (Wald $\chi^2_{(2)}$ = 13.62, p = 0.001; high: B = 0.64 kg ± 0.17 *SE* / moderate: B = 0.52 kg ± 0.17 *SE*) (Table 3.5).

I found no evidence that beat habitat quality did significantly affect muntjac fertility. Despite an improvement in model fit when replacing beat with ecological characteristics no significant effect of habitat suitability (Wald $\chi^2_{(1)}$ = 0.03, p = 0.87), proportion of calcareous soil (Wald $\chi^2_{(1)}$ = 0.66, p = 0.42) and muntjac density (Wald $\chi^2_{(2)}$ = 1.57, p = 0.46) were found (Table 3.6a, Table A3.2).

For roe deer I found a positive effect of proportion of calcareous soil (1000m-buffer) (Wald $\chi^2_{(1)}$ = 5.65, p = 0.02, B = 0.36 ± 0.15 *SE*) and a negative effect of low roe deer density (Wald $\chi^2_{(1)}$ = 5.61, p = 0.02, B = -0.13 ± 0.05 *SE*) on fertility. No significant effect of habitat suitability (Wald $\chi^2_{(1)}$ = 2.12, p = 0.15) or muntjac density (Wald $\chi^2_{(2)}$ = 5.04, p = 0.08) could be detected (Table 3.6b, Table A3.2).

Table 3.6b. Best model overview (Generalized linear models with poisson error) showing the effect of landscape structure and forest beat configuration on (a) adult female roe deer fertility (foetuses per female) (*n* = 198) in 2006-09 and (b) adult female roe deer fertility (foetuses per female) (*n* = 414) in 2001-09.

Model	Model predictors	*n*	B ± SE	Wald χ^2	*p*	ΔAIC	Log-likelihood	Dev/df	df
(a)									
1	Model			18.60	0.48	-	-254.28	0.32	178
	Access farmland 500m			0.52	0.47				
	Yes	125	-0.06 ± 0.09						
	No	73	-						
	Beat			17.99	0.46				
2	Model			18.07	0.52	0.15	-254.36	0.32	178
	Access farmland 1000m			0.03	0.87				
	Yes	167	-0.02 ± 0.11						
	No	31	-						
	Beat			17.27	0.51				
(b)									
1	Model			49.63	< 0.001	-	-529.49	0.40	399
	Access farmland 1000m No	69		1.77	0.18	1100.99			
	Yes	351	-0.12 ± 0.09						
	Beat			32.62	0.02				
	Year period			18.10	< 0.001				
2	Model			48.12	< 0.001	0.53	-529.76	0.40	399
	Access farmland 500m No	148		0.40	0.53				
	Yes	272	-0.04 ± 0.07						
	Beat			32.62	0.02				
	Year period			17.65	< 0.001				

Table 3.6b.

5	Model			20.05	< 0.001	-22.50	-535.22	0.41	416
	Access farmland 500m No	148		0.71	0.40				1
	Yes	272							
	Year period			12.80	< 0.001				1
	Habitat quality		0.36 ± 0.15	5.65	0.02				1
6	Model			19.98	< 0.001	-22.44	-535.23	0.41	416
	Access farmland 500m No	148		0.10	0.76				1
	Yes	272							
	Year period			14.75	< 0.001				1
	Roe density[1]			5.61	0.02				1
	Low	203	-0.13 ± 0.05						
	High	217	-						

[1] Fertility roe deer Sequential Sidak test comparing Roe deer density classes (low / high) are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.01$).

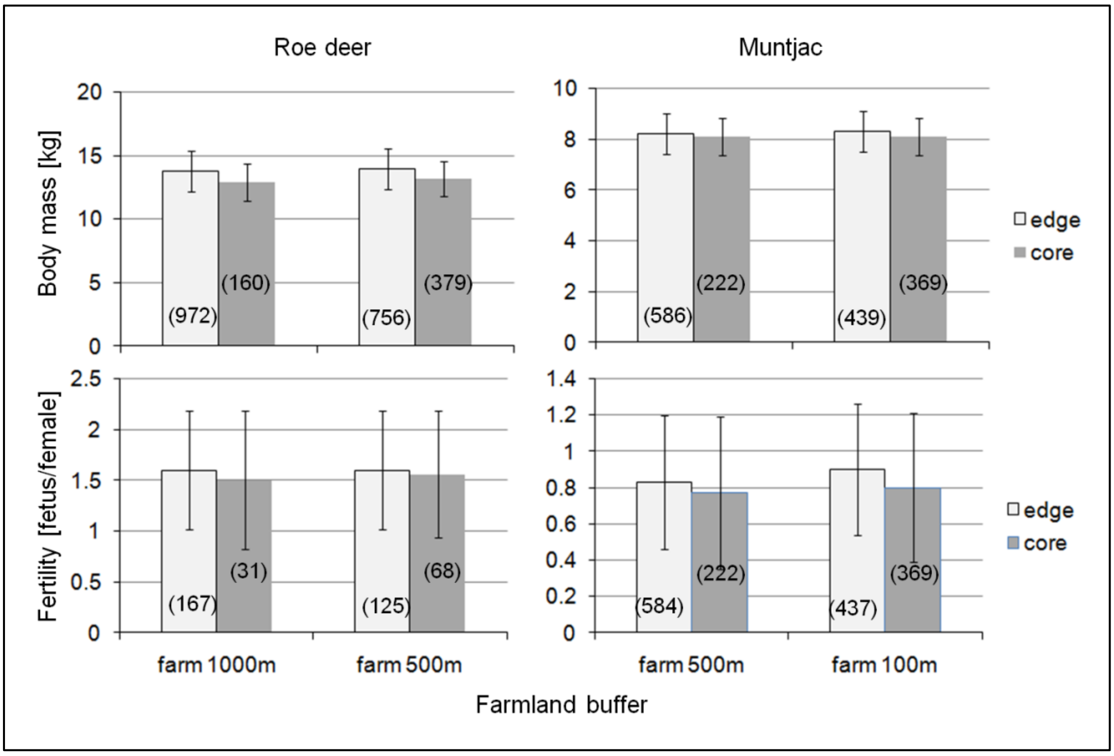

Fig. 3.1. Mean ± *SD* of (a) roe deer body mass [kg] (*n* = 1132) in 2001-09 and fertility [foetuses/female] (*n* = 198) in 2006-09 and (b) Reeve's muntjac body mass [kg] (*n* = 808) and fertility [foetuses/female] (*n* = 806) in 2006-09 in relation to edge and core areas in different farmland buffer in Thetford Forest.

Discussion

In support for our hypothesis I found that access to farmland affects deer performance significantly. Hereby, effects of landscape structure showed stronger effects on body mass than on fertility of adult female roe deer and female Reeve's muntjac.

Access to farmland positively influenced adult female roe deer and female Reeve's muntjac body mass. Body mass of adult female roe deer (1000m-buffer) and female Reeve's muntjac (100m-buffer) having access to farmland was 4% (0.5 kg) and 3% (0.2 kg) higher respectively than compared to animals culled in core woodland beyond the farmland-buffer. According to home-range sizes (Chapman et al., 1993) roe deer body mass was significantly affected by access to farmland within a 1000m-buffer whereas Reeves' muntjac was only affected within a 100m-buffer. The effect of the buffer zones suggests that roe deer is actively travelling to use farmland as feeding source whereas muntjac use farmland only when it is within their home-range. Hemami et al. (2005) found higher muntjac density in forest blocks with greater ratio to open habitat perimeter to forest area but no relationship for roe deer. In this study I found for both species a significant effect of forest beat on body mass (Table 3.5). However, I did not detect any differences between forest beats in analyses of female muntjac body mass but I did for roe deer. Body mass of roe deer was generally higher in small forest blocks (<15 km^2) surrounded by farmland than in larger blocks. Hewison et al. (2009) did analyse variation in body mass along a gradient with variable degree of woodland fragmentation in south-west France. Similarly to my study they found that roe deer body mass were generally heavier in the most open areas and lightest in the forest environment. In France, forest roe deer body mass was about 1 kg lower than body mass of deer in the woodland areas or in farmland (Hewison et al., 2009). In Thetford Forest female adult roe deer in core forest blocks with limited access to farmland was about mean = 0.8 kg ± 0.1 *SE* (6%) (maximum difference between island and core forest beat = 2.6 kg ± 0.4 *SE*, 17%) lighter than deer in small forest blocks surrounded by farmland. Although, Reeve's muntjac body mass was affected by farmland the influence of cull year on body mass was greater in this study. Animals culled in 2006 were generally 4% (0.3 kg) heavier than in 2009. This suggests weather effects next to food availability may play an important role for the introduced Reeve's muntjac. Muntjac seem not to be able to accumulate fat reserves to withstand longer periods of severe cold weather (Cooke et al., 1996).

Similarly to female muntjac body mass, muntjac fertility was significantly affected by cull year. Females in 2006 had a 0.1 higher fertility (14%) than females in 2009. This implies that here also annual effects (e.g. weather, increasing risk of predation through dogs) are more important than landscape structure.

In 2001-09 female roe deer fertility was significantly affected by forest beats but no significant difference between beats was found and only a weak negative effect of island beats was detected. However, I found a maximum mean difference in fertility of mean = 0.4 ± 0.2 *SE* (23%) between a small island forest block (here higher fertility) (low roe deer density, high muntjac density, low red deer density, surrounded by farmland) and a large island forest block (here lower fertility) (high roe deer density, moderate muntjac density, high fallow deer density, surrounded by farmland). Despite the influence of access to farmland on body mass of adult female roe deer and female

Reeve's muntjac no significant influence of access to farmland on fertility of both species could be found in 2006-09. In contrast the length of forest edge adjoining open habitats and roads has been reported to positively influence pregnancy rates in sika deer in Japan (Miyashita et al., 2008). In France McLoughlin et al. (2007) found a positive impact of high quality forage, cover and high edge density (meadow, thickets, roads) on life time reproductive success of roe deer.

In support of our hypothesis I found a positive effect of proportion of calcareous soil in each beat on adult female roe deer body mass (c 0.7 kg/proportion of calcareous soil) and fertility in 2001-09. Higher proportion of calcareous soil enhances food availability for the concentrate selector roe deer as plant species diversity on calcareous soils is higher than on acid soils (Eycott et al., 2006). In general higher habitat quality has been reported to enhance deer fertility. In Norway Nilsen et al. (2004) reported that roe deer females in high quality winter home-ranges more often produce litter sizes of 2 and 3 juveniles than individuals in low quality winter home-ranges.

Intra-specific high deer densities negatively impacted on roe deer body mass. Adult female roe deer were about 0.5 kg (3%) heavier when roe deer density (< 10 km^{-2}) was low compared to areas with high roe deer density (> 10 km^{-2}). Density dependent effects on adult roe deer body mass have been reported in several studies (Kjellander et al., 2006, Pettorelli et al., 2002). For example, Pettorelli et al. (2002) found an improvement in adult female roe deer body mass of 4.7 kg over a 13 year period following a reduction in deer numbers. Surprisingly, I found a positive impact of higher Reeve's muntjac densities (> 10 km^{-2}) on adult female roe deer body mass. Roe deer in areas with moderate or high deer numbers (< 10 km^{-2}) were circa 1 kg heavier than roe deer in areas with low muntjac density implying no negative effects of Reeve's muntjac on roe deer. High roe deer body mass combined with low roe deer density and high Reeve's muntjac densities occurred mainly in island beats where farmland is easily accessible for roe deer suggesting that high muntjac densities where supported by access to farmland and high habitat quality. Therefore, no interspecific effects of Reeve's muntjac on roe deer could be detected. Hemami et al. (2004) pointed out the potential for exploitation competition between roe deer and muntjac due to substantial habitat overlap especially in winter (aggregation on bramble). Competition between roe deer and muntjac has been also suggested in other studies (Hemami et al., 2005, Chapman et al., 1993). Also, roe has been reported to be susceptible to competition with other deer species (Dolman and Wäber, 2008, Focardi et al., 2006). In contrast no effects of habitat suitability, proportion of calcareous soil or deer density on female

Reeve’s muntjac and adult female roe deer fertility or Reeve’s muntjac body mass were detected in 2006-09.

Our results suggest that Reeve’s muntjac population demography is mainly influenced by annual changes and weakly by density dependent impacts but is not influenced by landscape structure. This would imply that even in less favourable habitats with high Reeve’s muntjac population densities dependent effects would difficult to detect or no such responses would occur and therefore population growth may be continue. Although forest beats significantly affected roe deer body mass the impacts on fertility were not significant. Landscape structure and beat configuration did have greater impacts on roe deer body mass than on roe deer fertility. Simard et al. (2008) found a significant decline in body mass but only a small decline in reproductive rates in an insular high density population of white-tailed deer *Odocoileus virginianus* in Anticosti, Quebec, Canada over 25 years. Similar results have been found in previous studies (reviewed in Gaillard et al., 2000, Clutton-Brock et al., 1983) suggesting that a decline in reproduction under nutritional stress at high population densities is not sufficient enough to regulate the population and deer impacts will continue (Sinclair and Parkes, 2008).These findings have important implications for deer biodiversity impacts and deer management as a growing and spreading deer population will extend herbivory impacts (Gill and Fuller, 2007). Carrying capacity as amount of available food resources that induce density-dependent demographic responses such that the population is regulated (Sinclair et al 2008) can differ within one landscape and may create areas with varying deer density. Deer managers have to incorporate this knowledge to induce higher cull targets in high productive areas avoiding building an artificial source-sink-system and to prevent further ecosystem changes through deer.

In this study only access to farmland has been specified at individual level whereas other ecological factors having possible impacts on deer body mass and fertility are defined at forest beat level or forest block level (DMU). Within one landscape research based on smaller spatial scales (home-range level) is needed to acquire detailed knowledge about ecological factors influencing deer demography and population growth to understand how neighbouring areas are affected by each other.

References

Aitken, R. J. (1974) Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility,* **39,** 225-233.

Aitken, R. J. (1975) Cementum layers and tooth wear as criteria for aging deer. *Journal of Zoology,* **175,** 15-28.

Allombert, S., Stockton, S. & Martin, J. L. (2005) A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology,* **19,** 1917-1929.

Alverson, W. S., Waller, D. M. & Solheim, S. L. (1988) Forest too deer - edge effects in Northern Wisconsin. *Conservation Biology,* **2,** 348-358.

Andersen, R. & Linnell, J. D. C. (2000) Irruptive potential in roe deer: Density-dependent effects on body mass and fertility. *Journal of Wildlife Management,* **64,** 698-706.

Chapman, N. G. (1991) Chinese muntjac *Muntiacus reevesi*. *The handbook of British mammals* (eds G. B. Corbet & S. Harris), pp. 526-532. Blackwell Scientific, 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.

Chapman, N. G., Furlong, M. & Harris, S. (1997) Reproductive strategies and the influence of date of birth on growth and sexual development of an aseasonally-breeding ungulate: Reeves' muntjac (*Muntiacus reevesi*). *Journal of Zoology,* **241,** 551-570.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1983) The costs of reproduction to red deer hinds. *Journal of Animal Ecology,* **52,** 367-383.

Cooke, A. S., Green, P. & Chapman, N. G. (1996) Mortality in a feral population of muntjac *Muntiacus reevesi* in England. *Acta Theriologica,* **41,** 277-286.

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

Cote, 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.

Dolman, P. M. & Sutherland, W. J. (1992) The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* **29,** 402-413.

Dolman, P. M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research,* **35,** 202-214.

Eycott, A. E. (2005) Plant population and community processes in a forested landscape. University of East Anglia, Norwich.

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.

Feber, R. E., Brereton, T. M., Warren, M. S. & Oates, M. (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. *Forestry,* **74,** 271-276.

Flowerdew, J. R. & Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry,* **74,** 277-287.

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.

Focardi, S., Pelliccioni, E. R., 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.

Fuller, R. J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. *Forestry,* **74,** 289-298.

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

Gill, R. M. A. & Fuller, R. J. (2007) The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis,* **149,** 119-127.

Gordon, I. J. (2003) Browsing and grazing ruminants: are they different beasts? *Forest Ecology and Management,* **181,** 13-21.

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, Norwich.

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. (1993) The reproductive performance of roe deer in relation to environmental and genetic factors. University of Southampton, Southampton.

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., 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.

Kie, J. G., Bowyer, R. T., Nicholson, M. C., Boroski, B. B. & Loft, E. R. (2002) Landscape heterogneity at different scales: Effects on spatial distribution of mule deer. *Ecology,* **83,** 530-544.

Kjellander, P., Gaillard, J. M. & Hewison, A. J. M. (2006) Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia,* **146,** 521-530.

Mayle, B. A. (1996) Progress in predictive management of deer populations in British woodlands. *Forest Ecology and Management,* **88,** 187-198.

McLoughlin, P. D., Gaillard, J.-M., 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.

McShea, W. J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology,* **81,** 228-238.

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.

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.

Pettorelli, N., Gaillard, J.-M., Duncan, P., Ouellet, J.-P. & van Laere, G. (2001) Spatial variations in habitat quality, local density and phenotypic quality in roe deer. *Oecologia,* **128,** 400-405.

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

Putman, R. J. & Moore, N. P. (1998) Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. *Mammal Review,* **28,** 141-163.

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

Said, S., Gaillard, J. M., Widmer, O., Debias, F., Bourgoin, G., Delorme, D. & Roux, C. (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos,* **118,** 1299-1306.

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

Sempéré, A. J., Mauget, R. & Mauget, C. (1998) Reproductive physiology of roe deer. *The European roe deer: the biology of success* (eds R. Andersen, P. Duncan & J. D. C. Linnell), pp. 161-188. Scandinavian University Press, Oslo.

Simard, M. A., Côte, S. D., Weladji, R. B. & Huot, L. J. (2008) Feedback effects of chronic browsing on life-history traits of a large herbivore. *Journal of Animal Ecology,* **77,** 678-686.

Sinclair, A. R. E. (1997) Carrying capacity and overabundance of deer. *The science of overabundance: deer ecology and population management* (eds W. J. McShea, H. B. Underwood & J. H. Rappole). Smithsonian Institution, Washington and London.

Sinclair, A. R. E. & Parkes, J. P. (2008) On being the right size: food-limited feedback on optimal body size. *Journal of Animal Ecology,* **77,** 635-637.

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

Appendix

Table A3.1. Model overview (general linear model with normal error) showing the effect of landscape structure and forest beat configuration on (a) female Reeve’s muntjac body mass [kg] (*n* = 808) in 2006-09 and (b) adult female roe deer body mass [kg] (*n* = 1125) in 2001-09.

Model no.	Model predictors	*n*	B ± SE	Wald χ^2	p	ΔAIC	Log-likelihood	Dev/df	df
(a) Reeve’s muntjac body mass									
1	Model			89.21	< 0.001	-	-901.84	0.56	784
	Access farmland 100m			12.30	< 0.001				
	Yes	439	0.21 ± 0.06						
	No	369	-						
	Beat			29.05	0.05				
	Year[1]			29.80	< 0.001				
	2006^{a}	160	0.33 ± 0.08						
	2007^{a}	206	0.29 ± 0.08						
	2008^{b}	218	0.03 ± 0.07						
	2009^{b}	224	-						
	Month			16.23	< 0.001				
2	Model			85.28	< 0.001	3.94	-903.81	0.57	784
	Access to farmland and (‘A’)-roads 100m			8.31	0.004				
	Yes	476	0.18 ± 0.06						
	No	332	-						
	Beat			26.99	0.08				
	Year[1]			29.89	< 0.001				
	2006^{a}	160	0.33 ± 0.08						
	2007^{a}	206	0.30 ± 0.08						
	2008^{b}	218	0.03 ± 0.07						
	2009^{b}	224	-						
	Month			15.77	< 0.001				
3	Model			83.01	< 0.001	6.21	-904.95	0.57	784

Table A3.1.

	Access farmland 500m			6.02	0.01				
	Yes	586	0.18 ± 0.08						
	No	222	-						
	Beat			28.58	0.05				
	Year[1]			27.60	< 0.001				
	2006[a]	160	0.33 ± 0.08						
	2007[a]	206	0.29 ± 0.08						
	2008[b]	218	0.04 ± 0.07						
	2009[b]	224	-						
	Month			18.18	< 0.001				
4	Model			79.88	< 0.001	9.33	-906.51	0.57	784
	Access to farmland and ('A')-roads 500m			2.88	0.09				
	Yes	649	0.14 ± 0.08						
	No	159	-						
	Beat			26.06	0.10				
	Year[1]			28.43	< 0.001				
	2006[a]	160	0.33 ± 0.08						
	2007[a]	206	0.30 ± 0.08						
	2008[b]	218	0.04 ± 0.07						
	2009[b]	224	-						
	Month			17.62	< 0.001				
5	Model			59.95	< 0.001	23.26	-916.47	0.58	787
	Access farmland 100m			11.79	0.001				
	Yes	439	0.21 ± 0.06						
	No	369	-						
	Beat			36.55	0.006				
	Month			23.54	< 0.001				
6	Model			55.93	< 0.001	27.29	-918.48	0.58	787

Table A3.1.

	Access farmland and (‘A’)-roads 100m			7.72	0.01				
	Yes	476	0.17 ± 0.06						
	No	332							
	Beat			34.08	0.01				
	Month			23.00	< 0.001				
7	Model			55.87	< 0.001	27.35	-918.52	0.58	787
	Access farmland 500m			7.65	0.006				
	Yes	586	0.21 ± 0.08						
	No	222	-						
	Beat			36.65	0.006				
	Month			25.83	< 0.001				
8	Model			51.94	< 0.001	31.28	-920.48	0.59	787
	Access farmland and (‘A’)-roads 500m			3.70	0.05				
	Yes	649	0.16 ± 0.08						
	No	159	-						
	Beat			33.11	0.02				
	Month			25.16	< 0.001				
9	Model			51.22	< 0.001	-7.15	-920.84	0.58	801
	Access farmland 100m No	369	-	8.47	0.004				1
	Yes	439	0.15 ± 0.05						
	Year			39.53	< 0.001				3
	Month			2.72	0.09				1
	Habitat quality		-0.07 ± 0.14	0.23	0.63				1
10	Model			50.99	< 0.001	-6.93	-920.95	0.58	801
	Access farm 100m No	369		7.84	0.01				1

Table A3.1.

	Yes	439	0.15 ± 0.05						
	Year			39.78	< 0.001				
	Month			2.81	0.09				3
	Habitat suitability		-0.03 ± 0.23	0.01	0.92				1
11	Model			57.55	< 0.001	11.49	-917.67	0.57	800
	Access farmland 100m	369		12.65	< 0.001				1
	No								
	Yes	439	0.15 ± 0.05						
	Year			37.16	< 0.001				
	Month			3.15	0.08				3
	Muntjac density[2]			6.59	0.04				2
	High[a]	413	-0.15 ± 0.09						
	Moderate[a]	270	-0.01 ± 0.08						
	Low[a]	125	-						
(b) Roe deer body mass									
1	Model			153.97	< 0.001	-	-2064.94	2.30	1109
	Access farmland 1000m			9.28	0.002				
	Yes	972	0.49 ± 0.16						
	No	160	-						
	Beat			124.02	< 0.001				
2	Model			168.10	< 0.001	1.87	-2057.88	2.28	1101
	Access farmland 1000m			10.81	0.001				
	Yes	972	0.53 ± 0.16						
	No	160	-						
	Beat			117.50	< 0.001				
	Year			14.22	0.08				
3				161.09	< 0.001	3.91	-2066.98	2.28	1112

Table A3.1.

	Access farmland 500m			15.83	< 0.001				
	Yes	756	0.46 ± 0.12						
	No	379	-						
	Beat			107.15	< 0.001				
4	Model			174.31	< 0.001	6.87	-2060.38	2.27	1104
	Access farmland 500m			16.42	< 0.001				
	Yes	756	0.47 ± 0.12						
	No	379							
	Beat								
	Year			13.29	0.10				
5	Model			49.81	< 0.001	66.16	-2117.02	2.47	1128
	Access farmland 1000m No	160		22.19	< 0.001				1
	Yes	972	0.69 ± 0.15						
	Muntjac density[3]			13.62	0.001				2
	High[a]	568	0.64 ± 0.17						
	Moderate[a]	461	0.52 ± 0.17						
	Low[b]	103	-						
6	Model			38.55	< 0.001	75.42	-2122.65	2.50	1129
	Access farmland 1000m No	160		37,43	< 0.001				1
	Yes	972	0.82 ± 0.14						
	Habitat suitability			2.27	0.13				1
7	Model			38.54	< 0.001	75.44	-2122.66	2.50	1129
	Access farmland 1000m No	160		36.46	< 0.001				1
	Yes	972	0.81 ± 0.14						
	Roe density			2.26	0.13				1

Table A3.1.

	Low	373	0.15 ± 0.10						
	High	759	-						
8	Model			36.36	< 0.001	77.61	-2123.75	2.50	1129
	Access farmland 1000m No	160		35.73	< 0.001				1
	Yes	972	0.81 ± 0.14						
	Habitat quality			0.08	0.78				1

[1] Body mass Reeve's muntjac Sequential Sidak test comparing cull year 2006-09 are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.05$).

[2] Body mass Reeve's muntjac Sequential Sidak test comparing Reeve's muntjac density classes (low / medium / high) are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.05$).

[3] Body mass roe deer Sequential Sidak test comparing Reeve's muntjac density classes (low / medium / high) are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.05$).

Table A3.2. Model overview (General Linear Models with poisson error) showing the effect of landscape structure and forest beat configuration on (a) female Reeve’s muntjac fertility (foetuses per female) (*n* = 806) in 2006-09, (b) adult female roe deer fertility (foetuses per female) (*n* = 198) in 2006-09 and (c) adult female roe deer fertility (foetuses per female) (*n* = 414) in 2001-09.

Model	Model predictors	*n*	B ± SE	Wald χ^2	*p*	ΔAIC	Log-likelihood	Dev/df	df
(a) Reeve’s muntjac fertility 2006-09									
1	Model				0.90	-	-784.27	0.32	23
	Access farmland and (‘A’)-roads 100m No	332		0.30	0.58				1
	Yes	474							
	Month			5.22	0.02				1
	Beat			5.17	0.99				18
	Year			4.26	0.24				3
2	Model				0.90	0.09	-784.31	0.32	23
	Access farmland 100m No	369		0.22	0.64				1
	Yes	437							
	Month			5.23	0.02				1
	Beat			5.08	0.99				18
	Year			4.23	0.24				3
3	Model				0.91	0.30	-784.42	0.32	23
	Access farmland 500m No	222		0.001	0.98				1
	Yes	584							
	Month			5.12	0.02				1
	Beat			5.31	0.99				18
	Year			4.11	0.25				3

Table A3.2.

4	Model					0.30	-784.42	0.32	23
	Access farmland and ('A')-roads 500m No	159		0.01	0.93				1
	Yes	647							
	Month			5.13	0.02				1
	Beat			5.65	0.99				18
	Year			4.12	0.25				3
5	Model				0.96	0.43	-786.47	0.33	20
	Access farmland and ('A')-roads 500m No	159		0	1.0				1
	Yes	647	-0.001 ± 0.12						
	Month			4.16	0.04				1
	Beat			5.01	0.99				18
6	Model				0.96	1.61	-786.47	0.33	20
	Access farmland 500m No	222		0	1.0				1
	Yes	584	0.11 ± 0.16						
	Month			4.16	0.04				1
	Beat			4.61	0.99				18
7	Model				0.96	1.71	-786.42	0.33	20
	Access farmland 100m No	369		0.10	0.76				1
	Yes	437	0.03 ± 0.09						
	Month			4.23	0.04				1
	Beat			4.49	0.99				18

Table A3.2.

8	Model				0.96	1.77	-786.39	0.33	20
	Access farmland and (‘A’)-roads 100m No	332		0.15	0.69				1
	Yes	474	0.03 ± 0.05						
	Month			4.23	0.04				1
	Beat			4.57	0.99				18
9	Model				0.11	-29.45	-786.55	0.32	6
	Access farmland 100m No			1.01	0.31				1
	Yes								
	Month			6.04	0.01				1
	Habitat quality			0.66	0.42				1
	Year			3.90	0.27				3
10	Model				0.14	-28.67	-786.86	0.32	6
	Access farmland 100m No			1.10	0.30				1
	Yes								
	Month			5.70	0.02				1
	Habitat suitability			0.03	0.87				1
	Year			3.70	0.30				3
11	Model				0.13	-28.38	-786.08	0.32	6
	Access farmland 100m No			0.38	0.54				1
	Yes								
	Month			5.11	0.02				1
	Muntjac density Low			1.57	0.46				1
	High	411	0.04 ± 0.13						3
	Moderate	270	-0.08 ± 0.13						
	Year	125	-						

Table A3.2.

(b) roe deer fertility 2006-09									
1	Model			18.60	0.48	-	-254.28	0.32	178
	Access farmland 500m			0.52	0.47				
	Yes	125	-0.06 ± 0.09						
	No	73	-						
	Beat			17.99	0.46				
2	Model			18.07	0.52	0.15	-254.36	0.32	178
	Access farmland 1000m			0.03	0.87				
	Yes	167	-0.02 ± 0.11						
	No	31	-						
	Beat			17.27	0.51				
3	Model			18.51	0.68	5.93	-254.49	0.32	175
	Access farmland 500m			0.52	0.47				1
	Yes	125	-0.06 ± 0.09						
	No	73	-						
	Beat			17.25	0.51				
	Year			0.20	0.98				3
	2006	35							
	2007	62							
	2008	59							
	2009	42							
4	Model			17.97	0.71	6.09	-254.33	0.32	175
	Access farmland 1000m			0.03	0.86				
	Yes	167	-0.02 ± 0.11						
	No	31	-						
	Beat			16.55	0.55				
	Year			0.19	0.98				
	2006	35							
	2007	62							
	2008	59							

Table A3.2.

	2009	42							
5	Model			2.44	0.30	-28.86	-256.85	0.32	195
	Access farmland 500m No	73		0.15	0.70				1
	Yes	125							
	Habitat quality			2.29	0.13				1
6	Model			1.36	0.51	-28.52	-257.02	0.32	195
	Access farmland 500m No	73		0.38	0.54				1
	Yes	125	0.04 ± 0.08						
	Roe density			1.22	0.27				1
7	Model			0.42	0.81	-28.22	-257.17	0.32	195
	Access farmland 500m No	73		0.08	0.77				1
	Yes	125							
	Habitat suitability			0.29	0.59				1
8	Model			0.76	0.86	-26.33	-257.11	0.32	194
	Access farmland 500m No	73		0.38	0.54				1
	Yes	125							
	Muntjac density			0.63	0.73				2
(c) roe deer fertility 2001-09									
1	Model			49.63	< 0.001	-	-529.49	0.40	399
	Access farmland 1000m No	69		1.77	0.18				
	Yes	351	-0.12 ± 0.09						
	Beat			32.62	0.02				
	Year period			18.10	< 0.001				
2	Model			48.12	< 0.001	0.53	-529.76	0.40	399
	Access farmland 500m No	148		0.40	0.53				
	Yes	272	-0.04 ± 0.07						
	Beat			32.62	0.02				
	Year period			17.65	< 0.001				

Table A3.2.

3	Model			67.47	< 0.001	7.59	-526.29	0.39	392
	Access farmland 1000m No	69		0.51	0.48				
	Yes	351	-0.06 ± 0.09						
	Beat			32.22	0.02				
	Year[1]			33.14	< 0.001				
	2001^{a}	31	-0.54 ± 0.14						
	2002^{b}	42	-0.11 ± 0.12						
	2003^{a,b}	63	-0.29 ± 0.11						
	2004^{a,b}	47	-0.28 ± 0.12						
	2005^{b}	39	-0.04 ± 0.12						
	2006^{b}	35	-0.02 ± 0.12						
	2007^{b}	62	-0.01 ± 0.11						
	2008^{b}	59	0.01 ± 0.11						
	2009^{b}	42	-						
4	Model			67.08	< 0.001	7.72	-526.35	0.39	392
	Access farmland 500m No	148		0.17	0.68				
	Yes	272	-0.03 ± 0.07						
	Beat			32.60	0.02				
	Year[1]			33.58	< 0.001				
	2001^{a}	31	-0.55 ± 0.14						
	2002^{b}	42	-0.10 ± 0.12						
	2003^{a,b}	63	-0.29 ± 0.11						
	2004^{a,b}	47	-0.28 ± 0.12						
	2005^{b}	39	-0.04 ± 0.12						
	2006^{b}	35	-0.02 ± 0.12						
	2007^{b}	62	-0.01 ± 0.11						
	2008^{b}	59	0.01 ± 0.11						
	2009^{b}	42	-						

Table A3.2

5	Model			20.05	< 0.001	-22.50	-535.22	0.41	416
	Access farmland 500m No	148		0.71	0.40				1
	Yes	272							
	Year period			12.80	< 0.001				1
	Habitat quality		0.36 ± 0.15	5.65	0.02				1
6	Model			19.98	< 0.001	-22.44	-535.23	0.41	416
	Access farmland 500m No	148		0.10	0.76				1
	Yes	272							
	Year period			14.75	< 0.001				1
	Roe density[2]			5.61	0.02				1
	Low	203	-0.13 ± 0.05						
	High	217	-						
7	Model			19.33	0.001	-20.21	-535.35	0.41	415
	Access farmland 500m	148		0.001	0.97				1
	Yes	272							
	Year period			14.27	< 0.001				1
	Muntjac density			5.04	0.08				2
8	Model			16.35	0.001	-21.02	-535.94	0.41	416
	Access farmland 500m	148		1.09	0.30				1
	Yes	272							
	Year period			15.19	< 0.001				1
	Habitat suitability			2.12	0.15				1

[1] Fertility roe deer Sequential Sidak test comparing cull year 2001-09 are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.01$).

[2] Fertility roe deer Sequential Sidak test comparing Roe deer density classes (low / high) are shown with superscripts, classes that do not share a superscript differ significantly ($p < 0.01$).

Chapter Four

Deer population assessment using distance sampling thermal imaging in a lowland pine forest

Abstract

Knowledge of deer density is important for evidence based deer control. Reliable measures of deer density are also important in order to understand non-linear impacts and biodiversity responses. However, estimating deer densities is still problematic especially in forested landscapes. Here I tested in a lowland pine forest in East England, UK across three winters the performance of distance sampling thermal imaging to calculate deer densities. I considered results from three different analysis designs: (1) detection function stratified by years but pooled across forest blocks, (2) detection function stratified by forest block but pooled across years and (3) detection function stratified by habitat class but pooled across forest blocks and years in seven out of twelve forest blocks. I made a number of refinements to previous published thermal imaging distance sampling methodology: transects routes were designed to provide visibility along, rather than across, tree planting rows, and perpendicular distance to detected deer was measured by laser range-finder mounted with a night vision monocular rather than by triangulation. I surveyed a mean of 529.4 km ± 40.3 *SD* of transect each year and observed a total of *n* = 2210 Reeve's muntjac *Muntiacus reevesi* groups and *n* = 921 roe deer *Capreolus capreolus* groups. Observed group size did not differ significantly at greater perpendicular distances for both deer species. The effective strip width (ESW) for roe deer was about 25-30% wider than for Reeve's muntjac. For both deer species ESW did not significantly differ between years but did differ amongst forest blocks and among habitats being about 45% wider in open habitat than dense habitat. Estimated deer densities did not differ significantly between analysis designs for either species. Density estimates based on observed mean group size were lower, with narrower Confidence Intervals, than default estimates that incorporate a size-bias adjustment for roe deer and Reeve's muntjac. It is concluded that the method is robust to monitor deer densities at a landscape scale.

Introduction

Deer impacts on vegetation (Gill and Beardall, 2001, Joys et al., 2004), birds (Gill and Fuller, 2007, McShea and Rappole, 2000, Holt et al., 2010), small mammals (Flowerdew and Ellwood, 2001, McShea, 2000) and insects (Cote et al., 2004, Feber et al., 2001, Pollard and Cooke, 1994) have been reported in both Europe and North America. Hereby, deer effects are assessed by comparing fenced areas with no browsing and unfenced areas with unknown deer density. Knowledge of deer densities at landscape-scale is needed to assess the management of the steadily increasing deer population (Ward, 2005, Milner et al., 2006) and to evaluate non-linear biodiversity responses to deer impacts. Setting objective and defendable cull targets in deer management requires reliable estimates to assess population trends (Marques et al., 2001). Estimating deer densities is still problematic especially in forested landscapes.

Conventional deer census techniques have limitations. Methods based on direct observations such as simple counts or spotlight counts are compromised by dense vegetation. Mark-resighting or drive counts are too labour-intensive to be applied at larger scales (e.g. Focardi et al. (2002b)). Accuracy of faecal pellet group methods is reduced by uncertain estimates of parameters such as defecation and decay rate (Campbell et al., 2004, Hemami and Dolman, 2005) and is further compromised by rapid decay rates in warm winters of lowland Britain (Hemami and Dolman (2005), K. Wäber pers. obs.).

In recent years the use of distance sampling method combined with thermal image equipment has been recommended as alternative cost effective method (Gill et al., 1997, Hemami et al., 2007, Smart et al., 2004, Focardi et al., 2001). No study to our knowledge has tested the performance of distance sampling thermal imaging at a landscape scale investigating the effect of different analysis designs on the detection function and the resulting estimates of animal densities within one landscape.

There are a number of potential problems with the distance sampling methodology. If animals show avoidance behaviour, moving away from the observer prior to detection, density may be underestimated. For example, roe deer were found to avoid observer during distance sampling thermal imaging surveys in nine conifer forests (*n* = 107 observed roe groups, total transect length = 131 km) in north east England by Ward et al. (2004). In this study fewer roe deer groups were observed within the first 20 m of the transect line. To avoid violating the assumptions of distance sampling that assumes the greatest probability of detection is close to the transect line two different approaches have been tested by Ward et al. (2004) and then compared with the right truncated data only. The data left truncated at 20 m increased the error surrounding the density estimate about 22% and pooling the observations from the first 25 m into one bin whilst treating the other data unconstrained increased the error of the density estimate about 3% compared to the right truncated data only (Ward et al., 2004). The study did not account for possible effects of habitat or forests in their analyses.

While testing thermal imaging distance sampling in seven different forest areas ranging from 8 km^2 to 11 km^2 across the UK Gill et al. (1997) pointed out that detection probability and distances are related to vegetation density and therefore differ between habitat types. In East England, UK, Hemami et al. (2007) showed that in a conifer dominated plantation (13 km^2) open habitats (n = 30 groups) resulted in higher detection probability and wider effective strip width (ESW) than dense (n = 30) and mature (n = 229 groups) habitats when using pooled observations of Reeve’s muntjac and roe deer from thermal imaging distance sampling. Thus, Hemami et al. (2007) suggested a possible increase in accuracy of density estimates may be achieved through stratification by habitat. Thermal imaging distance sampling (total transect line = 50 km) carried out by Focardi et al. (2002a) classified four habitat types in a Mediterranean forest (60 km^2) near Rome, Italy, to reduce variance of density estimates. The results showed that ESW of animals differed with habitat type for fallow deer *Dama dama*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa* but density results and confidence intervals of stratified and unstratified data were very similar for fallow deer. Only a slightly bias for the density estimate in roe deer and wild boar were found. For roe deer habitat-stratified density estimates were 10% higher and for wild boar 18% lower than density estimates without habitat stratification. However, a large sample size is needed to calculate a robust detection function for each habitat and improve overall density estimates.

To test the robustness of distance sampling thermal imaging and assess possible influential sources on the detection function such as differences of forest block composition, varying detectability of deer in different forest growth stages and annually varying weather conditions which may influence the vegetation cover between years, I conducted repeated surveys in a lowland pine forest in Eastern England, UK in 2008-10. In seven forest blocks (total 125 km^2) of Thetford Forest I investigated the effects of different analysis designs on the detection function and density estimates. Forest blocks differed in habitat composition, soil composition, and relative abundance of deer species. Our main hypotheses are (1) distance sampling thermal imaging can be used to estimate deer numbers at landscape-scale, therefore calculated density estimates will be similar in all three analyses designs and (2) using specific habitat densities to calculate area weighted density estimates would improve the precision of the density estimate due to variation in ESW among habitats.

Methods

Study area

The study was conducted in Thetford Forest (195 km^2) (0°40'E, 52°27'N), the largest lowland conifer forest in England, UK (Eycott et al., 2006). Corsican pine (*Pinus nigra* var. *maritima*) (59%) and Scots pine (*Pinus sylvestris*) (15%) are the dominant tree species; other conifers comprise 5% and deciduous species 10% of the area. Thetford Forest is currently managed by rotational clearfelling and replanting, creating a mosaic of even aged growth stages (sub-compartments) subdivided by a ride network. The forest is surrounded by farmland, grass-heath and scattered coniferous and mixed woodlands.

Thetford Forest is divided into twelve deer management units (DMU's), separated by roads. Distance sampling thermal imaging surveys were carried out in seven (mean = 17.5 km^2 ± 9.9 SD, range 7.1 km^2 to 34.7 km^2, total area = 125 km^2) of twelve DMU's in 2008-2010. Four DMU's were located in the core of Thetford Forest, with farmland abutting only a small proportion of the forest perimeter whereas the three island blocks were completely surrounded by farmland (Fig. 4.1).

Within the coniferous forest I distinguished five growth stages: restock (1-5 years); pre-thicket (6-10 years); thicket (11-20 years); pole stage (21-45 years) and mature (> 45 years) (Hemami et al., 2005, Hemami et al., 2004). Mature mixed broad leaved stands (> 45 years) were considered as an additional habitat type. Detailed data (crops species, planting year, area and soil type) of each management sub-compartment (part of a single even aged planted coupe separated by trackways, mean area = 3.1 ± 3.1 ha SD) were retrieved from a GIS database managed by the Forestry Commission (FC). Forest blocks differed in the proportion contributed by different growth stages (Table 4.1).

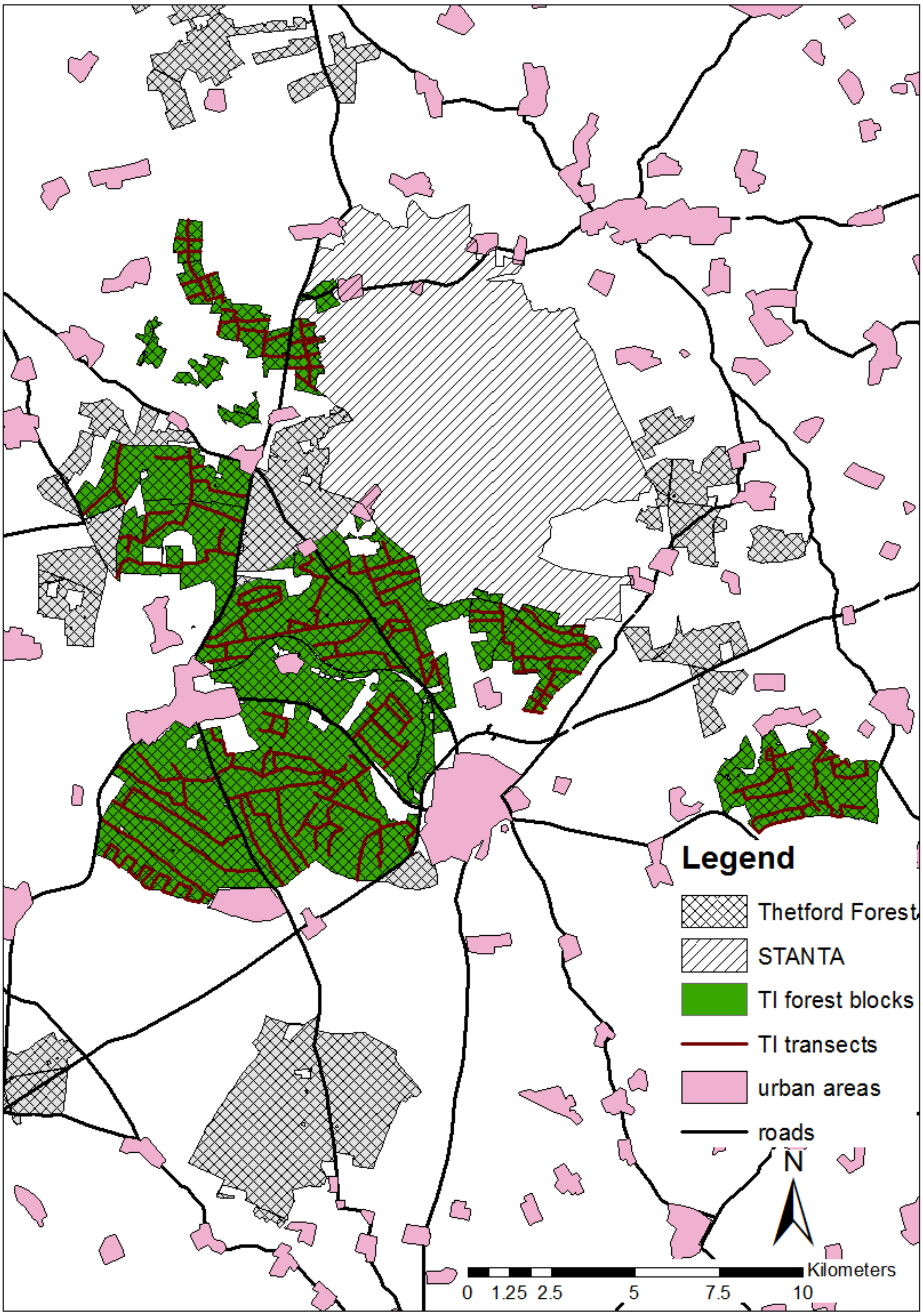

Fig. 4.1. Thetford Forest showing the seven forest blocks surveyed by distance sampling thermal imaging (TI forest blocks) and the driven transect routes (TI transects) in 2008-2010.

Table 4.1. Blocks of Thetford Forest sampled by thermal imaging distance transects, showing block area [km^2], transect length (mean ± SD [km]), total transect length surveyed [km], sampling effort (transect length [km] / block area [km^2]) in each of three survey years and growth stage composition [%].

Block	Block area [km^2]	Transect length [km] $\bar{x}$ ± SD			Total length surveyed [km]			Transect length [km] / block area [km^2]			Composition of sampled areas [%] (pooled $\bar{x}$ ± SD 2008-10)						
											Coniferous stands						Deciduous
		2008	2009	2010	2008	2009	2010	2008	2009	2010	Felled/ unplanted	Restock	Pre-thicket	Thicket	Pole	Mature	Mature
Cro	7.1	3.2 ± 1.3	3.2 ± 1.3	3.0 ± 1.3	68.2	68.2	85.2	9.6	9.6	12.0	1.2 ± 2.2	5.1 ± 0.1	10.2 ± 0.1	25.0 ± 8.8	36.5 ± 7.6	13.2 ± 0.2	8.7 ± 0.3
Did	9.2	4.4 ± 1.8	4.4 ± 1.8	4.4 ± 1.8	78.3	63.1	41.6	8.5	6.9	4.5	1.0 ± 1.7	6.0 ± 1.3	6.6 ± 1.1	7.3 ± 1.9	46.8 ± 3.1	23.1 ± 1.0	9.1 ± 1.0
Elv	16.5	4.1 ± 1.0	4.1 ± 1.0	4.1 ± 1.0	45.2	45.2	45.2	2.7	2.7	2.7	5.1 ± 1.4	4.4 ± 2.1	9.8 ± 1.4	24.1 ± 2.9	39.2 ± 0.7	14.4 ± 0.3	3.0 ± 0.03
Har	9.8	3.9 ± 1.1	3.9 ± 1.1	3.9 ± 1.1	77.9	68.2	71.9	7.9	7.0	7.3	3.6 ± 6.2	7.9 ± 2.2	1.4 ± 1.3	19.0 ± 0.5	24.3 ± 2.9	25.4 ± 2.9	18.5 ± 1.3
HiLo	34.7	4.1 ± 1.2	4.4 ± 1.1	4.6 ± 1.4	66.1	78.0	69.2	1.9	2.2	2.0	2.8 ± 3.1	6.5 ± 2.3	5.5 ± 1.5	18.7 ± 3.3	38.6 ± 1.9	22.2 ± 0.6	5.8 ± 1.9
Lyn	21.1	4.2 ± 1.3	4.2 ± 1.3	4.2 ± 1.3	138.6	139.7	108.6	6.6	6.6	5.2	0.5 ± 0.8	6.4 ± 1.1	5.7 ± 0.8	9.8 ± 0.9	52.3 ± 5.2	19.2 ± 3.5	6.2 ± 1.1
Mun	24.1	4.0 ± 0.8	4.0 ± 0.8	4.0 ± 0.8	96.6	53.8	58.1	4.0	2.2	2.4	4.3 ± 5.2	4.8 ± 3.1	6.5 ± 3.5	15.2 ± 1.0	37.4 ± 4.0	18.4 ± 1.5	13.4 ± 1.0
Total	122.5	39.0 ± 16.7	40.5 ± 17.2	40.4 ± 18.5	570.9	516.2	479.8	4.7	4.2	3.9	2.6 ± 3.4	5.9 ± 2.0	6.5 ± 3.1	17.0 ± 7.1	39.3 ± 9.0	19.4 ± 4.5	9.2 ± 5.0

Study species

Four deer species are present in Thetford Forest: roe deer, Reeve's muntjac *Munticacus reevesi*, red deer *Cervus elaphus* and fallow deer. In this study I focus on the two smaller deer species Reeve's muntjac and roe deer as they are abundant throughout the study area.

Distance transects

Line transect distance sampling thermal imaging was carried out at night (20.00 hrs-04.00 hrs) between January and March at the end of the cull season in 2008-10. During this time period most of the ground vegetation layer which may hide the deer away from detection has died (e.g. bracken) given a better detectability of deer. Best results were obtained in cold weather as this supports the brightness of the images shown by the thermal imager. Mean temperature differed between surveys in all three years (2008: mean = 3.8 °C ± 2.4 SD, range: -1.0 °C and 9.9 °C; 2009: mean = 2.4 °C ± 2.1 SD, range: -0.5 °C and 7.1 °C; 2010: mean = -1.4°C ± 2.7 SD, range: -6.9°C and 5.9°C).

Transect lines followed the widespread network of tracks and management rides within Thetford Forest (Fig. 4.1). Existing tracks were split in three different categories: fire routes (track ways surfaced with ballast acting as fire breaks), forest tracks (mainly grassy rides) and forest paths (driveable pathways). In each block thermal imaging transect routes were planned covering all compartments as far as possible along the orientation of the plant rows. The length of the surveyed transects routes varied among blocks (Table 4.1). Transect routes in five forest blocks were repeated at least twice in each winter and in two other blocks only surveyed once in each winter. The mean length of driven transects across all surveyed blocks was 529.4 km ± 40.3 *SD* per year.

Deer numbers feeding on adjacent fields were also recorded scanning from vantage points. Field counts were treated as 100% visibility. Deer numbers of field counts were estimated separately.

The equipment used was a Recon long range thermal imager (manufactured by FLIR Systems) designed for light weight applications such as target acquisition and surveillance (for further details see: www.gs.flir.com/products/land/reconi.cfm). As surveys were carried out during the night distance between observer and deer was measured using a Leica Laser Range Finder 'LEICA LRF 800' and a night vision 'Maxi-Kite Mk 4' (light weight for use as portable long range surveillance and weapon sight, manufactured by THALES) fitted with a infrared illuminator. Hereby, the laser beam was sighted in with the reticle of the night vision equipment. Angle from observer to deer was measured using an angle board (accuracy 5°).

Distance surveys were conducted using thermal imaging equipment, from the front passenger seat of an off road car with the observer eye level circa 1.5 m above the ground and a maximum speed of 15mp hr^{-1}. The position of the observer on the passenger seat gave the advantage to look into forest compartment under dense canopy cover compared to an observer on the top of a car. Only one side of the transect line was sampled (sampling fraction = 0.5). During the survey only the side lights of the car were used not to frighten deer away. One of the assumptions in distance sampling is that individuals should not move prior to detection (Buckland et al., 2001) therefore behaviour of deer when first seen was recorded. If deer moved away from its original position observation was disregarded (n = 20; < 1%) when the original position was unknown or not evident from heat radiation on the ground where the animal had been lying (Gill et al., 1997). Care was taken not to double count animals which moved away after being approached by the vehicle. All animals on the line ($g(0) = 1$) were detected. The survey was carried out by a single observer using an exacting field protocol.

For each individual or group of deer detected the following information were recorded: date, time, block, transect number, species, number of individuals in group, distance [m] and angle from observer, habitat type and behaviour (walking / running away from observer). Sighting distance and angle were transformed to perpendicular distance y_p for analysis using following equation:

$$y = \sin(\alpha_d)\, x_d$$

where α_d is the angle between direction to observed deer and, and line perpendicular to the transect route, and x_d is the distance between deer and observer.

Deer were always classified into species during thermal imaging distance surveys.

Analysis

Distance from observer to the edge of the planted forest stand differed between types of track-ways in all forest blocks. Generally, on fire routes and forest tracks distance from observer to habitat was between 2 m and 10 m whereas the distance on pathways was < 1 m. Therefore I subtracted the individual distance measured separately for each undivided track between observer and edge of the planted forest stand from the perpendicular distance for observed individuals on fire routes and forest tracks. Appearance of tracks may also influence the detection distance of animals as deer might avoid or prefer edges near tracks. For Reeve's muntjac and roe deer I tested whether perpendicular distance of detected animals differed between class of track ways whilst controlling for habitat and forest block using Generalized Linear Models with negative binomial distribution and log link function. For Reeve's muntjac perpendicular distance (n = 1828 groups) did not differ significantly among track-way types ($\chi^2_{(2)}$ = 4.61, p = 0.10) when controlling for habitat ($\chi^2_{(6)}$ = 149.87, p < 0.001) but was significantly affected by forest block ($\chi^2_{(6)}$ = 13.11, p = 0.04). Excluding the one forest block (n = 290 groups) with the lowest mean perpendicular distance (mean = 30.7 ± 1.75 m *SE*), across the remaining forest blocks detection distances for muntjac did not differ between track-way classes ($\chi^2_{(2)}$ = 2.06, p = 0.36) or forest blocks ($\chi^2_{(5)}$ = 4.75, p = 0.45) whilst controlling for habitats ($\chi^2_{(5)}$ = 128.08, p < 0.001). The forest block with the lowest detection distance was therefore analysed separately for further muntjac distance sampling calculation. For roe deer (n = 795 groups), mean perpendicular distance did not differ among track-way classes ($\chi^2_{(2)}$ = 0.67, p = 0.71) whilst controlling for habitat ($\chi^2_{(6)}$ = 99.95, p < 0.001) and forest block ($\chi^2_{(6)}$ = 12.0, p = 0.06). I therefore conclude that neither muntjac nor roe deer differ in their response to different classes of track-way: fire route, forest track or path.

Data collected from the line transect surveys were analysed using the software program DISTANCE 6.0 release 2 (Thomas et al., 2010, 2010). Avoiding bias in the detection function prior to analysis, exploratory examination of the distance data were carried out following (Buckland et al., 2001) searching for evidence of evasive movement prior detection, rounding and heaping of data, and to truncate outlier observations by investigating the distribution of perpendicular distances (Fig. 4.4-4.5 and A4.1-A4.2) and q-q-plots. The distribution of perpendicular distances showed possible movement prior to detection for roe deer. Although, animals may have moved away from the transect line they were still detected. Extreme observations can be difficult to model therefore deletion of these extreme observations is useful (Buckland et al., 2001).The truncation distance was chosen after searching the histogram for outliers (Fig. 4.4-4.5 and A4.1-A4.2) and 5% of the largest observation were discarded if this improved the fit of the detection function following (Buckland et al., 2001).

Distance sampling data were analysed using three different analytical methods for the detection function: (1) analysis design "Year", (2) analysis design "Block" and (3) analysis design "Habitat" (Table 4.3). Stratifying distance sampling data by habitat requires a sample size of more than 90 group observations in each habitat type in order to calculate a robust detection function (Buckland et al., 2001). Therefore I classified and grouped habitat classes as follows: (1) open habitat (open, felled unplanted areas and restocks), (2) dense (pre-thicket and thicket) and (3) mature habitats (pole, mature pine and mature broadleaf) using the ESW of each habitat as classification criteria. I did not fit separate detection functions for deer activities but pooled all deer activity observations.

Mean density stratified by forest blocks using the detection function in method (1) and (2) was estimated by the DISTANCE program calculated as

$$D = \frac{n \int(0)\, \bar{s}}{2L} \times 0.5$$

where n is the number of objects detected, $\int(0)$ is the value of the probability density function of perpendicular distances evaluated at zero distance, $\bar{s}$ the size of cluster of objects, L is the total line length in a line transect survey and the sampling fraction is specified by *0.5* (Buckland et al., 2001).

However, DISTANCE cannot handle stratification with more than one layer (Buckland et al., 2004). Therefore, to obtain mean density for each forest block the habitat area weighted mean D_{aw} (1) and variance (2) were calculated from habitat-specific density estimates following the equations:

$$D_{aw} = \sum_{i=1}^{n} c_i\, y_i$$

where c_i is the proportion of habitat i in a particular forest block and y_i is the density calculated from DISTANCE in habitat i of the same forest block;

$$var(D_{aw}) \approx D_{aw}^2 \sum \left(\frac{var\,(y_i)}{y_i^2} \right)$$

where $var\,(y_i)$ is the variance of density y_i (Buckland et al., 2001) in a particular forest block. The standard error SE of the area weighted mean D_{aw} is defined by

$$SE(D_{aw}) = \sqrt{var(D_{aw})}$$

And the 95% confidence intervals (CI) were calculated using

$$CI = D_{aw} \pm 1.96 * SE(D_{aw}).$$

For each data set the best model was chosen using Akaike's information criterion (AIC) and the goodness-of-fit tests (Kolmogorov-Smirnov test and Cramer-von Misés test) generated by the DISTANCE program. Model selection was carried out after truncation distances have been set as the AIC cannot be used to choose between models with different truncation distances (Buckland et al., 2001). The models tested were uniform function (alone; or with cosine adjustment), half-normal function (alone; or with hermite polynomial / cosine adjustment), and the hazard-rate function (alone; or with simple polynomial adjustment) following (Thomas et al., 2010 2010).

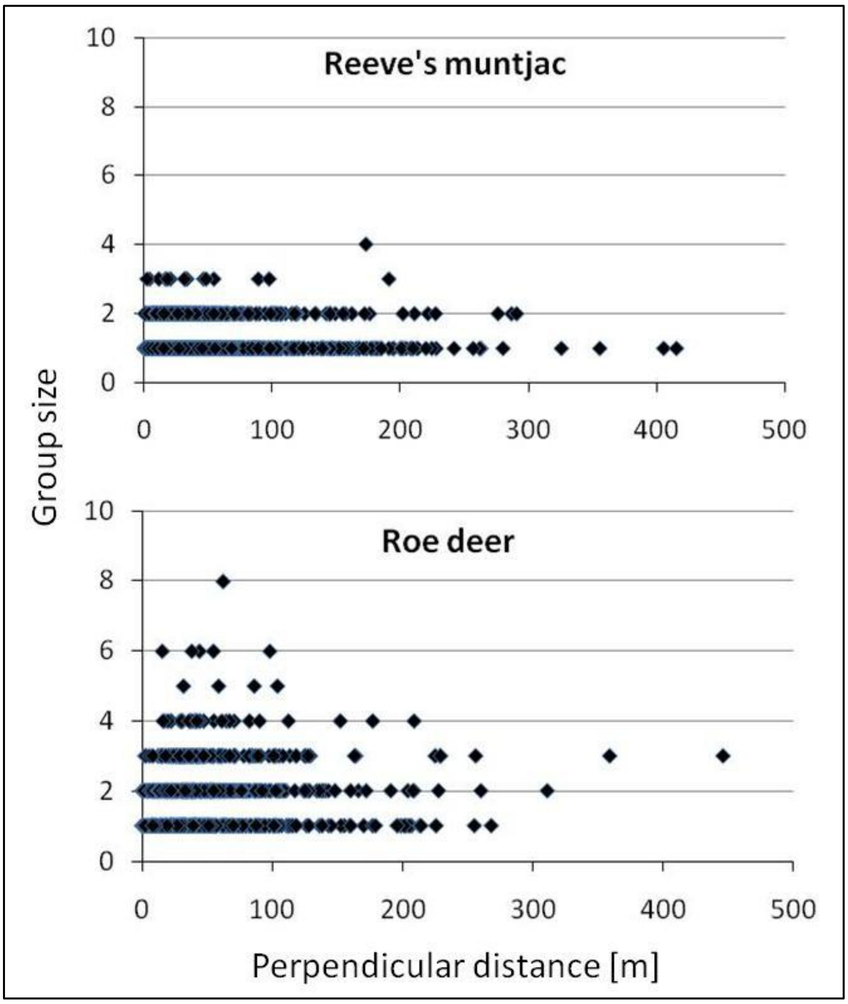

Fig. 4.2. Relationship between observed group size of Reeve's muntjac (*n* = 2209) and roe deer (*n* = 919) and perpendicular distance [m] from the line transect.

Both roe deer (*n* = 919; mean group size = 1.9 ± 0.9 SD; range: 1-8) and Reeve's muntjac (*n* = 2209; mean group size = 1.2 ± 0.4 SD; range: 1-4) can occur in clusters (Fig. 4.2). Group size can affect the density estimate as smaller clusters may be missed at greater distances or cluster size may be underestimated at larger distances (Buckland et al., 2001). I tested if the observed group size for roe deer and muntjac was affected by distance after 5% right truncation of the most distant observations using General Linear Models with poisson error.

I found that the detection of roe deer and Reeve's muntjac group size (dependent) was not affected by distance (continuous; roe: Wald $\chi^2_{(1)} = 1.70$, $p = 0.19$; muntjac: Wald $\chi^2_{(1)} = 1.02$, $p = 0.31$) whilst controlling for forest block (categorical; roe: Wald $\chi^2_{(6)} = 5.83$, $p = 0.44$; muntjac: Wald $\chi^2_{(6)} = 1.73$, $p = 0.94$) and year (categorical; roe: Wald $\chi^2_{(2)} = 2.79$, $p = 0.25$; muntjac: Wald $\chi^2_{(2)} = 3.94$, $p = 0.14$) (Table 4.2). Group size was therefore based on observed mean group size in each analysis design as detailed in Table 4.3.

Density results of each block and ESW of each analysis designs were compared using the z-test following (Buckland et al., 2001):

$$z = \frac{\bar{d}_1 - \bar{d}_2}{\sqrt{\left(SE\ (\bar{d}_1)\right)^2 + \left(SE(\bar{d}_2)\right)^2}}$$

where $\bar{d}_b$ is the density estimate for block *b*; and $SE(\bar{d}_b)$ the standard error of this estimate. The same equation is used when comparing ESW between different analyses designs. Here $\bar{d}_b$ is the ESW for an analysis design and $SE(\bar{d}_b)$ represents the corresponding standard error.

Table 4.2. Relationship between group size for roe deer (n = 873) and Reeve's muntjac (n = 2010) in Thetford Forest in 2008-2010 (after 5% truncation of the most distant observations) and year, forest block and distance using GLM's with poisson error.

Model predictors		n (%)	$\bar{x} \pm SD$	$B \pm SE$	Wald χ^2	p	Likelihood ratio χ^2	Log-likelihood	Dev/df	df
(a) roe deer										
Model		873				0.36	9.92	-1244.71	0.39	9
Year	2010	242 (27.7)	2.0 ± 1.0	-	2.79	0.25				2
	2009	301 (34.5)	1.9 ± 0.8	-0.08 ± 0.06						
	2008	330 (37.8)	1.7 ± 0.9	-0.10 ± 0.06						
Block	Har	45 (5.2)	1.8 ± 0.7	-	5.83	0.44				6
	Did	101 (11.6)	1.8 ± 0.8	0.004 ± 0.14						
	Mun	294 (33.7)	2.0 ± 1.0	0.12 ± 0.12						
	Lyn	245 (28.1)	1.9 ± 0.8	0.05 ± 0.12						
	Cro	104 (11.9)	1.9 ± 1.0	0.05 ± 0.13						
	HiLo	42 (4.8)	1.8 ± 0.9	0.01 ± 0.16						
	Elv	42 (4.8)	1.5 ± 0.7	-0.14 ± 0.17						
Distance				0.001 ± 0.001	1.70	0.19				1
(b) Reeve's muntjac										
Model		2094				0.66	6.83	-2332.34	0.12	9
Year	2010	548 (26.2)	1.1 ± 0.35	-	3.94	0.14				2
	2009	690 (33.0)	1.2 ± 0.39	0.006 ± 0.05						
	2008	856 (40.9)	1.2 ± 0.45	0.08 ± 0.05						
Block	Har	502 (24.0)	1.2 ± 0.44	-	1.73	0.94				6
	Did	451 (21.5)	1.2 ± 0.44	0.02 ± 0.06						
	Mun	292 (13.9)	1.2 ± 0.40	-0.01 ± 0.07						
	Lyn	440 (21.0)	1.2 ± 0.37	-0.05 ± 0.06						
	Cro	180 (8.6)	1.1 ± 0.35	-0.05 ± 0.08						
	HiLo	134 (6.4)	1.2 ± 0.36	-0.05 ± 0.09						
	Elv	95 (4.5)	1.2 ± 0.38	-0.03 ± 0.10						
Distance				0.001 ± 0.001	1.02	0.31				1

Table 4.3. Overview of analysis designs and specification of detection function and group size for each design.

Analysis design	Description
“Year”	**Detection function** pooled by forest block and stratified by year **Group size** year-specific observed mean, pooled across forest blocks
“Block”	**Detection function** pooled by year and stratified by forest blocks **Group size** block-specific observed mean, pooled across years
“Habitat”	**Detection function** pooled by habitat across forest blocks and year **Group size** habitat-specific observed mean, pooled across forest blocks and years Deer density in each forest block is calculated as overall **habitat area-weighted mean**

Results

Overall a total of 1725 roe deer in 921 groups and a total of 2625 Reeve’s muntjac in 2210 groups were detected. Most deer groups (roe: 80.9%; muntjac: 73.2%) were stationary when first seen. Only 17.0% of roe deer and 24.8% of muntjac were walking, and 2.1% roe deer and 1.9% muntjac were running when first detected. Few deer appeared to have moved in response to the approaching vehicle (Fig. 4.3). Analysing the percentage of walking animals versus the ranked distance (rank 1: < 30 m; 2: 30 - 60 m; 3: 61 - 90; 4: > 90 m) no difference of percentage of walking animals in the four distance bands was found for Reeve’s muntjac (Spearman ρ = -0.200, p = 0.80) and roe deer (Spearman ρ = 0.400, p = 0.60).

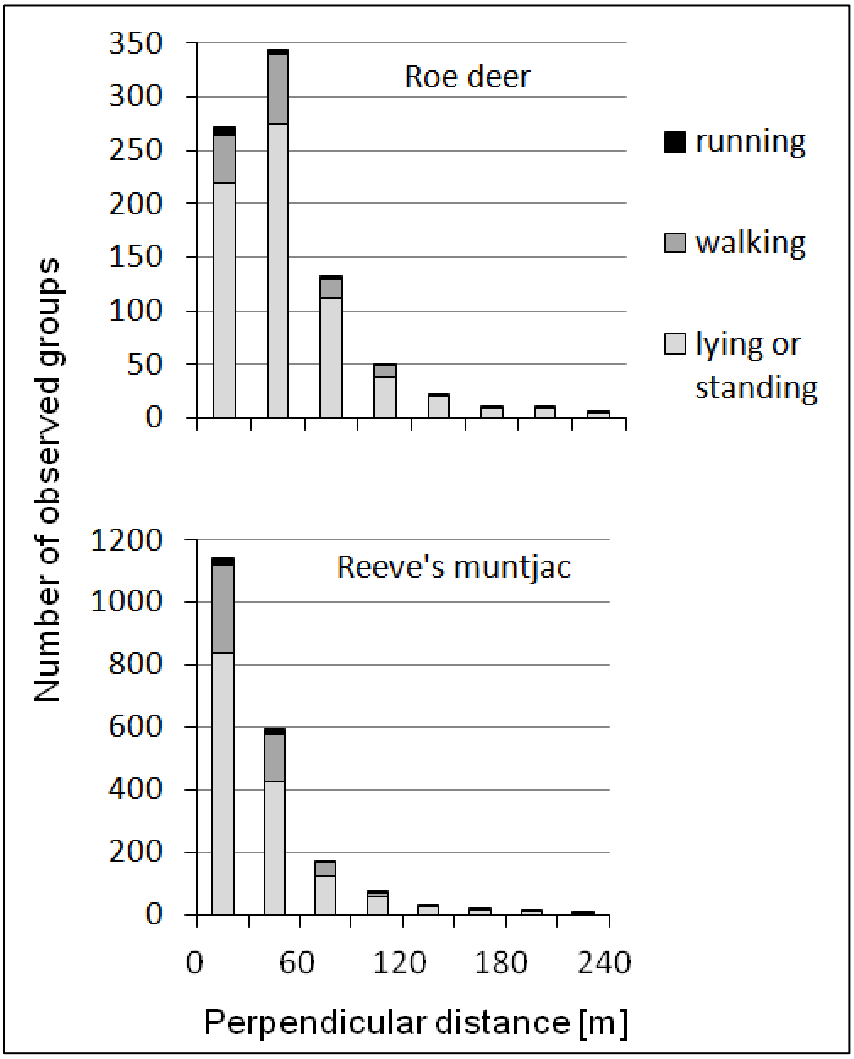

Fig. 4.3. Relationship between deer activity (lying, standing, walking, running) of roe deer (n = 851) and Reeve's muntjac (n = 2054) and perpendicular distance [m] grouped into distance bands of 30 m from the line transect.

For roe deer animals that were lying (mean = 43.1 m ± 2.3 *SD*) when detected tended to be located slightly closer to the transect line than those walking (mean = 48.4 m ± 3.1 *SD*) or standing (mean = 54.6 m ± 2.1 *SD*). Animals that were running (mean = 40.3 m ± 7.1 *SD*) when detected may have been responding to the vehicle as these were located closer than other activity classes (Wald $\chi^2_{(3)} = 17.2$, $p = 0.001$; standing^{a} > walking^{a,b} > running^{a,b} > lying^{b}; shared superscripts do not differ; Sequential Sidak $p < 0.05$).

Similar lying (mean = 30.5 m ± 1.4 *SD*) Reeve's muntjac were detected closer to the transect line than those walking (mean = 38.6 m ± 1.7 *SD*) or standing (mean = 43.8 m ± 1.5 *SD*). Running muntjac's (mean = 32.8 m ± 4.7 *SD*) were also detected closer to the transect line than other activity classes suggesting response to the approaching vehicle (Wald $\chi^2_{(3)} = 56.3$, $p < 0.001$; standing^{a} > walking^{a,b} > running^{b,c} > lying^{c}; shared superscripts do not differ; Sequential Sidak $p < 0.05$).

In this study I did not stratify by deer activity although moving deer may affect the shape of the detection function and therefore the density estimate. Removing the activities walking and running did not change the shape of the detection function (Fig. 4.3) curve suggesting including walking and running did not affect the density estimate. Although, responding to the vehicle deer that were walking were not strongly alarmed and were moving slowly, and therefore detected at a similar distance to their original position.

Detection function stratified by year

In all three years the best fit for Reeve's muntjac observation was a hazard rate model after 5% right truncation (Table 4.4). Detections declined with increasing distance from the transect (Fig. 4.4). No indication of Reeve's muntjac avoiding roads was found (Fig. 4.4) as there was no "trough" immediately next to the transect line. ESW for muntjac were similar in all three years (Fig. 4.6) but differed significantly between 2008 and 2010 (z-test: $p < 0.05$) ranging between mean = 52.4 m and mean = 58.0 m and showed a considerable fit (Cramer- von Misés test: $p \geq 0.05$) (Table 2). Detection probability was highest in 2010 ($P = 0.51$) and lowest in 2009 ($P = 0.41$) (Table 4.4). The CV of the detection probability was in all three years $CV(P) < 5\%$.

The hazard rate model proved also to be the best fit for roe deer observation after 5% right truncation (Table 4.6). In contrast to muntjac I found slightly fewer deer in the immediate proximity of the transect (≤ 30 m) (Fig. 4.4) which may result from some movement of deer away from the vehicle. Qualitative examination of the trough suggests approximately 10% of deer in the first distance band (0-30 m) had displaced into the second band (30-60 m) with 100% detection of individuals in both of these

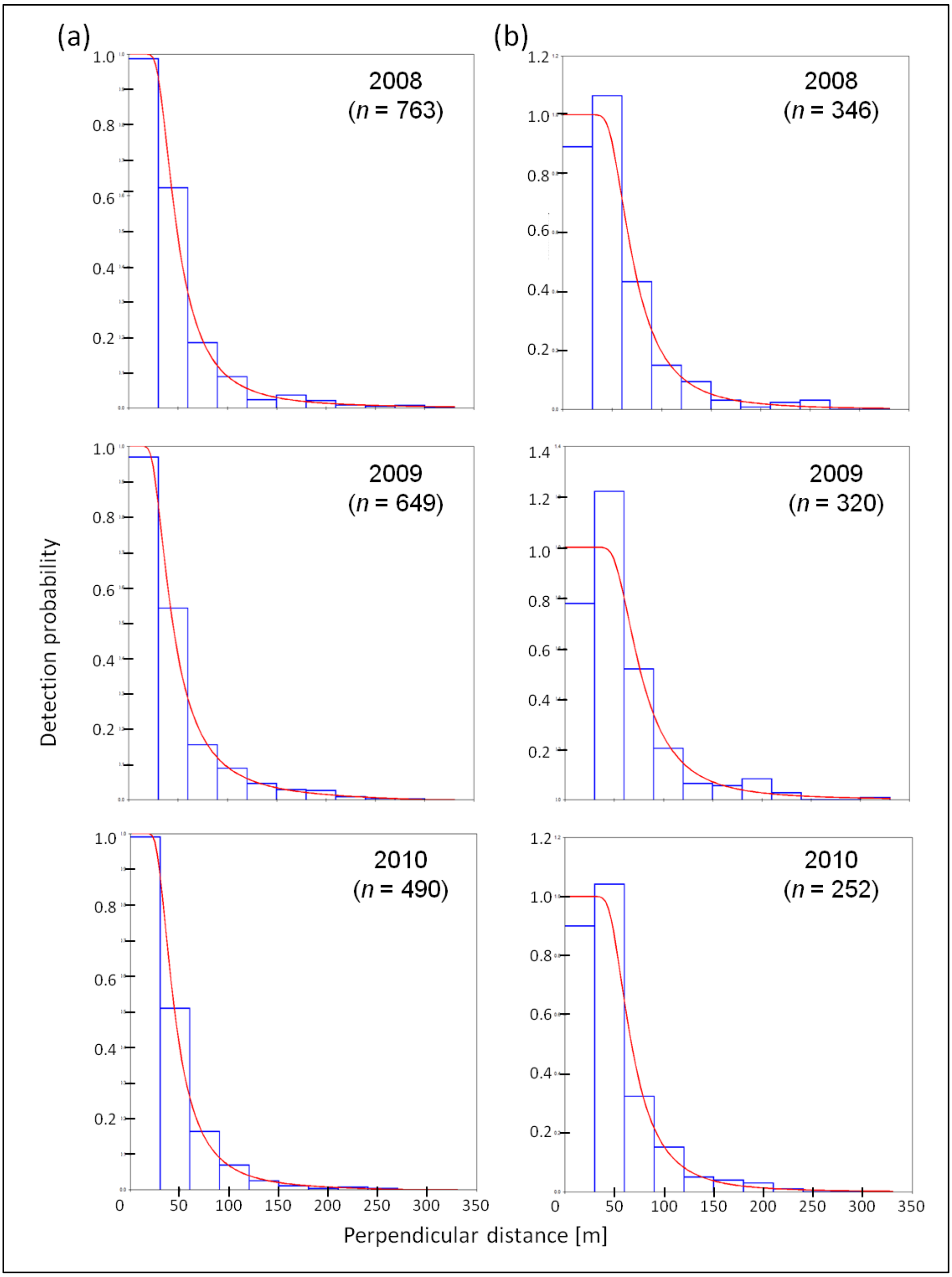

Fig. 4.4. Distribution of perpendicular distances and probability of detection obtained by observation stratified by year for (a) Reeve’s muntjac showing no avoidance and (b) roe deer showing minor avoidance with less than 5% of observed deer running between 0 m and 60 m.

Table 4.4. Results of density estimation for Reeve's muntjac (n = 1811) in Thetford Forest in 2008-10 with analysis design "year": with separate detection function and observed group size in each year and deer density stratified by forest block within years.

Block	Sample size (n)	Model fitted	Effective strip width ESW [m] (CI)	Detection probability P (CV(P) [%])	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Components of variation [%]			Estimated sampling intensity [%]*
					C-sq	p				P	n/L	E(S)	
(a) 2008													
Cro	69	Hazard rate	58.0 (54.1 - 62.2)	0.44 (3.5)	0.24	0.15	1.0 (0.8-1.3)	1.3 (1.2-1.3)	21.9 (16.4-29.1)	6.4	92.6	0.9	59
Did	163						2.0 (1.5-2.5)		42.2 (33.1-53.8)	9.0	89.7	1.3	49
Elv	36						0.8 (0.5-1.2)		17.2 (11.6-25.5)	3.9	95.6	0.6	16
Har	239						3.3 (2.6-4.1)		70.6 (55.7-89.5)	9.5	89.1	1.4	46
HiLo	60						0.5 (0.4-0.7)		11.3 (8.7-14.7)	7.6	91.3	1.1	14
Lyn	159						1.2 (0.9-1.5)		24.8 (19.5-31.7)	8.6	90.2	1.2	38
(b) 2009													
Cro	56	Hazard rate	55.9 (51.3-60.8)	0.41 (4.3)	0.32	0.05	0.8 (0.5-1.2)	1.2 (1.1-1.2)	15.6 (10.2-23.8)	4.3	95.3	0.4	54
Did	168						2.3 (1.7-3.1)		46.8 (34.6-63.3)	8.9	90.2	0.9	38
Elv	29						0.8 (0.6-1.1)		16.0 (11.4-22.4)	8.1	91.1	0.8	15
Har	160						2.3 (1.8-3.1)		48.2 (36.3-64.0)	10.0	89.1	1.0	39
HiLo	41						0.5 (0.4-0.8)		10.8 (7.3-16.0)	5.2	94.3	0.5	16
Lyn	165						1.2 (1.0-1.4)		23.6 (19.1-29.2)	16.8	81.5	1.6	37

Table 4.4.

(c) 2010													
Cro	59	Hazard rate	52.4 (47.8-57.4)	0.51 (4.7)	0.30	0.10	0.6 (0.4-0.7)	1.1 (1.1-1.2)	12.3 (9.4-16.1)	12.1	86.9	1.0	63
Table 4.4													
Did	118						2.2 (1.5-2.8)		44.2 (31.9-61.1)	9.2	90.0	0.8	24
Elv	29						0.6 (0.4-1.2)		13.8 (7.7-24.9)	2.9	96.8	0.3	14
Har	107						1.5 (1.0-2.2)		32.0 (21.6-47.6)	5.9	93.6	0.5	38
Table 4.4													
HiLo	35						0.5 (0.3-0.7)		10.4 (6.9-15.7)	5.7	93.8	0.5	13
Lyn	118						1.0 (0.8-1.3)		21.4 (16.3-28.1)	11.7	87.3	1.0	27

*Calculated as the (total length of transect used x ESW)/Block area

bands. The model fit for roe deer was less good as for the muntjac detection function (Cramer- von Misés test: $p \leq 0.03$). ESW was higher for roe deer (Fig. 4.7) than for muntjac ranging between ESW = 68.8 m and ESW = 80.7 m (Table 4.6). Only between 2009 and 2010 I found significant differences in the detection distance (z-test: $p < 0.05$). Detection probability for roe deer in all three years was $P \geq 0.51$ and CV(P) ranged between 5.3% and 6.4% (Table 4.6).

Detection function stratified by block

For all forest blocks the hazard rate model provided the best fit for Reeve's muntjac observations after 5% right truncation (Table 4.5). Mean ESW ranged from 43.7 m (block Mun) to 61.3 m (block Elv) (Table 4.5). Mean ESW for muntjac differed between blocks in 2008-10 whereby ESW of block Mun was significant lower than in the other forest blocks (z-test: $p < 0.05$) (Table 4.5). Although, the widest ESW was found in block Elv (a heavily browsed block with minimal understorey and no bramble) no significant differences with other forest blocks apart from block Mun were detected due to the high SE in block Elv. Overall the CI's of the ESW for the detection function pooled by year are smaller to the CI's for the detection function pooled by block.

Detection probability for muntjac within six forest blocks was generally lower than $P = 0.51$ (detection function pooled by year in 2009). Only one block showed a higher detection probability $P = 0.61$ (block Elv). The lowest detection probability was found in block HiLo ($P = 0.32$) (Table 4.5). Detection probability for muntjac within the other forest blocks was similar to the detection probability for 2008 and 2009. The variation in the CV of the detection probability for the detection function pooled by block was higher than the CV for the detection pooled by year. Apart from block Lyn (Cramer- von Misés test: $p = 0.03$) observed muntjac data did not differ from the distribution predicted by the detection function (Cramer- von Misés test: $p > 0.1$) (Table 4.5). For Reeve's muntjac no heaping in some distance from the transect line was observed when data were stratified by block (Fig. A4.1).

As for muntjac observations the hazard rate model provided the best fit for roe deer data after 5% right truncation. Only in forest block Cro the hazard rate model was fitted without truncation. The mean ESW ranged between 67.2 m (block Mun) and 85.1 (block Har) (Table 4.7). Generally, ESW in all models was greater for roe deer than for Reeve's muntjac (z-test: $p < 0.05$) (Table 4.5). Similar to Reeve's muntjac the lowest ESW for roe deer was found in block Mun; with the ESW of block Mun lower than those for blocks Har and Lyn (z-test: $p < 0.05$).

Table 4.5. Results of density estimation for Reeve's muntjac (*n* = 2110) in Thetford Forest in 2008-10 with analysis design "block": with separate detection function and observed group size in each block and deer density stratified by forest block within years.

Block	Year	Samp. size (*n*)	Model fitted	Effective strip width ESW [m] (CI)	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Components of variation [%]			Estimated sampling intensity [%]*
						C-sq	*p*				P	*n*/L	E(S)	
Cro	2008	69	Hazard rate	51.9 (45.4-59.4)	0.45 (6.8)	0.07	0.60	1.0 (0.8-1.3)	1.2 (1.1-1.2)	22.4 (16.5-30.4)	20.1	77.6	2.3	50
	2009	54						0.7 (0.5-1.1)		16.2 (10.4-25.2)	9.7	89.2	1.1	50
	2010	60						0.6 (0.5-0.8)		12.9 (9.7-17.1)	22.6	74.8	2.6	62
Did	2008	163	Hazard rate	54.3 (48.9-60.3)	0.44 (5.3)	0.14	0.30	2.0 (1.5-2.5)	1.2 (1.2-1.3)	44.0 (34.1-56.7)	18.1	80.0	1.8	46
	2009	167						2.3 (1.7-3.1)		51.2 (37.5-69.9)	12.4	86.4	1.3	37
	2010	122						2.1 (1.6-2.9)		47.9 (34.5-66.5)	11.7	87.2	1.2	25
Elv	2008	35	Hazard rate	61.3 (49.8-75.5)	0.61 (10.5)	0.19	0.15	0.8 (0.5-1.1)	1.2 (1.1-1.2)	14.6 (9.6-22.2)	27.1	70.2	2.7	17
	2009	29						0.7 (0.5-1.0)		13.7 (9.1-20.6)	28.2	69.0	2.8	17
	2010	39						0.6 (0.4-1.2)		12.2 (6.6-22.3)	13.3	85.3	1.3	17
Har	2008	238	Hazard rate	55.2 (50.8-60.0)	0.46 (4.2)	0.20	0.15	3.3 (2.6-4.1)	1.2 (1.2-1.3)	71.2 (55.9-90.7)	12.7	85.4	1.9	44
	2009	157						2.3 (1.7-3.0)		50.4 (37.8-67.3)	9.1	89.5	1.4	38
	2010	107						1.5 (1.0-2.2)		32.6 (22.0-48.4)	4.9	94.4	0.7	41

Table 4.5.

HiLo	2008	61	Hazard rate	52.9 (43.6-64.2)	0.32 (9.8)	0.02	1.00	0.5 (0.4-0.7)	1.2 (1.1-1.2)	11.6 (8.5-15.9)	38.1	59.1	2.8	13
	2009	41						0.5 (0.4-0.8)		11.5 (7.5-17.6)	21.7	76.7	1.6	15
	2010	36						0.5 (0.3-0.7)		10.8 (7.0-16.8)	21.0	77.4	1.5	13
Lyn	2008	158	Hazard rate	58.7 (53.5-64.5)	0.47 (4.8)	0.45	0.03	1.1 (0.9-1.4)	1.2 (1.1-1.2)	22.3 (17.3-28.6)	14.6	83.9	1.5	39
	2009	164						1.1 (0.9-1.4)		22.3 (17.1-26.4)	19.5	78.5	2.0	39
	2010	121						1.0 (0.8-1.3)		19.9 (15.1-26.3)	12.0	86.8	1.2	30
Mun	2008	132	Hazard rate	43.7 (39.0-48.9)	0.42 (5.8)	0.13	0.30	1.3 (1.2-1.6)	1.2 (1.2-1.3)	36.6 (30.3-44.1)	36.9	58.6	4.4	21
	2009	85						1.3 (0.9-1.9)		35.3 (24.1-51.6)	9.9	88.9	1.2	12
	2010	72						1.2 (0.9-1.7)		33.1 (23.6-46.4)	12.7	85.8	1.5	13

*Calculated as the (total length of transect used x ESW)/Block area

Table 4.6. Analysis design “year”: results of density estimation for roe deer (*n* = 874 groups) in Thetford Forest in 2008-10 with separate detection function and observed group size in each year and deer density stratified by forest block within years.

Block	Sample size (*n*)	Model fitted	Effective strip width ESW [m] (CI)	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Components of variation [%]			Estimated sampling intensity [%]*
					C-sq	*p*				P	*n*/L	E(S)	
(a) 2008													
Cro	25	Hazard rate	75.6 (68.2 – 83.9)	0.55 (5.3)	0.44	0.03	0.4 (0.2-0.6)	1.8 (1.7-2.0)	8.9 (5.8-13.7)	6.1	91.6	2.3	73
Did	49						0.6 (0.4-0.9)		15.2 (10.3-22.3)	7.9	89.1	3.0	64
Elv	18						0.4 (0.2-0.7)		9.6 (5.4-17.0)	4.0	94.5	1.5	21
Har	17						0.2 (0.2-0.4)		5.6 (3.6-8.7)	6.0	91.7	2.3	60
HiLo	22						0.3 (0.2-0.6)		8.1 (4.6-14.1)	3.8	94.8	1.4	18
Lyn	77						0.6 (0.4-0.7)		13.5 (9.9-18.2)	12.0	83.5	4.5	50
Mun	123						1.3 (1.0-1.6)		30.3 (23.7-38.6)	19.0	73.9	7.2	37
(b) 2009													
Cro	43	Hazard rate	80.7 (72.8-89.5)	0.51 (5.3)	0.94	0.001	0.7 (0.4-1.0)	1.8 (1.7-1.9)	15.0 (9.5-23.5)	5.7	92.9	1.4	78
Did	34						0.5 (0.3-1.1)		12.3 (6.1-24.5)	2.5	96.9	0.6	55
Elv	10						0.2 (0.2-0.3)		5.0 (3.3-7.7)	7.3	91.0	1.8	21
Har	16						0.2 (0.1-0.5)		5.3 (2.6-10.8)	2.4	97.1	0.6	56
HiLo	12						0.2 (0.1-0.3)		3.5 (2.1-5.9)	4.2	94.8	1.0	23

Table 4.6.

Lyn	103						0.7 (0.6-0.9)		16.0 (12.1-21.0)	14.8	81.6	3.6	53
Mun	86						1.3 (1.0-1.7)		29.8 (22.6-39.3)	15.3	81.0	3.7	21
(c) 2010													
Cro	35	Hazard rate	68.8 (60.7-78.0)	0.58 (6.4)	0.73	0.01	0.4 (0.3-0.6)	2.0 (1.9-2.1)	11.9 (7.8-18.1)	9.4	88.3	2.3	83
Did	18						0.4 (0.2-0.6)		10.0 (5.9-17.0)	6.5	91.9	1.6	31
Elv	16						0.4 (0.2-0.7)		10.3 (5.1-20.7)	3.8	95.3	0.9	19
Har	12						0.2 (0.1-0.3)		4.8 (2.4-9.9)	3.3	95.9	0.8	51
HiLo	9						0.1 (0.1-0.3)		3.9 (1.5-9.9)	1.9	97.6	0.5	17
Lyn	65						0.6 (0.4-0.8)		16.6 (11.3-24.3)	11.5	85.7	2.8	35
Mun	84						1.4 (1.0-2.1)		41.0 (27.1-62.1)	10.4	87.1	2.6	20

*Calculated as the (total length of transect used x ESW)/Block area

Table 4.7. Analysis design “block”: results of density estimation for roe deer (*n* = 881) in Thetford Forest in 2008-10 with separate detection function and observed group size in each block and deer density stratified by forest block within years.

Block	Year	Sample size (*n*)	Model fitted	Effective strip width ESW [m] (CI)	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Components of variation [%]			Estimated sampling intensity [%]*
						C-sq	*p*				P	*n*/L	E(S)	
Cro	2008	25	Hazard rate no truncation	77.8 (63.5-95.4)	0.38 (10.3)	0.79	0.01	0.4 (0.2-0.6)	1.8 (1.7-2.0)	8.6 (5.4-13.8)	19.5	76.0	4.5	75
	2009	45						0.7 (0.4-1.1)		16.2 (9.7-27.0)	16.5	79.7	3.8	75
	2010	38						0.5 (0.3-0.6)		10.5 (7.0-15.8)	25.0	69.3	5.7	93
Did	2008	49	Hazard rate	78.6 (66.1-93.4)	0.71 (8.7)	0.19	0.20	0.6 (0.4-0.9)	1.8 (1.6-1.9)	14.0 (9.3-21.1)	18.5	76.1	5.4	67
	2009	33						0.5 (0.3-1.1)		11.7 (5.7-24.0)	6.3	91.9	1.8	54
	2010	18						0.3 (0.2-0.6)		7.7 (4.5-13.3)	11.2	85.5	3.3	36
Elv	2008	18	Hazard rate [1]	72.8 (58.4-90.7)	0.44 (11.1)	0.18	0.20	0.4 (0.2-0.7)	1.7 (1.5-1.8)	9.0 (5.0-16.3)	15.3	81.5	3.1	20
	2009	10						0.2 (0.2-0.3)		5.0 (3.2-7.9)	25.1	69.9	5.1	20
	2010	16						0.4 (0.2-0.7)		8.0 (3.9-16.5)	5.6	93.3	1.1	20
Har	2008	17	Hazard rate [2]	85.1 (75.9-95.5)	0.60 (5.8)	0.87	0.001	0.2 (0.2-0.4)	1.9 (1.8-1.9)	5.0 (3.2-7.8)	7.4	91.2	1.4	68
	2009	16						0.2 (0.1-0.5)		5.1 (2.5-10.3)	2.9	96.5	0.6	59
	2010	13						0.2 (0.1-0.4)		3.9 (1.8-8.4)	2.5	97.1	0.5	62

Table 4.7.

HiLo	2008	22	Hazard rate [1]	72.8 (58.4-90.7)	0.44 (11.1)	0.18	0.20	0.3 (0.2-0.6)	1.7 (1.5-1.8)	7.5 (4.2-13.6)	14.7	82.3	3.0	17
	2009	13						0.2 (0.1-0.3)		3.8 (2.0-7.0)	13.4	83.9	2.7	21
	2010	9						0.1 (0.1-0.3)		3.0 (1.2-7.9)	5.6	93.3	1.1	18
Lyn	2008	78	Hazard rate	84.2 (74.6-95.2)	0.59 (6.2)	0.70	0.01	0.6 (0.4-0.8)	1.9 (1.8-2.0)	12.4 (9.1-17.0)	15.8	80.8	3.4	55
	2009	102						0.7 (0.5-0.9)		15.4 (11.6-20.4)	19.0	76.9	4.1	56
	2010	67						0.6 (0.4-0.8)		13.1 (9.1-18.8)	11.7	85.8	2.5	43
Mun	2008	122	Hazard rate	67.2 (60.6-74.6)	0.49 (5.3)	0.34	0.05	1.2 (1.0-1.5)	2.0 (1.9-2.1)	36.7 (28.7-46.9)	19.0	74.9	6.1	33
	2009	86						1.3 (1.0-1.7)		38.8 (29.4-51.2)	15.3	79.8	4.9	18
	2010	84						1.4 (1.0-2.1)		41.9 (27.8-63.1)	7.4	90.2	2.4	20

*Calculated as the (total length of transect used x ESW)/Block area

[1] data set block 3 (ESW: mean = 75.0m; CI: 52.0-108.0) and block 5 (ESW: mean = 70.4m; CI: 51.4-96.5) pooled to increase sample size for calculating detection function for both blocks

[2] data set block 4 (ESW: mean = 81.2m; CI: 63.3-104.2) and block 6 (ESW: mean = 84.2m; CI: 74.6-95.2) pooled to increase sample size for calculating detection function of block 4

For roe deer the CI's of the ESW of the detection function stratified by block were generally wider than the CI's of the detection function stratified by year. In analysis design "block" the detection probability for roe deer varied widely between P = 0.71 (block Did) and P = 0.38 (block Cro) (Table 4.7). The CV of the detection probability ranged from 5.3 to 11.1 in analysis design "block" (Table 4.7). In four out of seven forest blocks the CV of the detection probability was higher when roe deer data were stratified by block (CV(P) > 6.4) rather than by year. Only in three of seven forest blocks an adequate fit of the observed roe deer data was found (Cramer- von Misés test: $p = 0.20$) in analysis design "block" (Table 4.7). In four forest blocks I observed a peak in detections in some distance away (> 30 m) from the transect line (Fig. A4.2).

Detection function stratified by habitat

For both deer species the Hazard rate model again provided the best fit for all three habitat classes after 5% truncation. The habitat-specific ESW for Reeve's muntjac was constantly less than that for roe deer (z-test: $p < 0.05$) and for roe deer ESW in all three habitats were constantly larger than those for muntjac. These findings are consistent with the two other analysis designs "year" and "block". For roe deer and muntjac ESW varied more strongly among habitats than between analysis designs "year" and "block".

For Reeve's muntjac the highest ESW was found in open habitats (mean = 78.7 ± 8.7 m SE), mature stands were mean = 51.9 ± 1.3 m *SE* and the lowest ESW was found in dense habitats (mean = 41.4 ± 2.1 m *SE*). Similarly, for roe deer ESW in open habitats was mean = 103.5 ± 7.4 m *SE*, in mature stands mean = 70.2 ± 2.6 m *SE* and in dense habitats mean = 55.9 ± 4.5 m *SE* (Table A4.1.a-A4.2.c). The ESW of dense habitats was approximately half the width of the ESW of open habitats.

Detection probability was about P = 0.50 for Reeve's muntjac and about P = 0.60 for roe deer. CV of the detection probability was highest for open habitats CV(P) = 11.1 for muntjac and highest in dense habitats CV(P) = 8.0 for roe deer. For both species lowest CV of the detection probability was found in mature stands CV(P) = 2.4 and CV(P) = 3.7 for muntjac and roe deer respectively. The goodness of fit for observed data of Reeve's muntjac was adequate for open habitats and dense habitats (Cramer-von Mises test: $p \geq 0.10$). Due to fewer observed deer in the immediate proximity of the transect (≤ 30 m) the goodness of fit was poor for observed data in mature stands of observed Reeve's muntjac detection distances and for all three habitat classes of roe deer data (Cramer- von Mises test: $p \leq 0.03$) (Table A4.1.a-A4.2.c, Fig. 4.5).

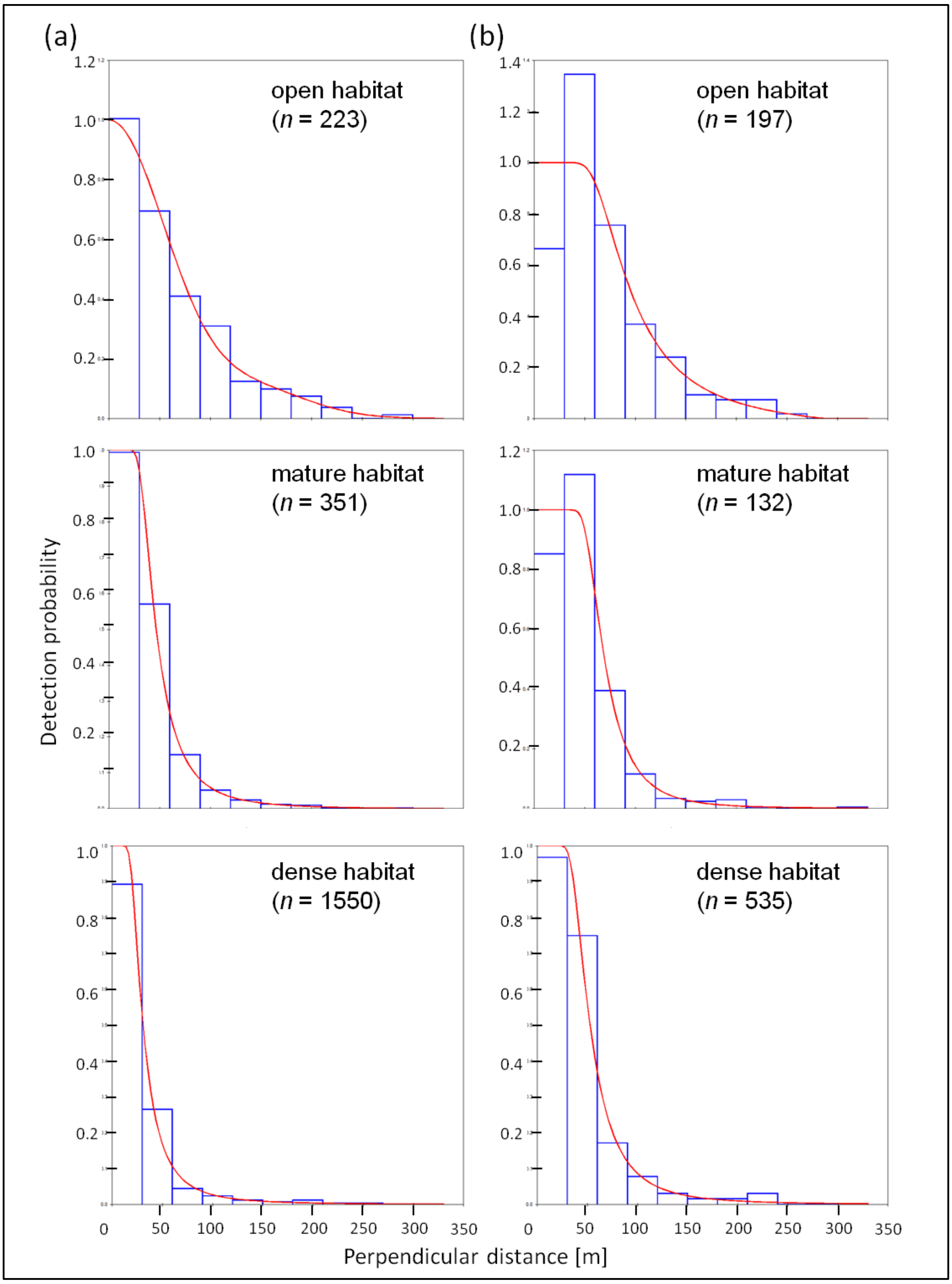

Fig. 4.5. Distribution of perpendicular distances and probability of detection obtained by observation stratified by habitat across forest blocks and years for (a) Reeve's muntjac and (b) roe deer.

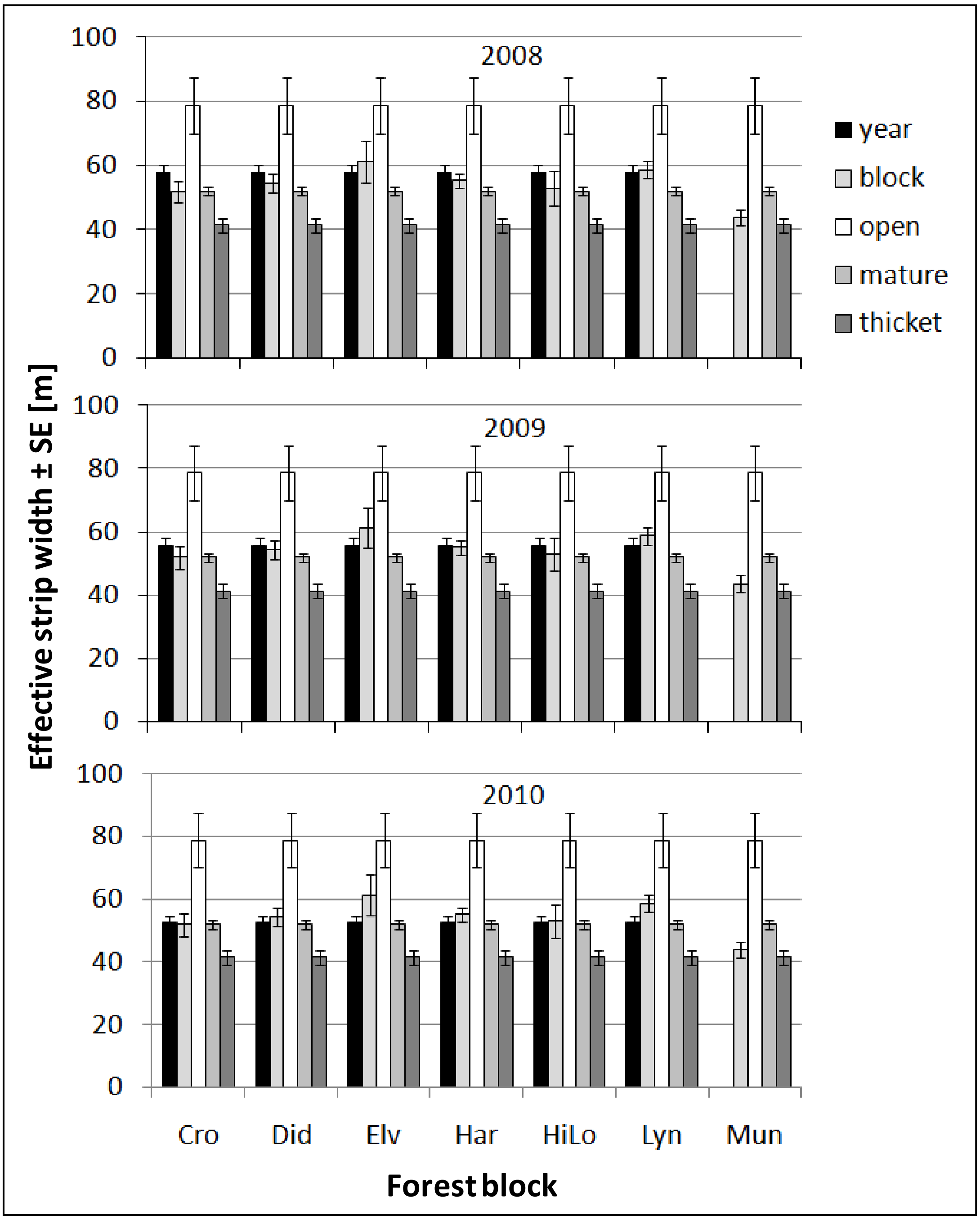

Fig. 4.6. Reeve's muntjac effective strip width ESW ± *SE* [m] in seven forest blocks in Thetford Forest in 2008-10 established by using distance sampling thermal imaging data analysed using three different analytical methods for the detection function: (1) stratifying the observations for the detection function by **year** pooling across forest blocks, (2) stratifying the observations by forest **block** pooling across years and (3) stratifying observations by **habitat** pooling across years and blocks, to calculate an overall habitat area-weighted mean.

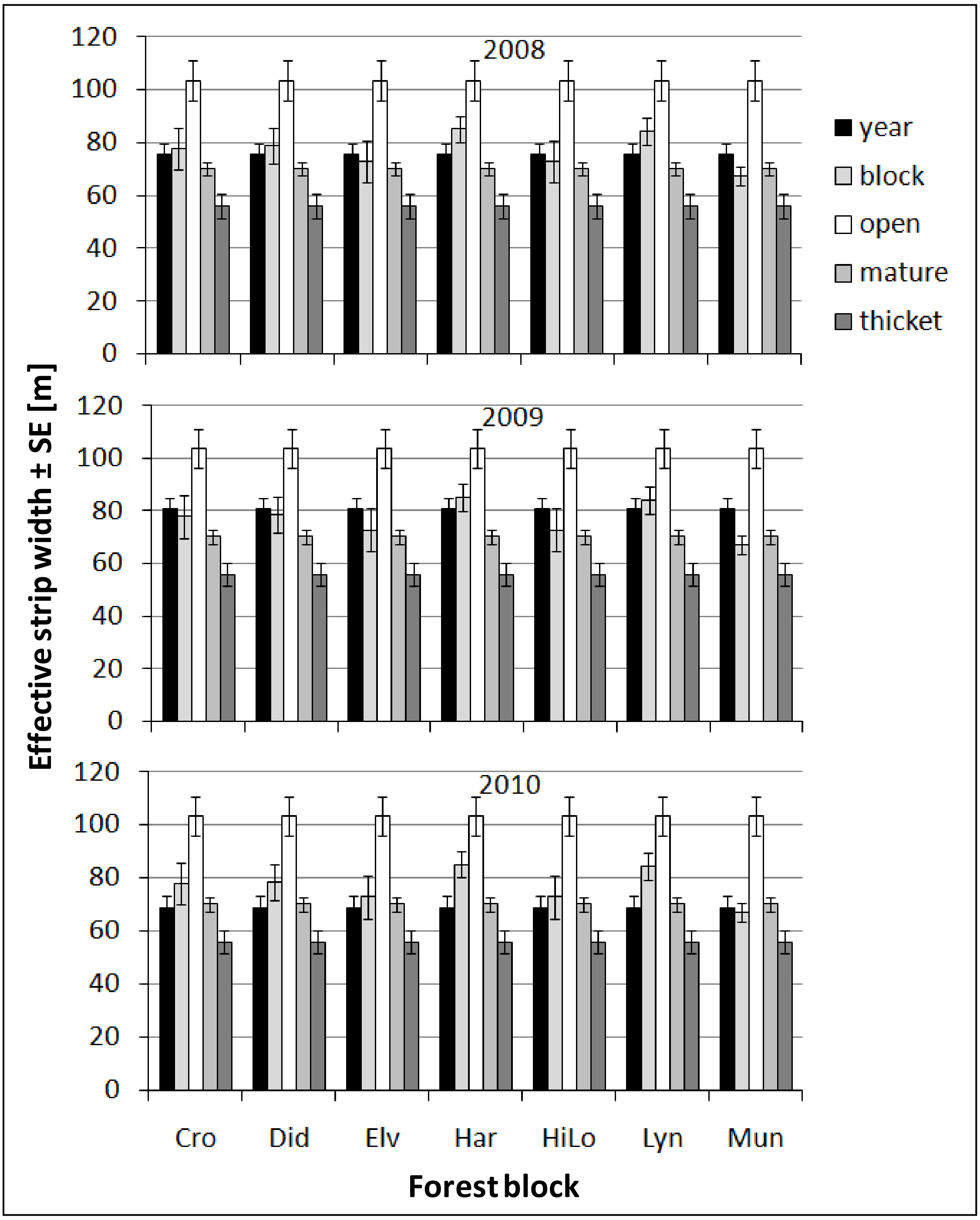

Fig. 4.7. Roe deer effective strip width ESW ± *SE* [m] in seven forest blocks in Thetford Forest in 2008-10 established by using distance sampling thermal imaging data analysed using three different analytical methods for the detection function: (1) stratifying the observations for the detection function by **year** pooling across forest blocks, (2) stratifying the observations by forest **block** pooling across years and (3) stratifying observations by **habitat** pooling across years and blocks, to calculate an overall habitat area-weighted mean.

Cluster size

The default option in DISTANCE to incorporate cluster size in the calculation of the density estimate is the group size regression method. However, I preferred to use the observed mean cluster size in our calculations. Thus, for Reeve's muntjac and roe deer I compared density estimates and 95% CI's between these two methods for all three analysis designs "year", "block" and "habitat". Generally, I found less variation of density estimates and 95% CI's between the two group size designs for the mainly solitary living muntjac than for roe deer which is living in small family groups during the winter.

For Reeve's muntjac I found that density estimates comparing the observed group size to the size-bias method differed less than 10% for all three analyses designs. In analysis design "habitat" I detected differences between density estimates greater than 10% when comparing the observed group size to the size-bias method in block Elv in 2009 (12%) and in 2010 (15%), in block Cro in 2010 (11%), and in block Did in 2008 (11%). In two cases (Elv and Did) the density estimates decreased when using the observed group size.

For muntjac I found a decrease in 95% CI's in block Did (2008: 11%; 2009: 12%) and in block HiLo (2008: 11%) whilst I detected an increase in 95% CI in block Cro (2009: 12%) when using the observed group size for calculations compared to the size-bias method in analysis design "habitat". For all other comparisons of 95% CI's between the observed group size and the size-bias method less than 10% variation was detected.

For roe deer analyses using the size bias regression method for group size and the observed group size mean provided density estimates that differed by greater than 10% in all three analysis designs "year", "block" and "habitat".

Comparisons of roe density estimates and 95% CI's between the two cluster size designs showed that in 38% (n = 24) and in 40% (n = 25) of all cases the mean difference ranged between 11%-31% and 11%-47% respectively. In 50% of these cases the density estimate and in 76% of these cases the 95% CI decreased comparing the observed group size to the size-bias method.

Encounter rate

Encounter rates for Reeve's muntjac and roe deer was similar in analysis designs "year" and "block" but differed between individual blocks and surveyed years (Table

4.4-4.7). For Reeve’s muntjac the highest encounter rates were found in block Did and Har ranging between 1.5 groups/km and 3.3 groups/km. The lowest encounter rates were observed in block Elv and HiLo ranging between 0.5 groups/km and 0.8 groups/km for muntjac.

In analysis design “habitat” encounter rate of Reeve’s muntjac and roe deer differed among habitats, blocks and years (Table A4.1.a-A4.2.c). Generally muntjac encounter rate was higher in mature stands (range from 0.5 to 3.7 groups/km) and open habitats (range from 0.2 to 3.2 groups/km) than in dense habitats (range from 0.2 to 2.5 groups/km). This reflects the night feeding behaviour of muntjac. Roe deer encounter rate was highest in open habitats (range from 0.1 to 4.1 groups/km) and lower in mature stands (range from 0.1 to 2.5 groups/km) and dense habitats (range from 0.1 to 1.3 groups/km). This suggests that open habitats offer a good feeding source for roe deer.

Sampling intensity

Sampling intensity was influenced by ESW and total length of transect surveyed (Table 4.4-4.7). Generally, mean sampling intensity was similar between analysis designs “year” and “block” for muntjac mean = 33% ± 16% SD vs. mean = 33% ± 15% SD and roe deer mean = 45% ± 22% SD vs. mean = 48% ± 24% SD when excluding block Mun (Table 4.4-4.7). Overall, the lowest sampling intensity for roe deer was about 20% and for muntjac was about 17% in block Elv and HiLo which were only surveyed once (Table 4.4-4.7). The sampling intensity was about 14% higher in roe deer than in Reeve’s muntjac due to the wider ESW for roe deer.

Components of variation

In all three analysis designs the encounter rate (Reeve’s muntjac: range from 49.0% to 99.0%; roe deer: range from 69.3% to 99.3%) was the highest source of variation of the density estimates. Probability of detection was mainly influenced by vegetation cover (e.g. roe deer in mature stands versus dense habitats). The effect of the cluster size on the variation of the density estimates of both species was < 8% in all analysis designs (Table 4.4-4.7 and A4.1.a-A4.2.c) when using the observed group mean.

Density estimates

Density estimates were similar between analysis designs “year”, “block” and “habitat” (z-test: n.s.). Generally, density estimates were stable among years but differed between forest blocks (Table 4.88, Fig. 4.8-4.9).

The general pattern of deer density distribution throughout the forest was similar for Reeve’s muntjac and roe deer in all three analysis designs in 2008-10 (Table 8, Fig. 4.8-4.9). Muntjac density was highest in blocks Did and Har (mean ≥ 30 deer km^{-2}) and lowest in blocks Elv and HiLo (mean ≤ 20 deer km^{-2}). The highest roe deer density was observed in block Mun (mean ≥ 30 deer km^{-2}) and the lowest densities in blocks Elv, Har and HiLo (mean ≤ 10 deer km^{-2}) (Table 4.8).

In analysis design “year” changes in Reeve’s muntjac density throughout time were detected in forest block Cro where density decreased about 44% from 2008 to 2010 (z-test: $p < 0.01$) and in forest block Har where density decreased about 32% from 2008 to 2009 (z-test: $p < 0.05$) and about 34% from 2009 to 2010 (z-test: $p < 0.05$). Analysis design “block” suggest a similar decline of 42% in muntjac density in forest block Cro from 2008 to 2010 (z-test: $p < 0.01$) and in forest block Har of 29% from 2008 to 2009 and 35% from 2009 to 2010 (z-test: $p < 0.001$). No significant decline in muntjac density in forest block Cro was found in analysis design “habitat”. However, a significant reduction of muntjac density in forest block Mun from 2008 to 2009 and 2009 to 2010 of 21% and 38% respectively was observed in analysis design “habitat” (z-test: $p < 0.05$).

For roe deer, in analysis design “year” I detected a significant density increase of 41% in block Cro from 2008 to 2009 and in block HiLo a decrease of 57% from 2008 to 2009 (z-test: $p < 0.05$). Similarly, in analysis design “block a significant increase (47%; z-test: $p < 0.05$) of roe deer density from 2008 to 2009 was observed in block Cro and a significant decrase in block HiLo (21%; z-test: $p < 0.05$)”. But I also found a significant decrease in roe deer density (34%; z-test: $p < 0.05$) in block Did. For roe deer in analysis design “habitat” I observed a significant increase of 30% (z-test: $p < 0.05$) in block Mun from 2008 to 2010 and a significant decrease of 45% (z-test: $p < 0.05$) in block Did from 2008 to 2010.

Table 4.8. Habitat-area weighted densities from models with separate detection function in each of three habitat types, showing mean and 95% CI's for Reeve's muntjac and roe deer.

	Density per forest block [deer km^{-2}] (95% CI)						
Year	Cro	Did	Elv	Har	HiLo	Lyn	Mun
(a) Muntjac							
2008	26.1	53.3	18.4	77.2	19.0	26.4	31.5
	(14.3-37.9)	(32.8-73.8)	(5.7-31.0)	(58.8-95.7)	(8.5-29.6)	(18.7-34.1)	(23.2-39.7)
2009	18.1	54.4	14.8	60.8	10.8	26.1	28.9
	(4.9-31.4)	(20.5-88.4)	(5.3-24.3)	(46.6-75.0)	(0-23.6)	(16.4-35.7)	(17.1-40.7)
2010	18.0	51.0	13.2	37.8	11.5	25.1	36.8
	(7.3-28.6)	(32.0-70.1)	(5.6-20.8)	(20.9-54.6)	(1.7-21.2)	(14.3-35.9)	(9.2-64.3)
(b) Roe deer							
2008	10.2	18.8	8.7	5.8	8.2	12.3	31.7
	(5.2-15.1)	(10.3-27.3)	(0-17.4)	(0.5-11.0)	(0.9-15.5)	(6.9-17.7)	(23.1-40.3)
2009	14.4	11.5	5.7	6.2	3.2	15.6	34.1
	(4.8-24.0)	(1.8-21.1)	(1.2-10.2)	(2.2-10.2)	(0-7.4)	(8.4-22.8)	(26.2-41.9)
2010	8.6	10.3	8.4	3.0	3.3	14.0	48.8
	(3.1-14.0)	(5.7-15.0)	(0.9-15.9)	(0-7.0)	(0-9.5)	(6.6-21.4)	(30.0-67.5)

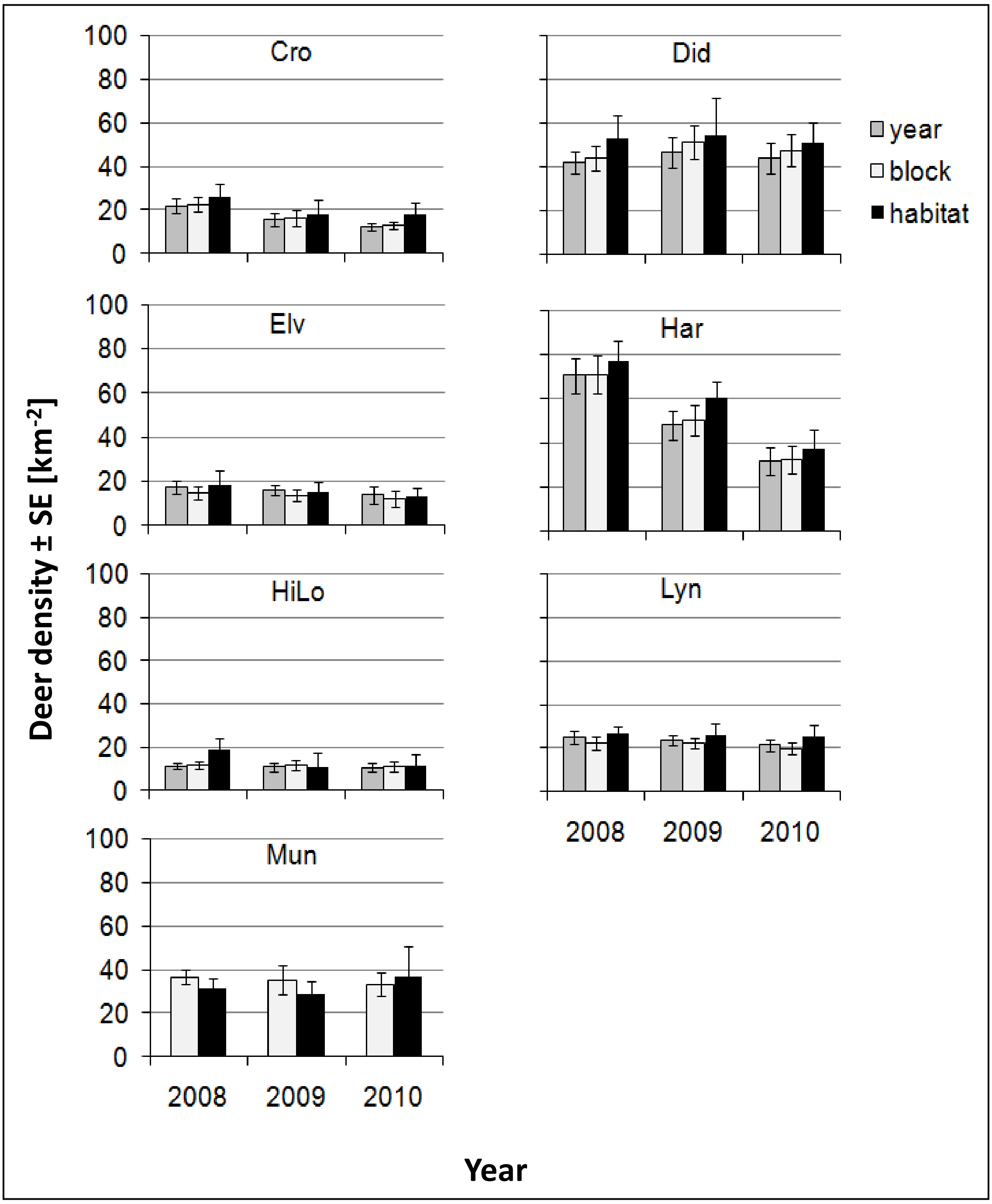

Fig. 4.8. Reeve's muntjac density ± *SE* [km^{-2}] in seven forest blocks in Thetford Forest in 2008-10 established by using distance sampling thermal imaging data analysed using three different analytical methods for the detection function: (1) stratifying the observations for the detection function by **year** pooling across forest blocks, (2) stratifying the observations by forest **block** pooling across years and (3) stratifying observations by **habitat** pooling across years and blocks, to calculate an overall habitat area-weighted mean.

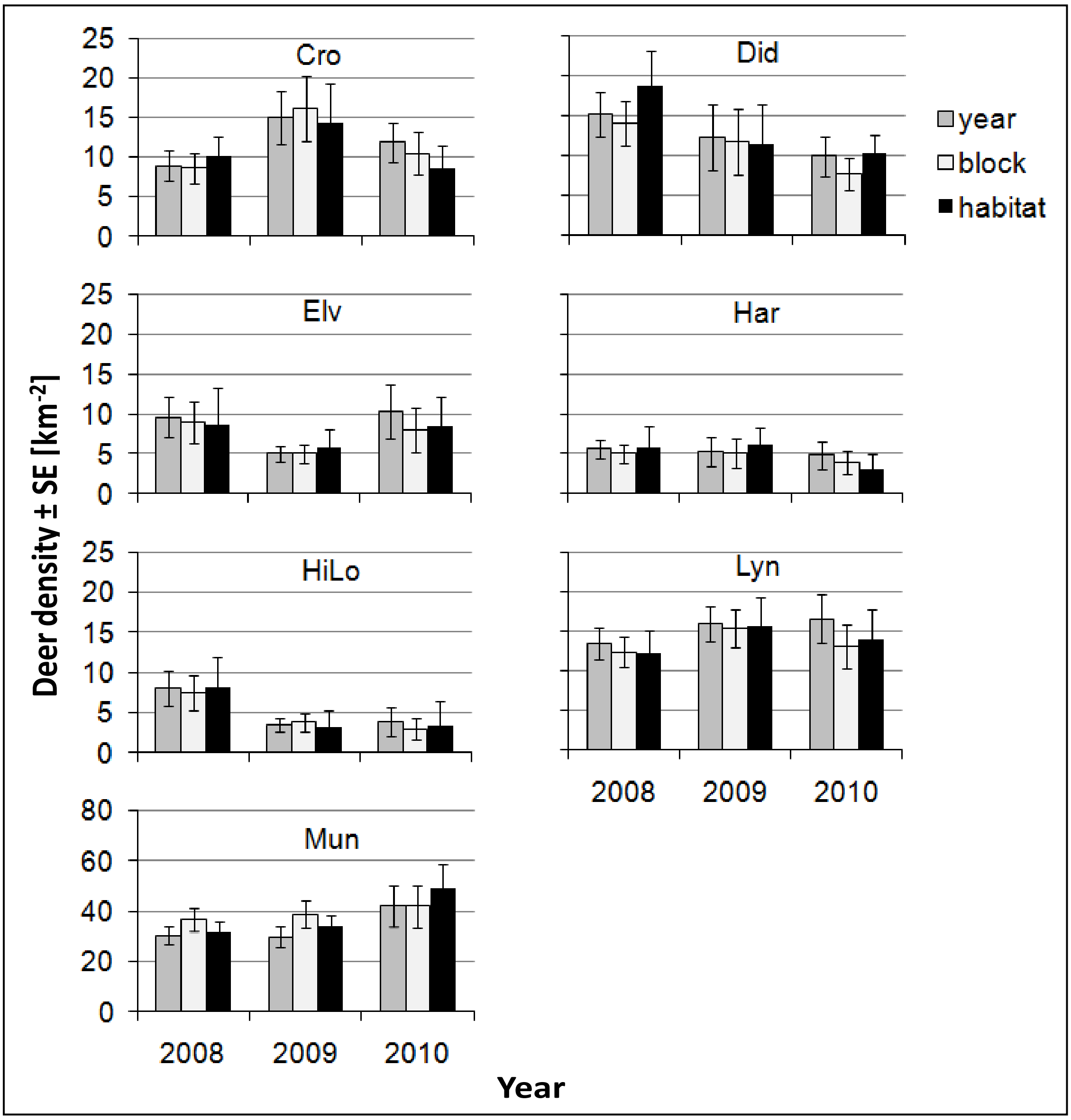

Fig. 4.9. Roe deer density ± *SE* [km^{-2}] in seven forest blocks in Thetford Forest in 2008-10 established by using distance sampling thermal imaging data analysed using three different analytical methods for the detection function: (1) stratifying the observations for the detection function by **year** pooling across forest blocks, (2) stratifying the observations by forest **block** pooling across years and (3) stratifying observations by **habitat** pooling across years and blocks, to calculate an overall habitat area-weighted mean.

Discussion

For the first time deer density of Reeve's muntjac and roe deer has been estimated using thermal imaging distance sampling data contrasting three different analysis designs, with the detection function (1) stratified by year but pooled across forest blocks, (2) stratified by forest block but pooled across years and (3) stratified by habitat type but pooled across both forest blocks and years (Table 4.3). No significant differences of estimated deer densities between analyses designs have been found suggesting that thermal imaging distance sampling is a robust method to establish deer densities and can be used for intensive monitoring at landscape scale.

In particular, deer densities calculated using analysis designs "year" and "block" were nearly identical, however there was less variance in analysis design "year" than "block" (for definition see Table 4.3). Sample size, encounter rate and group size were very similar in these two analysis designs. Thus, although enough observations (> 90 groups) had been available to calculate the detection function for Reeve's muntjac and roe deer separately in each block, a detection function pooled across the forest is more robust and achieved greater precision. For roe deer the variance of the density estimate was more affected by cluster size than for muntjac as roe deer is living in small family groups during winter time.

Deer density estimates calculated using analysis design "habitat" that calculates an area-weighted mean from separate habitat-specific density estimates with differing ESW, reflected the configuration of forest blocks and the distribution of deer found during the survey. Most deer where located in mature habitats, that were the dominant habitats within forest blocks (mature stands across blocks: mean = 68.0 % ± 8.9 SD; range: 49.7% - 82.9%). This might explain why density estimates by the habitat area-weighted mean did not differ significantly from density estimates by analysis design "year" and "block" as expected. Although, enough observations were available to calculate the detection function in each of the three habitat classes (> 90 groups) the higher variance of the area weighted mean was due to lower observations within single forest blocks in some habitats especially in open and dense habitats. Similarly, higher densities of Reeve's muntjac and roe deer have been found in mature habitats using standing crop pellet-group counts in Thetford Forest (Hemami et al., 2005). However, in this study I did not find higher deer density in dense habitats for both species as proposed by Hemami et al. (2005). Animals are more likely to hide in dense habitats in daylight due to shooting and other disturbances and use more open habitats by night (Gill et al., 1997). Lower total numbers observed in open areas were most likely due to low availability (< 13% of forest block area) or the accessibility of fields adjacent to the forest. Fields act as additional feeding resource and are used by deer ranging within the forest at night. Therefore surveys of adjacent fields are important to establish deer numbers as also suggested by Hemami et al. (2007).

Block-specific population densities over a three year period were stable, increased or decreased. I did not detect strong fluctuations of population density over one or two years as suggested by Focardi et al. (2002a). Significant changes in population density were identified for muntjac in three forest blocks ranging from 21% to 42% and for roe deer in three forest blocks ranging from 21% to 47%. These changes were mainly due to increased cull targets.

Detection of deer

Although only a low number of deer moved away from the transect line as reaction to the observer, for roe deer but not for Reeve's muntjac I found slightly fewer animals in the immediate proximity of the transect line (≤ 30 m) irrespective of track width and appearance. They moved to the next distance band (30-60 m) and were detected there ($p > 1.0$ for 30-60 m). Research by Marini et al. (2009) suggested that deer were more likely to be detected by the approaching observer before the deer show any avoidance reaction by observing the behaviour of radio collared fallow deer on walked night transects. This suggests that movement of deer may occur possible due to other sources of disruption or interaction between deer. I recorded low numbers of running (< 5%) and walking (< 25%) animals. Also deer often walked parallel to the transect line and not away. Ward et al. (2004) observing similar heaping of roe deer in some distance from the transect suggested roe deer might avoid the near edge of tracks and simply cluster around 20-30m distance. These observations are in agreement with our findings that roe deer avoids the immediate edge of forest compartments and the curve of the detection function did not change when excluding the moving deer.

Detection function

In this study, I found that the ESW for roe deer was about 25%-30% wider than for Reeve's muntjac. Hemami et al. (2007) reported a difference of 40% between the ESW of roe deer and muntjac in forest block Mun. I found a similar difference of 34% between the ESW of roe deer and muntjac in the same forest block. The difference of the ESW between both species is most likely due to the appearance of the smaller species (Corbet and Harris, 1991). Due to differences in the detectability of the two species separate detection functions should be calculated to obtain robust density estimates for each species as also suggested by Hemami et al. (2007).

Stratifying the detection function by activity may improve accuracy of density estimates and lower the error around the estimates due to different detection probability given enough observations are collected.

Comparisons of annual detection functions stratified by year and pooled across forest blocks of Reeve’s muntjac showed that ESW was 10% wider in 2008 than in 2010 and roe deer ESW in 2009 was 15% wider than in 2010 possible due to weather impacts. Results of the ESW of analysis design “block” suggest that block configuration and vegetation cover might lead to different detectability of deer among forest blocks as shown for Reeve’s muntjac and roe deer in block Mun. The pooled mean ESW of analysis design “block” for the first six blocks (Cro to Lyn) was about 15% wider than the ESW of block Mun. Forest block Mun differed in understorey cover from the other forest blocks. Here bramble cover was higher than compared with the other six forest blocks (K. Wäber, unpublished). Using detection function stratified by “year” therefore might over- or underestimate deer density in individual blocks.

As shown by Hemami et al. (2007) I found significant differences in ESW between open, dense and mature habitats. The ESW of the detection function was widest in open habitats and narrower in dense and mature habitats for both deer species (muntjac: 53% and 66% respectively of that in open habitats; roe deer: 54% and 68% respectively of that in open habitats). ESW differed significantly between deer species but percentage of ESW reduction was similar in dense and mature habitats. Percentage of ESW reduction differed between this study and the ESW found by Hemami et al. (2007) (ESW of dense and mature habitat 71% and 74% respectively from that in open habitats). These differences might be due to survey designs as Hemami et al. (2007) only investigated habitat differences of the ESW within one forest block and pooled observations for Reeve’s muntjac and roe deer, and in this study I pooled habitats across seven forest blocks separately for each deer species given a more robust estimate of detection distances across the forest. Only the ESW for the detection function of open habitats showed broader CI’s than analyses design “year” and “block”. In addition I used a laser rangefinder whilst Hemami et al. (2007) used a graticule which may have greater error for more distant deer.

Encounter rate, Cluster size and sampling intensity

The high encounter rate variance in some forest blocks found for both deer species in all three analyses designs suggests that either deer were observed at or close by favourable areas (e.g. feeding grounds) or too few transects were surveyed within forest blocks as implied by Gill et al. (1997).

Reeve’s muntjac were generally solitary living individuals and are not living in family groups over the winter unlike roe deer (Chapman et al., 1993) suggesting that using detection distance of single individuals would reduce bias in cluster size on density estimates for Reeve’s muntjac.

Although the accuracy of the deer density estimates by using distance sampling thermal imaging will be unknown and has been questioned in other studies (Smart et al., 2004), Hemami et al. (2007) showed that for roe deer similar density estimates were obtained when using distance sampling thermal imaging and pellet-group accumulation plots (FAR). In this study I obtained similar density estimates for roe deer and Reeve’s muntjac when using distance sampling thermal imaging and a drive census in two forest blocks (K. Wäber, unpublished).

I have shown that thermal imaging distance sampling is a robust technique to obtain reliable estimations of deer densities at landscape-scale. Distance sampling thermal imaging will help to understand the impacts of local deer densities on biodiversity and control the effectiveness of deer management. More research is needed to investigate the performance of thermal imaging distance sampling in a range of landscapes such as farmland with small woods or broadleaf forests. The impact of weather, deer behaviour and time of observation on the detection of deer needs also further investigation to further improve density estimates.

References

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. (2001) *Introduction to Distance Sampling - Estimating abundance of biological populations,* Oxford University Press, Oxford.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. (2004) *Advanced Distance Samplling - Estimating abundance of biological populations,* Oxford University Press, Oxford.

Campbell, D., Swanson, G. M. & Sales, J. (2004) Comparing the precision and cost-effectiveness of faecal pellet group count methods. *Journal of Applied Ecology,* **41,** 1185-1196.

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.

Corbet, G. B. & Harris, S. (1991) *Handbook of British Mammals,* Blackwell Scientific, Oxford, UK.

Cote, 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.

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.

Feber, R. E., Brereton, T. M., Warren, M. S. & Oates, M. (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. *Forestry,* **74,** 271-276.

Flowerdew, J. R. & Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry,* **74,** 277-287.

Focardi, S., De Marinis, A. M., Rizzotto, M. & Pucci, A. (2001) Comparative evaluation of thermal infrared imaging and spotlighting to survey wildlife. *Wildlife Society Bulletin,* **29,** 133-139.

Focardi, S., Isotti, R., Pelliccioni, E. R. & Iannuzzo, D. (2002a) The use of distance sampling and mark-resight to estimate the local density of wildlife populations. *Environmetrics,* **13,** 177-186.

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

Gill, R. M. A. & Beardall, V. (2001) The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry,* **74,** 209-218.

Gill, R. M. A. & Fuller, R. J. (2007) The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis,* **149,** 119-127.

Gill, R. M. A., Thomas, M. L. & Stocker, D. (1997) The use of portable thermal imaging for estimating deer population density in forest habitats. *Journal of Applied Ecology,* **34,** 1273-1286.

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. *European Journal of Wildlife Research,* **51,** 19-24.

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.

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. *Mammal Review,* **37,** 246-254.

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.

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.

Marini, F., Franzetti, B., Calabrese, A., Cappellini, S. & Focardi, S. (2009) Response to human presence during nocturnal line transect surveys in fallow deer (*Dama dama*) and wild boar (*Sus scrofa*). *European Journal of Wildlife Research,* **55,** 107-115.

Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A. & Peace, A. J. (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology,* **38,** 349-363.

McShea, W. J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology,* **81,** 228-238.

McShea, W. J. & Rappole, J. H. (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology,* **14,** 1161-1170.

Milner, J. M., Bonenfant, C., Mysterud, A., Gaillard, J. M., Csanyi, S. & Stenseth, N. C. (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology,* **43,** 721-734.

Pollard, E. & Cooke, A. S. (1994) Impact of muntjac deer *Munitacus reevesi* on egg-laying sites of the white admiral butterfly *Ladoga camilla* in a Cambridgeshire Wood. *Biological Conservation,* **70,** 189-191.

Smart, J. C. R., Ward, A. I. & White, P. C. L. (2004) Monitoring woodland deer populations in the UK: an imprecise science. *Mammal Review,* **34,** 99-114.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. & Burnham, K. P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology,* **47,** 5-14.

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

Ward, A. I., White, P. C. L. & Critchley, C. H. (2004) Roe deer *Capreolus capreolus* behaviour affects density estimates from distance sampling surveys. *Mammal Review,* **34,** 315-319.

Appendix

Table A4.1a. Open habitat (open areas, felled areas, restock) results of density estimation for Reeve's muntjac (*n* = 212) in Thetford Forest in 2008-10 in analysis design "habitat". Deer density is stratified by forest block within years.

Block	Year	Sample size (*n*)	Model fitted	Effective strip width ESW [m]	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Density SE	Components of variation [%]		
						C-sq	*p*					P	*n*/L	E(S)
Cro	2008	6	Hazard rate	78.7 (63.3-97.9)	0.47 (11.1)	0.04	0.90	0.8 (0.3-2.3)	1.2 (1.2-1.3)	12.8 (4.8-34.6)	5.4	7.1	92.6	0.4
	2009	2						0.4 (0.1-1.7)		6.4 (1.6-26.1)	4.2	2.8	97.3	0.1
	2010	11						0.8 (0.3-2.5)		12.3 (3.9-38.8)	7.3	3.5	96.3	0.2
Did	2008	5						0.9 (0.3-2.2)		13.3 (5.3-33.7)	5.6	7.0	92.7	0.4
	2009	2						0.4 (0.1-2.1)		6.9 (1.5-31.8)	4.2	3.3	96.6	0.2
	2010	8						0.9 (0.3-2.5)		13.7 (5.0-37.8)	5.9	6.7	92.9	0.3
Elv	2008	2						0.6 (0.1-6.1)		9.7 (1.0-91.7)	8.0	1.8	98.1	1.0
	2009	3						2.8 (1.5-5.2)		30.9 (0.7-1468.5)	35.3	0.9	99.0	0.1
	2010	12						1.7 (0.5-5.2)		25.8 (8.3-80.3)	14.0	4.2	95.6	0.2
Har	2008	22						2.2 (1.1-4.3)		34.3 (17.2-68.6)	11.7	10.6	88.9	0.5
	2009	21						2.8 (1.5-5.2)		42.7 (22.2-82.3)	13.7	12.0	87.4	0.6
	2010	13						0.8 (0.3-1.8)		11.7 (4.9-27.7)	5.0	6.7	92.9	0.3

Table A4.1a.

HiLo	2008	4	0.5 (0.2-1.3)	8.4 (3.5-19.7)	3.4	7.4	92.2	0.4
	2009	2	0.2 (0.1-1.4)	3.6 (0.6-22.2)	3.7	1.1	98.8	0.1
	2010	4	0.4 (0.1-1.1)	5.6 (1.8-17.1)	3.1	3.9	95.1	0.2
Lyn	2008	28	2.1 (1.7-2.6)	32.3 (23.6-44.3)	5.1	48.5	49.0	2.5
	2009	18	1.3 (0.7-2.5)	20.5 (10.4-40.4)	6.9	10.8	88.6	0.6
	2010	15	0.8 (0.4-1.5)	12.1 (6.2-23.5)	4.0	11.1	88.3	0.6
Mun	2008	20	3.2 (1.8-5.7)	49.1 (26.7-90.0)	14.3	14.5	84.7	0.7
	2009	8	1.9 (0.9-4.2)	29.4 (13.4-64.8)	10.5	9.6	89.9	0.5
	2010	6	1.1 (0.5-2.8)	17.5 (7.2-42.7)	6.9	8.0	91.6	0.4

Table A4.1b. Mature stand (pole, mature pine, mature broadleaf) results of density estimation for Reeve’s muntjac (*n* = 1475).

Block	Year	Sample size (*n*)	Model fitted	Effective strip width ESW [m]	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Density SE	Components of variation [%]		
						C-sq	*p*					P	*n*/L	E(S)
Cro	2008	42	Hazard rate	51.9 (49.5-54.4)	0.54 (2.4)	0.97	0.001	1.2 (0.7-2.0)	1.2 (1.1-1.2)	26.2 (15.1-45.4)	7.0	0.8	99.1	0.8
	2009	35						1.0 (0.7-1.5)		22.3 (14.7-33.8)	4.5	1.4	98.4	0.2
	2010	40						1.1 (0.8-1.6)		25.1 (17.1-37.0)	4.8	1.7	98.1	0.2
Did	2008	109						2.5 (1.9-3.2)		55.7 (42.7-72.6)	7.0	3.7	95.8	0.5
	2009	128						2.6 (1.9-3.5)		58.7 (43.4-79.5)	8.3	2.9	96.7	0.4
	2010	96						2.4 (1.7-3.2)		53.5 (39.1-73.1)	7.7	2.9	96.8	0.4
Elv	2008	23						1.0 (0.6-1.6)		21.4 (13.0-35.2)	4.9	1.2	98.7	0.2
	2009	17						0.7 (0.4-1.4)		16.2 (8.2-31.8)	5.0	0.6	99.3	0.1
	2010	13						0.5 (0.3-1.1)		12.2 (6.2-24.1)	3.8	0.6	99.3	0.1
Har	2008	155						3.7 (2.9-4.8)		84.3 (65.8-107.9)	10.0	4.2	95.3	0.5
	2009	102						2.9 (2.1-3.9)		64.8 (47.8-87.9)	9.4	2.8	96.8	0.4
	2010	74						2.1 (1.5-3.0)		48.2 (33.6-69.2)	8.3	2.0	97.7	0.3
HiLo	2008	40						0.9 (0.5-1.7)		21.3 (12.1-37.4)	5.7	0.8	99.1	0.1
	2009	29						0.6 (0.3-0.9)		12.4 (7.5-20.5)	3.0	1.0	98.9	0.1
	2010	28						0.6 (0.4-0.9)		13.9 (9.2-21.1)	2.7	1.5	98.2	0.2

Table A4.1b.

Lyn	2008	100	1.2 (0.9-1.5)	26.3 (20.3-34.0)	3.3	3.7	95.9	0.5
	2009	120	1.2 (1.0-1.6)	27.5 (21.5-35.2)	3.3	4.0	95.5	0.5
	2010	92	1.2 (0.9-1.6)	27.9 (21.2-36.8)	3.8	3.2	96.3	0.4
Mun	2008	98	1.5 (1.3-1.7)	33.3 (28.3-39.1)	2.6	9.6	89.2	1.2
	2009	70	1.5 (1.0-2.1)	33.0 (22.6-48.2)	5.9	1.8	97.9	0.2
	2010	64	2.3 (1.4-3.8)	52.6 (31.8-87.1)	12.5	1.1	98.8	0.1

Table A4.1.c. Dense habitat (pre-thicket and thicket) results of density estimation for Reeve's muntjac (n = 300).

Block	Year	Sample size (*n*)	Model fitted	Effective strip width ESW [m]	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Density SE	Components of variation [%]		
						C-sq	*p*					P	*n*/L	E(S)
Cro	2008	17	Hazard rate	41.4 (37.5-45.7)	0.46 (5.0)	0.29	0.10	0.9 (0.5-1.7)	1.2 (1.2-1.3)	27.5 (14.9-50.9)	8.2	2.9	96.7	0.4
	2009	9						0.4 (0.2-0.8)		11.8 (6.2-22.4)	3.7	2.5	97.1	0.4
	2010	9						0.3 (0.2-0.5)		8.6 (4.7-15.9)	2.6	2.7	96.8	0.4
Did	2008	23						1.9 (1.1-3.2)		55.8 (32.9-94.7)	14.3	3.8	95.6	0.6
	2009	15						1.4 (0.6-3.2)		41.2 (18.3-92.9)	16.2	1.6	98.1	0.3
	2010	12						2.3 (1.6-3.3)		67.2 (47.2-95.5)	10.3	10.8	87.5	1.6
Elv	2008	6						0.6 (0.2-1.4)		16.0 (6.3-40.9)	7.0	1.3	98.5	0.2
	2009	5						0.4 (0.1-1.0)		10.0 (3.4-29.4)	5.1	1.0	98.9	0.2
	2010	5						0.4 (0.2-0.8)		10.2 (4.2-24.5)	4.1	1.5	98.2	0.2
Har	2008	47						2.5 (1.5-4.3)		73.5 (43.1-125.5)	18.9	3.8	95.6	0.6
	2009	34						1.9 (1.1-3.1)		54.1 (32.5-89.8)	13.1	4.3	95.0	0.7
	2010	22						1.2 (0.5-2.5)		33.5 (15.2-73.7)	12.9	1.7	98.0	0.3
HiLo	2008	9						0.6 (0.3-1.2)		17.8 (8.9-35.8)	6.0	2.3	97.4	0.4
	2009	5						0.3 (0.1-0.7)		8.0 (3.1-20.9)	3.9	1.1	98.7	0.2
	2010	4						0.2 (0.1-0.6)		6.4 (2.5-16.7)	3.0	1.2	98.6	0.2

Table A4.1.c.

Lyn	2008	23	0.9 (0.5-1.7)	26.2 (13.5-50.8)	8.6	2.3	97.3	0.4
	2009	19	0.7 (0.4-1.4)	21.4 (11.5-39.9)	6.7	2.6	97.0	0.4
	2010	11	0.5 (0.3-0.9)	15.5 (9.6-25.3)	3.7	4.4	94.9	0.7
Mun	2008	18	0.9 (0.5-1.4)	24.9 (15.2-40.8)	6.0	4.4	95.0	0.7
	2009	4	0.6 (0.2-1.4)	16.2 (6.6-39.8)	6.7	1.5	98.3	0.2
	2010	2	0.2 (0.1-0.7)	5.5 (1.5-20.1)	3.6	0.6	99.3	0.1

Table A4.2.a. Open habitat results of density estimation for roe deer (*n* = 187) in Thetford Forest in 2008-10 in analysis design “habitat”. Deer density is stratified by forest block within years.

Block	Year	Sample size (*n*)	Model fitted	Effective strip width ESW [m]	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Density SE	Components of variation [%]		
						C-sq	*p*					P	*n*/L	E(S)
Cro	2008	0	Hazard rate	103.5 (89.9-119.2)	0.59 (7.1)	0.54	0.01	-	2.1 (2.0-2.3)	0	-	-	-	-
	2009	3						0.6 (0.1-3.0)		12.8 (2.7-59.8)	9.4	0.9	98.8	0.3
	2010	16						1.2 (0.6-2.4)		23.7 (11.2-50.1)	8.7	3.8	95.1	1.1
Did	2008	7						1.2 (0.4-3.3)		24.7 (9.0-68.0)	11.2	2.5	96.8	0.7
	2009	5						1.1 (0.2-6.1)		22.7 (4.2-122.7)	15.4	1.1	98.6	0.3
	2010	0						-		0	-	-	-	-
Elv	2008	2						0.6 (0.1-11.7)		12.8 (0.7-237.4)	14.8	0.4	99.5	0.1
	2009	0						-		-	-	-	-	-
	2010	6						0.8 (0.3-2.7)		17.0 (5.3-55.1)	9.5	1.6	97.9	0.5
Har	2008	4						0.4 (0.2-1.1)		8.3 (2.0-22.6)	4.2	2.0	97.4	0.6
	2009	5						0.7 (0.2-2.0)		13.5 (4.4-41.0)	7.5	1.6	97.9	0.5
	2010	7						0.4 (0.2-1.1)		8.3 (3.1-22.4)	4.1	2.1	97.3	0.6
HiLo	2008	2						0.3 (0.1-0.9)		5.5 (1.7-18.5)	3.3	1.5	98.1	0.4
	2009	4						0.5 (0.2-1.3)		9.4 (3.2-27.4)	5.1	1.8	97.7	0.5
	2010	1						0.1 (0.1-0.6)		1.8 (0.3-11.4)	1.9	0.5	99.4	0.1

Table A4.2.a.

Lyn	2008	31		2.3 (1.6-3.4)		47.3 (31.7-70.7)	9.4	13.0	83.1	3.8
	2009	30		2.2 (1.5-3.2)		45.1 (30.7-66.4)	8.6	14.2	81.7	4.2
	2010	23		1.2 (0.8-1.9)		25.0 (15.8-39.6)	5.7	9.9	87.1	2.9
Mun	2008	21		3.3 (1.5-7.6)		68.2 (29.6-157.2)	27.1	3.2	95.8	1.0
	2009	17		4.1 (2.8-5.9)		82.8 (56.1-122.2)	14.8	16.0	79.3	4.7
	2010	4		0.8 (0.2-1.8)		15.4 (6.5-36.8)	5.8	3.6	95.3	1.1

Table A4.2b. Mature stand (pole, mature pine, mature broadleaf) results of density estimation for roe deer (*n* = 508).

Block	Year	Sample size (*n*)	Model fitted	Effective strip width ESW [m]	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Density SE	Components of variation [%]		
						C-sq	*p*					P	*n*/L	E(S)
Cro	2008	13	Hazard rate	70.2 (65.2-75-5)	0.65 (3.7)	1.46	0.001	0.4 (0.2-0.6)	1.8 (1.7-1.9)	9.2 (5.9-14.5)	2.0	2.9	96.3	0.9
	2009	22						0.6 (0.3-1.2)		16.0 (8.3-30.8)	5.2	1.3	98.3	0.4
	2010	13						0.4 (0.9-1.6)		9.9 (6.0-16.2)	2.4	2.4	96.9	0.7
Did	2008	31						0.7 (0.5-1.0)		18.7 (13.3-26.4)	3.1	5.2	93.3	1.6
	2009	22						0.5 (0.2-0.9)		11.5 (5.6-23.6)	3.9	1.2	98.5	0.4
	2010	12						0.3 (0.2-0.6)		7.6 (3.8-15.1)	2.4	1.4	98.2	0.4
Elv	2008	9						0.4 (0.2-0.9)		9.5 (3.9-23.1)	4.0	0.8	98.9	0.2
	2009	4						0.2 (0.1-0.4)		4.3 (1.8-10.4)	1.8	0.8	98.9	0.2
	2010	7						0.3 (0.1-0.8)		7.5 (2.7-20.4)	3.6	0.6	99.2	0.2
Har	2008	9						0.2 (0.1-0.4)		5.6 (2.9-10.7)	1.8	1.4	98.2	0.4
	2009	10						0.3 (0.1-0.8)		7.2 (2.7-19.6)	3.6	0.6	99.3	0.2
	2010	4						0.1 (0.1-0.3)		3.0 (1.2-7.6)	1.4	0.6	99.2	0.2
HiLo	2008	14						0.3 (0.2-0.6)		8.5 (4.5-16.1)	2.6	1.5	98.1	0.4
	2009	5						0.1 (0.1-0.2)		2.4 (1.1-5.3)	0.9	0.9	98.8	0.3
	2010	6						0.1 (0.1-0.4		3.4 (1.2-9.9)	1.8	0.5	99.4	0.2

Table A4.2b.

Lyn	2008	30	0.4 (0.2-0.6)	9.0 (5.2-15.5)	2.5	1.8	97.6	0.6
	2009	52	0.5 (0.4-0.8)	13.6 (9.2-19.8)	2.4	3.9	94.9	1.2
	2010	38	0.5 (0.3-0.8)	13.5 (8.6-21.2)	3.0	2.8	96.3	0.9
Mun	2008	81	1.2 (0.9-1.6)	31.3 (23.0-42.6)	4.7	6.1	92.0	1.8
	2009	57	1.2 (0.9-1.6)	30.6 (22.2-42.2)	4.7	5.8	92.4	1.8
	2010	69	2.5 (1.3-5.0)	64.6 (32.3-129.5)	21.4	1.3	98.4	0.4

Table A4.2c. Dense habitat (pre-thicket and thicket) results of density estimation for roe deer (*n* = 126).

Block	Year	Sample size (*n*)	Model fitted	Effective strip width ESW [m]	Detection probability P (CV(P) [%]	Goodness of fit (Cramer-von Mises)		Encounter rate n/L [groups/km]	Group size E(S) (95% CI)	Density [deer km^{-2}] (95% CI)	Density SE	Components of variation [%]		
						C-sq	*p*					P	*n*/L	E(S)
Cro	2008	7	Hazard rate	55.9 (47.7-65.4)	0.47 (8.0)	0.50	0.03	0.4 (0.2-1.0)	1.8 (1.6-1.9)	12.4 (4.9-31.4)	5.7	3.0	96.2	0.8
	2009	8						0.4 (0.2-0.8)		11.5 (4.9-26.7)	4.9	3.6	95.6	0.6
	2010	6						0.2 (0.1-0.4)		6.3 (2.8-14.0)	2.6	2.6	62.4	35.0
Did	2008	6						0.5 (0.2-1.2)		15.9 (6.8-37.0)	6.7	3.6	95.5	0.9
	2009	2						0.2 (0.1-0.8)		6.0 (1.4-25.4)	4.5	1.1	98.6	0.3
	2010	6						1.2 (0.5-2.7)		36.7 (15.7-85.9)	13.5	4.7	94.1	1.2
Elv	2008	2						0.2 (0.1-0.8)		5.8 (1.3-26.7)	4.4	1.1	98.6	0.3
	2009	4						0.3 (0.1-0.9)		8.8 (2.7-28.4)	4.9	2.0	97.4	0.5
	2010	3						0.2 (0.1-0.9)		6.7 (1.5-29.8)	5.0	1.2	98.6	0.3
Har	2008	3						0.2 (0.1-0.4)		5.1 (1.9-13.9)	2.5	2.7	96.6	0.7
	2009	0						-		0	-	-	-	-
	2010	2						0.1 (0.1-0.4)		3.3 (0.8-13.8)	2.5	1.1	98.6	0.3
HiLo	2008	4						0.3 (0.1-0.8)		8.7 (2.8-26.5)	4.8	2.1	97.4	0.5
	2009	2						0.1 (0.1-0.4)		3.5 (0.9-13.1)	2.4	1.3	98.3	0.3
	2010	2						0.1 (0.1-0.4)		3.5 (0.9-13.7)	2.5	1.3	98.4	0.3

Table A4.2c.

Lyn	2008	13	0.5 (0.3-0.8)	16.2 (9.6-27.3)	4.2	9.4	88.2	2.4
	2009	10	0.4 (0.2-0.9)	12.3 (5.1-30.0)	5.7	3.0	96.2	0.8
	2010	7	0.3 (0.1-0.9)	10.8 (4.1-28.6)	5.4	2.5	96.8	0.6
Mun	2008	19	0.9 (0.6-1.5)	28.8 (17.4-47.6)	7.2	10.3	87.1	2.6
	2009	9	1.3 (0.7-2.2)	39.8 (22.6-70.0)	10.4	9.3	88.4	2.3
	2010	11	1.0 (0.6-1.9)	33.0 (17.9-60.9)	9.6	7.5	90.6	1.9

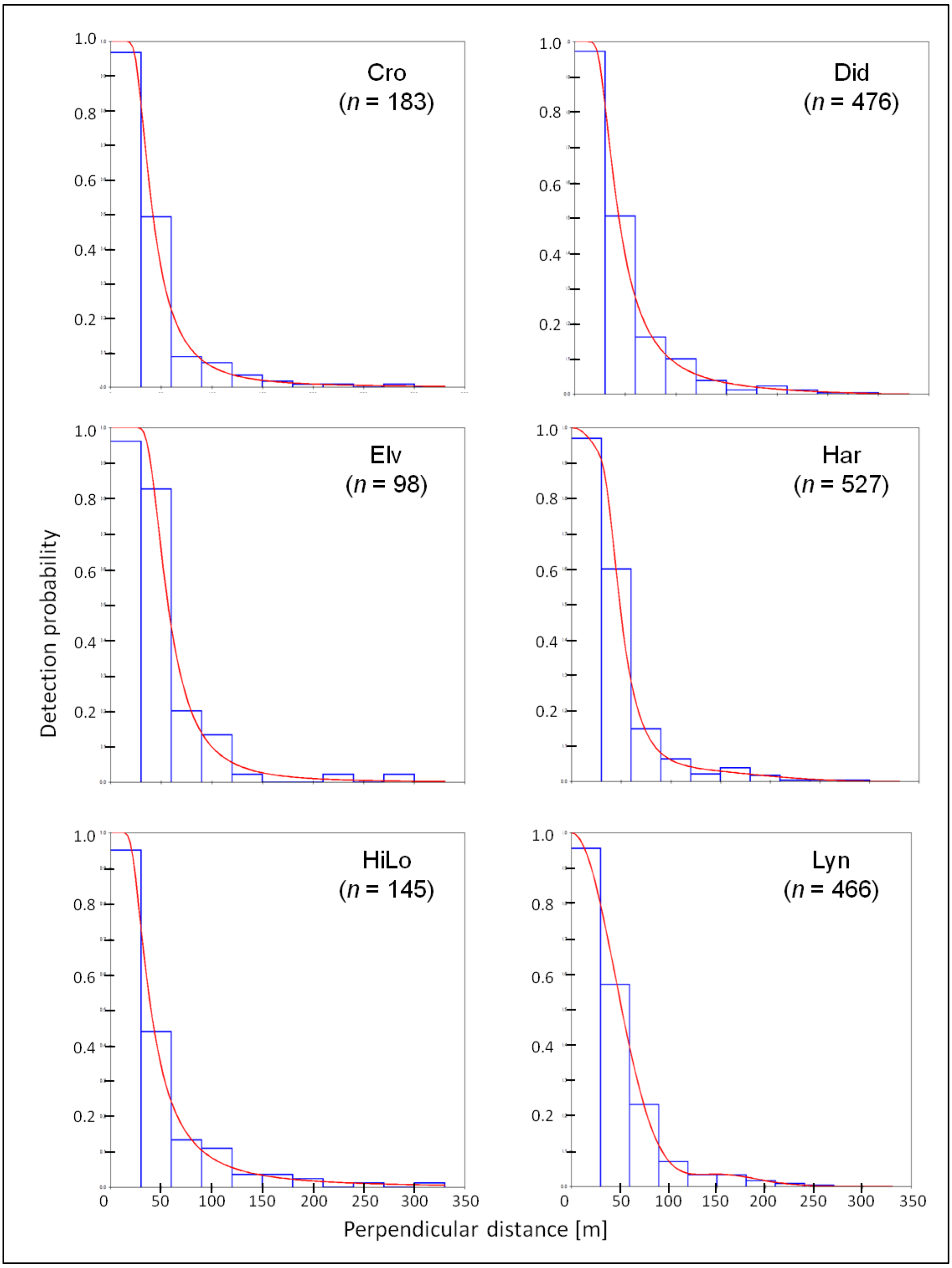

Fig. A4.1. Distribution of perpendicular distances and probability of detection obtained by observation stratified by block for Reeve’s muntjac.

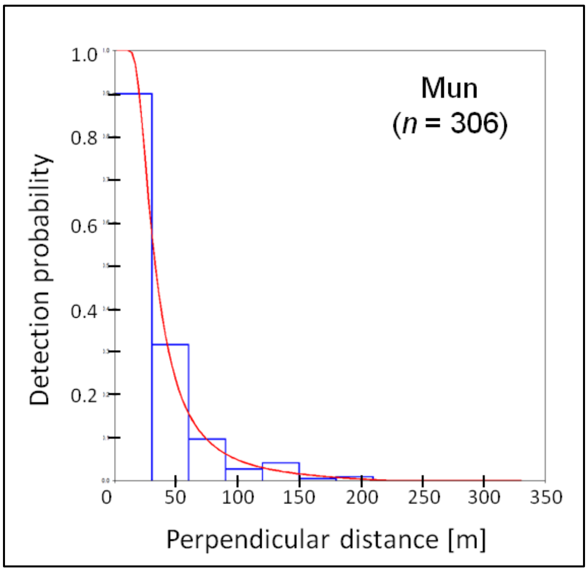

Fig. A4.1. (continued).

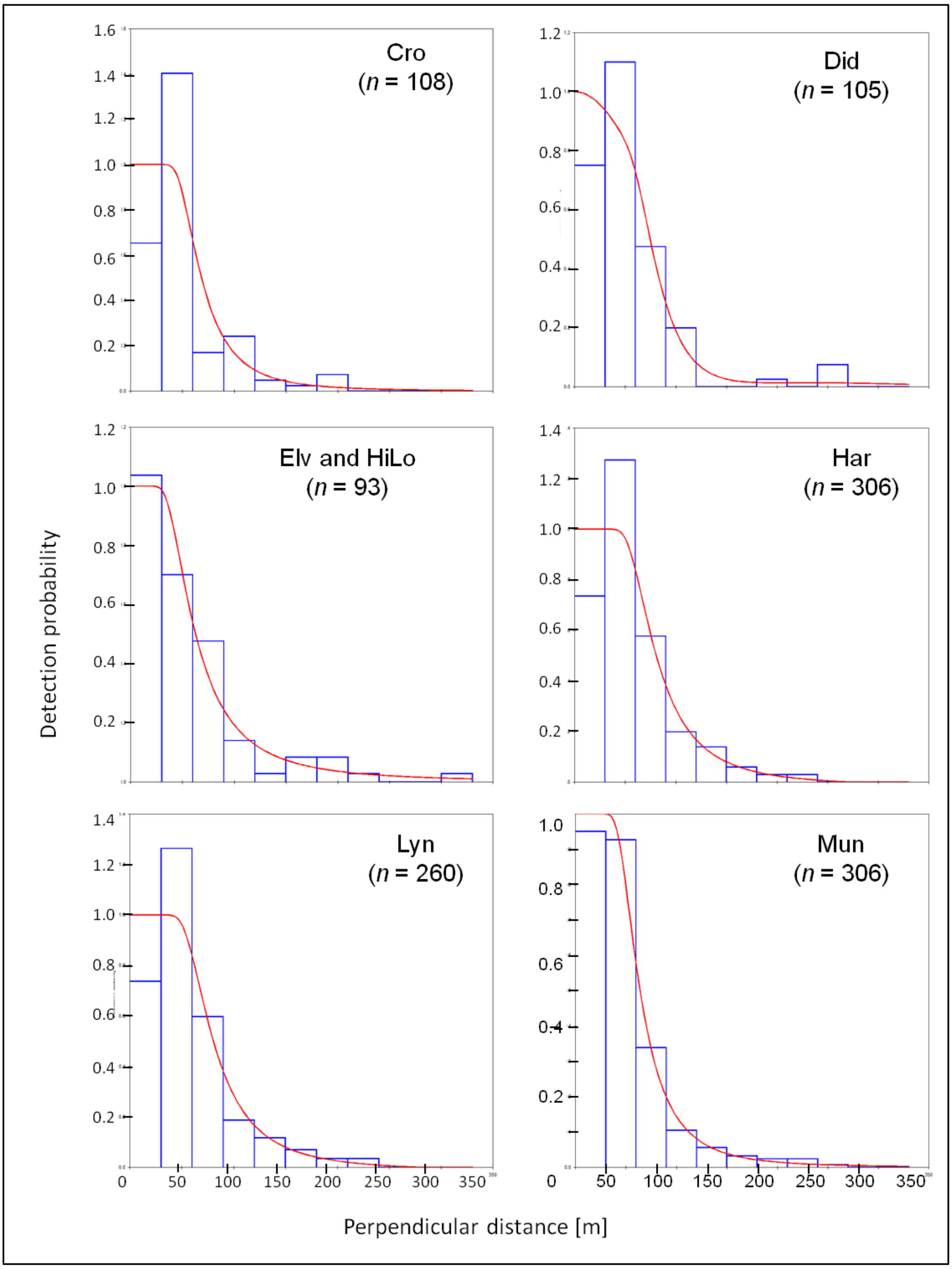

Fig. A4.2. Distribution of perpendicular distances and probability of detection obtained by observation stratified by block for roe deer.

Chapter Five

Roe deer *Capreolus capreolus* and Reeve’s muntjac *Muntiacus reevesi* source-sink dynamics within a forested landscape

Abstract

Deer management plans are often limited by landownership units, however impacts of deer management across borders or even across landscapes should be taken into account. Knowledge of source-sink dynamics within and across landscapes is important to effectively manage deer and reduce their impacts, but is poorly understood. Here I present a novel approach to calculate source-sink dynamics of roe deer *Capreolus capreolus* and Reeve's muntjac *Muntiacus reevesi* across seven forest blocks (totalling 120 km^{-2}) of a lowland pine forest in Eastern England, UK in 2008/09 and 2009/10. Annual changes in deer numbers, and estimates of fertility, juvenile survival and mortality due to culling were combined in a model to examine whether forest blocks have potential to act as sources (i.e. that contribute net emigrant recruits to the surrounding landscape) or sinks (that absorb dispersing individuals from surrounding areas). For roe deer estimated densities in 2008-2010 stayed stable in four forest blocks, increased in one forest block from 2008 to 2009 and, decreased in two forest blocks from 2008 to 2010. Muntjac densities were stable in five forest blocks and decreased in two forest blocks from 2008 to 2010. Roe deer potential population growth (defined as net production minus cull) was positive in all forest blocks for both 2008/09 and 2009/10. In 2008/09 the difference between potential density (deer density in year 1 plus production minus cull) and the observed density in year two was positive in five forest blocks (i.e. production was not recruited locally) and negative in one forest block (i.e. local recruitment was not produced locally) in 2008/09 and in 2009/10. Thus, one forest block in each year was a potential sink whereas the other six were potential sources. For muntjac (kid survival 65% and 70%) potential population growth was negative (cull exceeded production) in only one forest block in both years. This forest block was a weak source (< 20 animals emigrating) for muntjac when assuming a kid survival of 65% or 70% in 2009/10. Potential net emigration rates from individual forest blocks ranged from < 0 to several hundred for both roe deer and muntjac. Across the area of forest considered, potentially 430-440 roe deer and between 1200 to 1500 muntjac may have moved out into the wider landscape, each year. This is considerably greater than can be accounted for by road mortality or game management on neighbouring estates and likely represents a net export of dispersing deer, contributing to population growth and range expansion in the region. For both species, a cull of more than 50% of the deer population would be necessary to balance the annual production in each forest block. In 2008/9-2009/10, the cull intensity ranged from 8.1% to 48.9% of the total deer population per block for roe deer and 3.3% to 71.2% for Reeve's muntjac. Source-sink systems can be detected between landscapes and ownership boundaries with different management objectives; such understanding

has the potential to improve deer management at the wider landscape scale. Identifying source-sink dynamics at landscape scales can enable deer managers to concentrate culling effort on source areas in order to more successfully reduce deer numbers at landscape scale.

Introduction

Increasing deer numbers and spread are of increasing concern in Europe and North America (Dolman and Wäber, 2008). Deer numbers are still increasing in Europe (Ward, 2005, Suominen and Danell, 2006). In Europe deer cause about 507,000 road traffic accidents annually costing $ 1 billion in material damage as estimated in 1996 (Bruinderink and Hazebroek, 1996). In the UK deer are increasingly involved in road traffic accidents (RTA's) resulting in about 46,000 injuries each year and costing up to 40 million pound each year (Langbein, 2008). Increasing deer populations will also raise damage on agricultural and forestry crop (Gill and Beardall, 2001, Putman and Moore, 1998, Scott et al., 2009). Crop damage may reach between £1.1 million and £5.6 million per annum in England (Wilson, 2003). Defra is planning to establish around 60,000 ha of short rotation coppice (energy crops e.g. willow, hazel) within the UK (Defra, 2009) which are prone to deer browsing. In addition, Defra aims to increase woodfuel production by increasing the area of woodland in active management, this will be problematic in regions with high deer densities. Deer impacts on biodiversity due to grazing and browsing are widely recognised (Fuller et al., 2007, Barrett and Stiling, 2006, Cote et al., 2004, Dolman and Wäber, 2008). Through their impacts deer alter and reduce under-storey structure affecting under-storey dependent species including invertebrates (Feber et al., 2001, Allombert et al., 2005b), birds (Fuller, 2001, Holt et al., 2010) and small mammals (Flowerdew and Ellwood, 2001). Therefore, it is increasingly important to manage deer populations in order to control impacts and balance competing interests. To be publicly accountable and defensible in the public eye, such management must be based on sound and objective evidence.

Limited knowledge is available as to how deer densities differ among landscapes and how they are affected by habitat distribution and suitability, gradients of fertility and different cull pressures in different parts of the landscape. Most of our current understanding of deer management is based on research into the population dynamics of long-term monitored unharvested or fenced in populations (e.g. Kjellander et al. (2006) and Pettorelli et al. (2002)). Although, deer density in an area may be stable over a relatively long time period, suggesting that there has been no change in population size under the current management regime, this does not mean that the control measures are balancing population productivity; the area may still be a net exporter or importer of individuals (Pulliam, 1988, Runge et al., 2006). Assessing the impact of cull management on population growth and emigration-immigration or source-sink dynamics is therefore necessary to be able to successfully control population densities across wider landscapes. This knowledge will be useful to understand the non-linear relationship between biodiversity responses (Gordon et al., 2004) and exact deer densities.

Decisions in cull management are usually made on an annual basis often incorporating habitat damage, changes in deer density or deer population growth when determining cull targets. In France population-habitat-relationships are used to make deer management decisions which are based on monitoring temporal changes of ecological indicators such as deer performance, habitat quality and herbivore impacts (Morellet et al., 2007). If habitat damage due to deer continues the cull targets are usually increased. However, even if population density is stable within a landscape habitat damage may vary between years for example due to hard winters and increased immigration from neighbouring areas. Thus, cull targets may be increased the following year even though the population size is unchanged. Although, higher culling effort concentrating on areas with high crop or forest damage may be beneficial locally it may not reduce deer numbers across wider scales and instead may only shift deer impacts on a spatial scale. In Britain an approach for predictive deer management has been developed incorporating deer population size, sex ratio, age class distribution, fertility, mortality and habitat damage using a Leslie Matrix model (Mayle, 1996) to predict changes in population size; however, this approach is not widely used. This approach may be a useful tool to identify if population numbers are increasing or decreasing in a certain area but it is still unclear if this area may be acting as net exporter of deer and therefore add additional pressure on the deer management in neighbouring areas due an increase in deer numbers in these areas. Thus there is a need for management based in sound understanding of deer numbers.

Deer inhabit extensive heterogeneous landscapes and populations are linked by dispersal. This is especially evident for the wide ranging red and fallow deer (*Cervus elaphus* and *Dama dama*), but even the more territorial roe deer *Capreolus capreolus* and Reeve's muntjac *Muntiacus reevesi* show dispersal and recruitment at landscape scale. As deer movements do not stop at ownership boundaries, the effects of local deer management may be offset by inward migration and recruitment from neighbouring areas. This has been recognised as a particular problem in conservation management as a successful reduction in deer numbers is necessary to limit deer impacts on biodiversity.

Here I develop and present a novel approach to investigate the effectiveness of deer management using annual production, mortality and density estimates of a roe deer and Reeve's muntjac subpopulation to explore possible emigration-immigration or source-sink dynamics in a forested landscape. Data were obtained in seven forest blocks covering 120 km^2 in 2008/09 and 2009/10. I addressed the following questions:

(1) Do population density and population growth of roe deer and Reeve's muntjac differ among forest blocks under the same management strategy?

(2) Does the current magnitude of cull management exceed the population production? What does this imply for potential population trends?

(3) How do potential population trends predicted from productivity less culling relate to observed year to year changes in actual numbers? Therefore, is the forest a potential net exporter or importer of deer?

For the first time in any European landscape, this approach may allow to assess the effectiveness of deer cull management in terms of whether local management units are contributing to reduced deer abundance in the wider landscape, or instead are acting as sources for further population increase and range expansion.

Methods

(a) Study area

Thetford Forest (195 km^2), the largest lowland commercial pine forest in the UK, is located in the Breckland region of East England (52°30´N, 0°60´W). The region is characterised by semi-continental climate and sandy, nutrient-poor soils (Dolman and Sutherland, 1992). The forest is dominated by a mosaic of growth stages with Corsican pine (*Pinus nigra*) (59%) and Scots pine (*Pinus sylvestris*) (15%) being the dominant tree species, other conifers comprising 5% and deciduous tree species 10% of the area. The forest is managed by rotational clear-felling and replanting of even-aged stands (Eycott et al., 2006). The forest is subdivided into twelve deer management units (DMU's) (mean area = 15.6 ± 10.2 km^2 *SD*, range 4.5 km^2 to 34.7 km^2) by roads. Distance sampling thermal imaging has been carried out in seven of the DMU's, across a total area of 120 km^2.

Four deer species are resident in Thetford Forest: roe deer, red deer, Reeve's muntjac and fallow deer. Roe deer and Reeve's muntjac are wide-spread, with densities ranging from 3 km^{-2} to 42 km^{-2} and from 11 km^{-2} to 71 km^{-2} respectively in 2008-10. Red deer are widespread at the forest at low numbers (density < 5 km^{-2} in 2008-10), whereas fallow deer reaches higher densities in the Southern blocks of the forest (density between 5 km^{-2} and 10 km^{-2}) but are still scarce in the Northern blocks (density < 2 km^{-2}).

(b) Cull data and fertility

Roe deer and Reeve's muntjac cull data from 2008-10 were obtained from a database managed by FC providing the date shot, location (compartment or GPS), sex, age (only roe deer: juvenile, yearling, adult), body mass, reproductive status of females (presence and number of embryos, *corpora lutea*, milk) of each culled individual.

(c) Analysis

The following information are necessary to establish whether a forest block is a potential source or sink:

- potential population growth, that requires knowing:
    - annual production,
    - culled numbers,
- actual population trend, that requires knowing:
    - observed deer density in year 1 (estimated by distance sampling), and
    - observed deer density in year 2 (estimated by distance sampling).

To estimate the potential numbers of deer that may be immigrating or emigrating from a forest block, I subtracted the potential density in year 2 (observed deer density in year 1 plus annual production minus cull) from the observed density in year 2. A positive value showing that the observed density in year 2 was lower than the potential density that could have been achieved, indicating potential net emigration of deer. Thus, a positive value indicates that the forest block may act as a source. Conversely, a negative value indicated that net immigration is likely to have occurred as the observed density in year 2 was higher than the potential density that could have been achieved through *in situ* production in the face of the level of cull management that was imposed.

It should be emphasised that this method measures potential for source or sink dynamics, and does not prove that these have occurred. A potential net source, may either result in emigration and dispersal of individuals to the adjoining landscape, or may be accounted for by unmeasured sources of mortality (including unreported RTA's, illegal harvest, or disease). Similarly, a potential sink may result from net immigration rather than from a high cull rate, or instead may occur due to local demographic stochasticity, for example if local (block-specific) neonatal mortality was lower than the forest-wide estimated mean used in the model.

The potential net population growth from year *j* to year *j+1*, in forest block *i* (PPG_{ij} in km^{-2}) was calculated using the equation:

$$PPG_{i(t+1)} = \frac{D_{Mit} \times A_i + P_{Ait} - M_{Cit}}{D_{Mit} \times A_i} \times D_{Mit} - D_{Mit}$$

where D_{Mj} is the mean deer density for forest block *i*, A_i the area of the forest block, M_{Cij} is the annual cull in forest block *i* in year *j*, and the total annual production P_{Aji} across forest block *i* in year *j* was calculated by:

$$P_{Aji} = D_{MFi} \times A_i \times x_{Fj} \times S_K$$

where D_{MFi} is the mean adult female deer density for each forest block, x_{Fj} the fertility in year *j* and S_K the neonatal kid survival (i.e. from birth to first winter) estimated from pooled data for cull years 2008 and 2009. Mean adult female deer density D_{MFi} was calculated as:

$$D_{MFi\,=}\, D_{Mij} \times P_{obs} \times P_{Fcull}$$

from the mean density for each forest block (D_{Mij}) multiplied by the proportion of female roe deer (P_{obs}) in the surveyed population (restricted in this context to animals in Thetford Forest) in 2008-10 and the proportion of adult female roe deer (P_{Fcull}) within the total cull of female individuals in 2007-09.

Roe deer fertility

Roe deer kids are usually born in May/June (Fig. 5.1). By May, the kids of the previous calendar year are classified as yearlings, while all previous cohorts are classified as adults (Fig. 5.1). However, within these adults, those that were yearlings at the previous mating season potentially have lower fertility than those that were adults in year *j*-1. Therefore the proportion of older adults and yearlings was calculated. I first excluded data from one DMU managed by a private stalking club where most data had no age classification and further excluded two recorded pregnant kids from the cull database for roe deer in 2007-09. The recordings of pregnant kids were recognised as typing errors in the larder computer system after consultation with the wildlife ranger team. Adults comprised 73% (n = 166) of the remaining culled females, yearlings 8% (n = 19) and female kid a further 19% (n = 43) in 2007-09 (n = 2 years). The observed sex ratio for roe deer obtained from the distance sampling thermal imaging data (n = 1023 individuals) was female biased with 42% males and 58% females (Fisher Exact test: p

< 0.001). As 58% of all roe deer are females and of those 73% are adults, 8% are yearlings and 19% are female kids, 42% of the roe deer population are adult females, 5% of the roe population are yearling females and 11% are female kids, and together adult and yearling females comprise the reproductively active females (47% of the roe population).

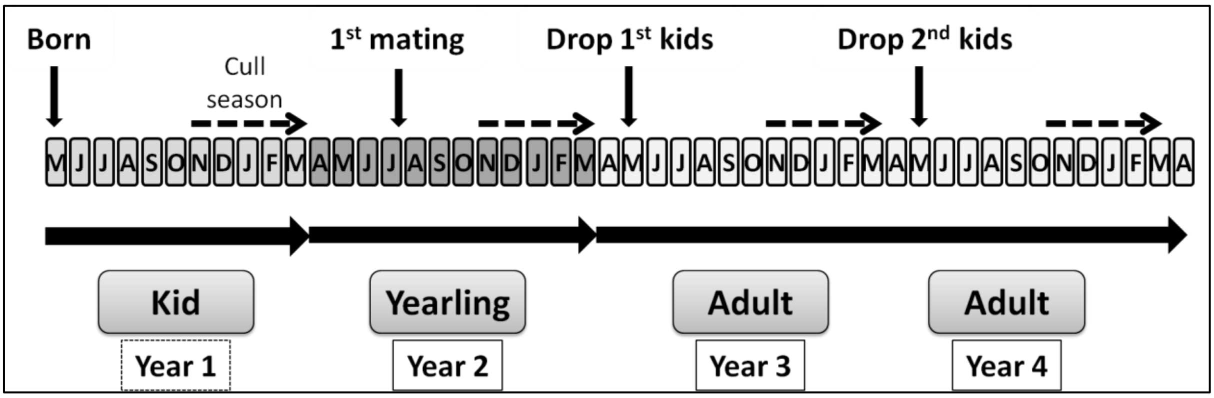

Fig. 5.1 Overview of roe deer classification for adult females and Yearling females.

Fertility per female was established by examining uterus contents of culled individuals. Roe deer embryos are not visible before January on opening the uterus (Ratcliffe and Mayle, 1992) due to delayed implantation (Aitken, 1974, Sempéré et al., 1998). As there is a risk of missing embryos in the early stages of development (Hemami, 2003) I only considered females shot from the 25th of January to the end of the cull season in March following (Hemami, 2003) and K. Wäber (unpublished, see Chapter 1 and 2).

Fertility data from one DMU managed by a private stalking club showed significant lower fertility estimates compared to the other forest blocks (see Chapter 2). Thus, these data were excluded from fertility analyses. No differences in adult female roe deer fertility between forest blocks were found (see Chapter 3) therefore I pooled fertility data across blocks separately for adults (n = 199) and yearlings (n = 23) in 2006-09. The mean fertility for adult females was $\overline{x}$ = 1.59 foetuses per female ± 0.60 *SD* and for yearling females $\overline{x}$ = 1.22 foetuses per female ± 0.85 *SD*. I found no significant difference between the fertilty of adult and yearling females ($\chi^2_{(1)} = 1.86$, p = 0.17) whilst controlling for cull year ($\chi^2_{(3)} = 0.30$, p = 0.96). The pooled mean fertility of adult and female yearlings (n = 222) was $\overline{x}$ = 1.55 foetuses per female ± 0.63 *SD* in 2006-2009 (Fig 5.4).

Neonatal survival roe deer

Calculating the annual net production requires knowledge about survivorship of roe deer kids. Neonatal survival was estimated by comparing observed autumn kid:doe ratios with those expected from fertility data (i.e. foetuses per doe). The ranger team in Thetford Forest was requested to record observations of the numbers of kids and adult does in replicate roe deer family groups in the beginning of October to the end of November in each of three years 2007-2009. For all groups observed, the date, time, location, group size, and the sex and age (juvenile/yearling/adult) of individuals within the group, were recorded. Overall 1003 roe deer in 473 groups were recorded, with 486 adult females and 517 kid followers (family groups 2007: $n = 166$; 2008: $n = 164$; 2009: $n = 143$).

A generalised linear model was used to explore whether kid:doe ratios differed among blocks or years. Number of kids (dependent; $n = 473$ groups) was significantly positively related to the number of adult females in the family group (predictor: Wald $\chi^2_{(1)} = 21.33$, $p < 0.001$), while there were no significant differences among cull years (Wald $\chi^2_{(2)} = 1.60$, $p = 0.66$) or among forest blocks (Wald $\chi^2_{(11)} = 9.91$, $p = 0.54$) (using generalised linear models with poisson loglinear distribution fitted in SPSS 18.0). Therefore, the pooled mean kid-female ratio (1.27 kids per adult female ± 0.03 SE, 2007-09) was used for all blocks and years when calculating neonatal mortality.

Neonatal survival of roe deer kids (S_K) from birth to their first winter was calculated using the following equation:

$$S_K = 1 - \left[\frac{x_F - x_{KF}}{(x_F)}\right]$$

where x_F is the mean pooled fertility (per doe) in 2006-09 observed in January/February and x_{KF} is the pooled kid-female ratio in October/November in 2007-09. Therefore neonatal kid survival was 79% in 2008 and in 2009 (Fig. 5.4).

Reeve's muntjac fertility

Reeve's muntjac derive from sub-tropical areas and do not show a seasonal reproductive cycle, instead births are distributed throughout the year (Chapman et al., 1997) (Fig. 5.2). During this study, newly born kids were observed in winter months (e.g. February-March, K. Wäber pers. obs.). (Chapman, 1991) found that captured female Reeve's muntjac are capable of breeding when they reach a live weight of 10 kg (around 8 months).

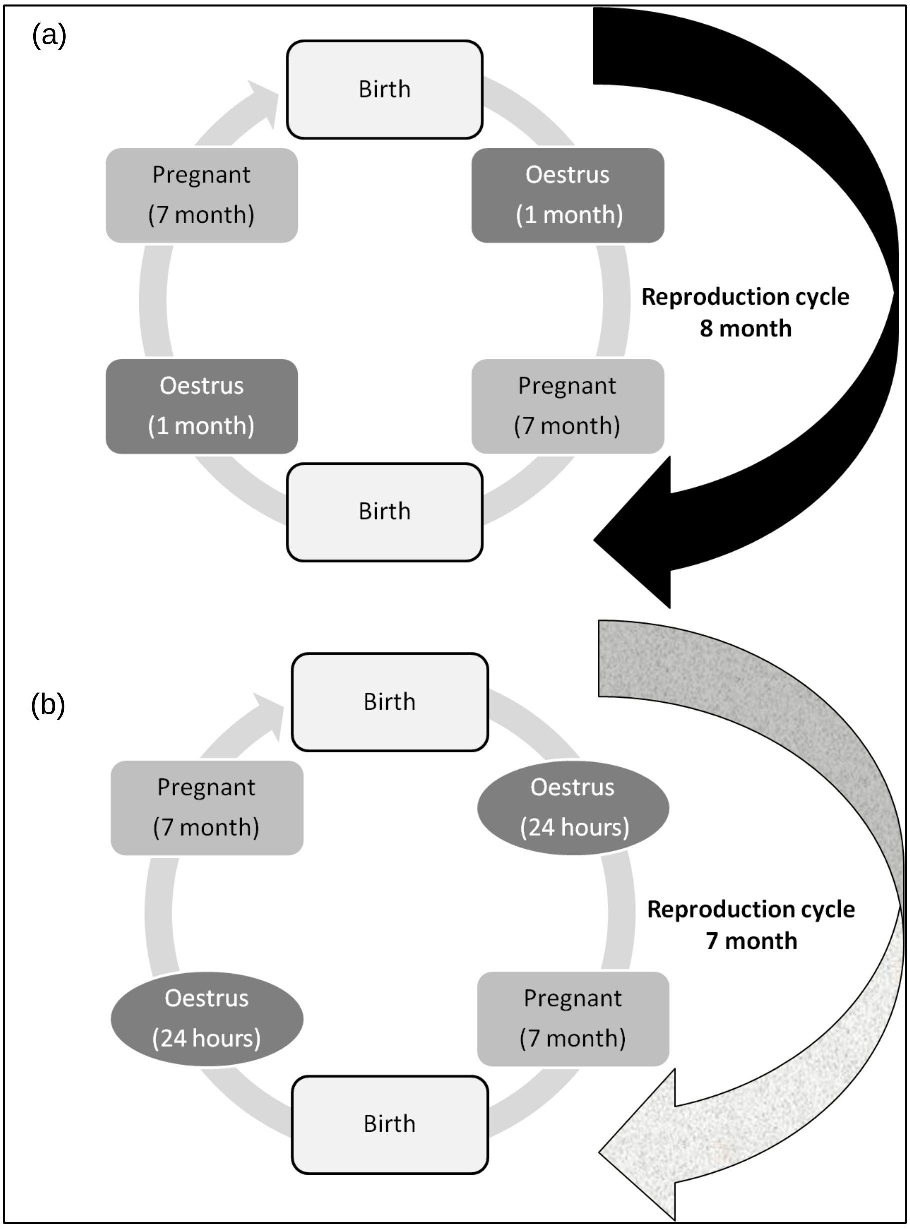

Fig. 5.2. Overview of Reeve's muntjac reproduction a) with maximum cycle length of 8 month following (Chapman et al., 1997); b) with plausible reproductive parameters.

No age classification between sub-adults and adult animals was possible within the larder data logging protocols as age-specific patterns of tooth eruption are not known. In order to define and quantify the proportion of reproductively active sub-adult and mature adult muntjac within the population, the influence of body mass classes (class 1: < 5 kg; 2: 5 - 6 kg; 3: 6 - 7 kg; 4: 7 - 8 kg; 5: 8 - 9 kg; 6: > 9 kg; see Chapter 3) on fertility was examined. For females culled during 2006-09, fertility (the number of foetuses per Reeve's muntjac female) did not differ beyond a larder mass of ≥ 7 kg (GLM with Poisson error: $n = 1172$, Wald $\chi^2_{(5)} = 123.80$, $p < 0.001$) [body mass class: $6^a \approx 5^a \approx 4^a > 3^b > 2^c > 1^d$; shared superscripts do not differ, Sequential Sidak test $p < 0.001$] (see Chapter 3). Female Reeve's muntjac with a larder mass ≥ 7 kg were therefore defined as reproductively mature females, whereas females with a larder mass ≥ 5 kg and < 7 kg were defined as reproductively active sub-adult females.

The mean observable foetuses at any one time for adult females was mean = 0.82 ± 0.39 *SD* foetuses per female and for sub-adult females was mean = 0.58 ± 0.50 *SD* foetuses per female in 2006-09. My model showed (see model for neonatal survival for Reeve's muntjac) all adult female muntjac were getting pregnant. Therefore, the fertility for adults is 1.0 foetus per female. But not all sub-adult females were getting pregnant for example either due to their body condition or environmental influences. I used the ratio of the mean observable foetuses for sub-adult females to adult females to calculate the fertility for sub-adults. The ratio between adult females and sub-adult females was 0.71 resulting in fertility for sub-adult female muntjac of 0.71 foetuses per female. The reproduction cycle for Reeve's muntjac is seven month. Thus, the annual mean fertility $\overline{x}_{AF}$ calculated as

$$\overline{x}_{AF} = \frac{12\,month}{7\,month} \times \overline{x}_{SA}$$

Where, $\overline{x}_{SA}$ is defined as the mean fertility per female (adult or sub-adult) per partuition event, was therefore 1.2 per sub-adult female and 1.7 foetuses per adult muntjac female (Fig. 5.4).

As in roe deer I detected a female biased sex ratio in the distance sampling thermal imaging data ($n = 1806$ individuals) with 41% of the observed animals being males and 59% females in 2008-10 (Fisher Exact test: $p < 0.001$). Within the larder data, muntjac females ($n = 1708$) comprised 66% adults (body mass ≥ 7 kg) and sub-adults comprised 26% (body mass ≥ 5 kg and < 7 kg) in 2006-09. The proportion of reproductively active female Reeve's muntjac females in the population was 54% (comprising 39% adults and 15% subadults).

Neonatal survival Reeve's muntjac

Counts of Reeve's muntjac kid-female ratio are difficult to achieve as females with kid followers are seldom seen, however the survival rates of newly born kids can be inferred from the lactating status of their mothers. Unlike for roe deer, there are still gaps in the knowledge of Reeve's muntjac biology making this approach far from straightforward. Therefore, the expected proportions of pregnant and / or lactating females under different assumptions of kid mortality and using plausible biological parameters (for gestation duration, rate of foetus development, duration of lactation, timing of subsequent pregnancy) were compared to the proportions observed in the population, in order to refine understanding of biology and then estimate neonatal mortality.

Most observations are made on captive animals in Britain. Only a few observations on non-captive animals exist (e.g. Chapman et al. (1993), Chapman et al. (1985)). The gestation period for Reeve's muntjac is seven months. Female Reeve's muntjac get into oestrus 24 hours after giving birth and again one month after birth, as observations of captive individuals showed (Chapman et al., 1997). It is unclear if females are mainly getting pregnant in their first or second oestrus after giving birth. Thus, the reproductive cycle (time difference between parturition) for wild animals, may be seven or eight month long. The maximal observed lactation period of captive animals is up to 17 weeks (4 month) (Chapman, 1991) (Fig. 5.2). However, due to differences in stress, competition, nutrition or weather influences this may be different for non-captive muntjac. It is also unknown how long after conception and implantation the foetus starts to be visible to a deer manager on opening the uterus of a culled animal. The length of the reproductive cycle of red and fallow deer (about 8 month) is similar to Reeve's muntjac. Therefore I investigated when the foetus is visible in the uterus in red and fallow deer.

From the larder data I extracted fertility data for adult red and fallow deer (> 1 year) in Thetford Forest in 2001-2009. The red deer and fallow deer rut is from September to November. To calculate after how many months the foetus will be visible in the uteri I set the 21st of September as the mean rutting date. I analysed the relationship of foetus per female (dependent) and following independent variables year (categorical) and number of month after the rut (categorical) (month code 1: 21 Sep. – 18 Oct.; 2: 19 Oct. – 15 Nov.; 3: 16 Nov. – 13 Dec.; 4: 14 Dec. – 10 Jan.; 5: 11 Jan. – 7 Feb.; 6: 8 Feb. – 30 Feb.) whilst controlling for species. For both species I found that after two month following the 21st of September a foetus was visible in the uterus in > 50% of the adult females (GLM with Poisson error: n = 482, year: Wald $\chi^2_{(8)}$ = 5,35, p = 0.72, species: Wald $\chi^2_{(1)}$ = 2.02, p = 0.16, month code: Wald $\chi^2_{(4)}$ = 42.29, $p < 0.001$) [month code: $6^a \approx 5^a \approx 4^{a,b} \approx 3^b > 2^c$; shared superscripts do not differ, Sequential Sidak test $p < 0.05$]. For Reeve's muntjac I assumed as an approximation that the foetus is visible two month after conception.

Thus, Reeve's muntjac kid survival was estimated using length of gestation period, length of lactation period and point in time when the foetus is visible in the uterus. I made use of the following observation of adult female muntjac (body mass ≥ 7 kg; n = 845) from the larder data:

- Adult females with milk and no foetus: 11%
- Adult females with milk and foetus: 22%
- Adult females with foetus and no milk: 59%
- Adult females with no milk, no foetus: 8%.

I started investigating Reeve's muntjac kid survival using the following assumptions: females conceive one month after parturition, the foetus is visible in the uterus two months after conception and therefore three months after parturition, the length of the lactation period is four months and the kid survival is 100% (Table 5.1, Fig. 5.3: Model (a)). However, when comparing the observed percentage of females lactating with no foetus yet visible, versus females lactating with a visible foetus in the uterus with the predicted proportions, it is clear that these observations are not possible unless I refine the underlying biological assumptions. First, I changed the assumptions about the time when the foetus is visible in the uterus from two month after conception and three month after parturition to 0.3 month after conception and 1.3 month after parturition (Table 5.1, Fig. 5.3: Model (b) and (c)). The foetus is visible after 25% (2 month) of the gestation period has elapsed, in > 50% of red deer and fallow deer females. In Reeve's muntjac a period of 1.3 months amounts to 19% of the overall gestation period. Thus it is plausible that the foetus in the majority of the females will be visible within 1.3

months. Model (c) showed a very high correlation and close agreement between predicted and observed data. However, the identification of a foetus in the uterus ten days after conception may be difficult and much more reliable when the pregnancy further advances. Then I changed the date of conception by assuming most females become pregnant immediately after giving birth, which Chapman (1991) said was a possibility also found in her captive animals. Finally, I changed the lactation period, which Chapman stated was ‘up to four months’. I altered this from the maximal four month in Model (d) to 3.5 month in Model (e) and three month in Model (f) (Table 5.1, Fig. 5.3).

The two models showing the highest correlation between predicted and observed values assuming 100% kid survival ($n = 4$ parameter pairs; Model (e): $r = 0.91$, $p = 0.09$; Model (f): $r = 0.96$, $p = 0.04$) where therefore selected as offering the best description of the basic biology. Of these, model (f) receives strongest support prior to varying neonatal mortality. Having adjusted the basic biological parameters the consequence of different values for mortality was then examined varying mortality levels. I primarily assume that mortality happens immediately after birth (Table 5.1). This is justified as a simplifying assumption on the following grounds: Muntjac females are very defensive of their offspring and will chase foxes away (P. Mason and B. Ball, pers. observation). I therefore expect that weather plays an important role in muntjac kid survival; for example kids born in winter may perish by cold and wet weather or starve as the female cannot find enough food to sustain both of them. Thus, I assume for our calculations that the Reeve’s muntjac kid mortality mainly takes place very shortly after birth. Following loss of a kid females cease lactating and enter the class: no lactation, no foetus visible. Thus, mortality does not change the ratio of lactating females without foetus *versus* lactating females with foetus.

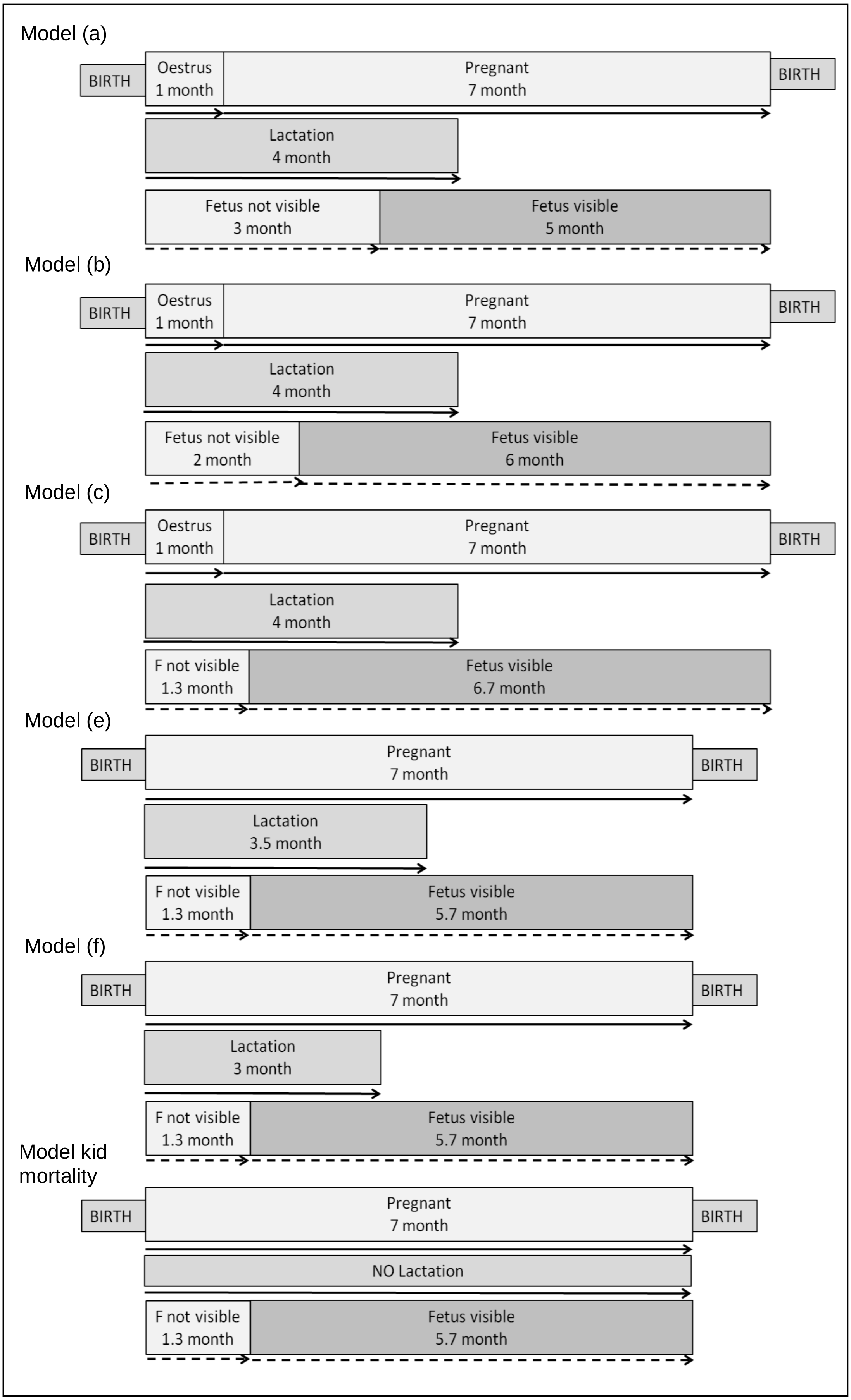

Fig. 5.3. Schematic overview of models used the calculation of kid survival with changes in conception time, length of lactation period and foetus visibility in the uterus.

I predicted the proportion of females in each category F (i.e. lactating and no foetus, etc.) by:

$$P_F = P_S \times PV_{KS} + P_M \times PV_{KM}$$

with P_S proportion of kids surviving, P_M proportion of kids suffering mortality shortly after birth, PV_{KS} as the predicted proportion of females in category F if their kids have survived, and PV_{KM} as the predicted proportion of females in category F if their kids suffered mortality shortly after birth (Table 5.1).

In model (e) I found that the highest correlation between predicted and observed data after testing varying neonatal mortality of kids for a kid survival of 70% (r = 1.0, p = 0.003), 65% (r = 1.0, p = 0.002) and 60% (r = 0.99, p = 0.004). In all other correlations the correlation coefficient was r < 1.0 and p ≥ 0.01. No significant differences between the correlations were found (z-test: n.s.).

I have evidence that most Reeve's muntjac females will conceive immediately after giving birth (Table 5.1) suggesting a reproduction cycle length of seven month (Fig. 5.2). Thus, the majority of female muntjac will give birth 1.7 times per year. Our data also suggest that the foetus in the uterus must be visible in < 2 month after conception most likely just after one month. Our data support a lactation period of 3.5 month rather than four month. I therefore suggest that the kid survival is most likely between 65% and 70% (Table 5.1, Fig. 5.4).

Table 5.1. Modelling of predicted proportions of adult culled females with observable lactation and developing foetus, for different parameters (length of reproductive cycle, visibility of foetus in uterus and length of lactation period) and different assumptions of neonatal mortality, compared to observed proportions in 2006-09. The shaded area showing the best fit for observed versus predicted data for kid survival.

Status of culled females:			**Observed in population [%] (*n*)**	**Predicted in population (%)**						
				If 100% kids survive	Kid mortality occurs soon after birth: % survival (% mortality)					
Lactating	Foetus visible	Duration (months)			*0 (100)*	90 (10)	80 (20)	70 (30)	65 (35)	60 (40)
Model (a) conception after 1 month, foetus visible 2 months after conception and 3 month after parturition, lactation period 4 month										
Yes	No	3	11 (92)	37.5						
Yes	Yes	1	22 (175)	12.5						
No	Yes	4	59 (479)	50.0						
No	No	0	8 (62)	0						
Model (b) conception after 1 month, foetus visible 1 months after conception at 2 month after parturition, lactation period 4 month										
Yes	No	2	11 (92)	25.0						
Yes	Yes	2	22 (175)	25.0						
No	Yes	4	59 (479)	50.0						
No	No	0	8 (62)	0						
Model (c) conception after 1 month foetus visible 0.3 months after conception and 1.3 month after parturition, lactation period 4 month										
Yes	No	1.3	11 (92)	16.7						
Yes	Yes	2.7	22 (175)	33.3						
No	Yes	4	59 (479)	50.0						
No	No	0	8 (62)	0						
Model (d) conception 24 hours after birth, foetus visible 1.3 month after conception, lactation period 4 month										
Yes	No	1.3	11 (92)	19.0						
Yes	Yes	2.7	22 (175)	38.1						
No	Yes	3	59 (479)	42.9						
No	No	0	8 (62)	0						

Table 5.1.

Model (e) conception 24 hours after birth, foetus visible 1.3 month after conception, lactation period 3.5 month										
Yes	No	1.3	11 (92)	19.0	0	17.1	15.2	13.3	12.4	11.4
Yes	Yes	2.2	22 (175)	31.0	0	27.9	24.8	21.7	20.2	18.4
No	Yes	3.5	59 (479)	50.0	81.0	53.1	56.2	59.3	60.9	62.4
No	No	0	8 (62)	0	19.0	1.9	3.8	5.7	6.7	7.6
Model (f) conception 24 hours after birth, foetus visible 1.3 month after conception, lactation period 3 month										
Yes	No	1.3	11	19.0	0	17.1	15.2	13.3	12.4	11.4
Yes	Yes	1.7	22	23.9	0	21.5	19.1	16.7	15.5	14.3
No	Yes	4	59	57.1	81.0	59.5	61.9	64.3	65.5	66.7
No	No	0	8	0	19.0	1.9	3.8	5.7	6.7	7.6

Deer densities

Roe deer and Reeve’s muntjac densities in each forest block were assessed using thermal imaging distance sampling in 2008, 2009 and 2010. The surveys were conducted between January and March at night (8pm-4am) using Recon long range thermal imager (manufactured by FLIR Systems) and a Leica Laser Range Finder ‘LEICA LRF 800’ mounted with the night vision ‘Maxi-Kite Mk 4’ (manufactured by THALES) fitted with a infrared illuminator.

Transect lines were placed on the widespread forest track-way network. Average length of driven transects per year was mean = 529.4 km ± 40.3 *SD*. Transects in five forest blocks were repeated two to four times and once in two blocks. Total transect length driven differed between blocks and ranged between 41.6 km and 139.7 km (see Chapter 4). Survey was carried out on one-sided-transects as camera work took place from the front passenger seat of a 4-wheel-drive vehicle at a maximum speed of 20mp/hr.

Roe deer and Reeve’s muntjac distance sampling data were analysed applying a detection function stratified by forest blocks and pooled across years to obtain density estimates for each block in each year, following the procedure described by (Buckland et al., 2001) with the computer software DISTANCE 6.0 release 2 (Thomas et al., 2010).

Overall 1725 roe deer and 2625 Reeve’s muntjac were observed. Of these the sex could be detected for 85% and 70% respectively.

For further details on distance sampling thermal imaging see Chapter 3.

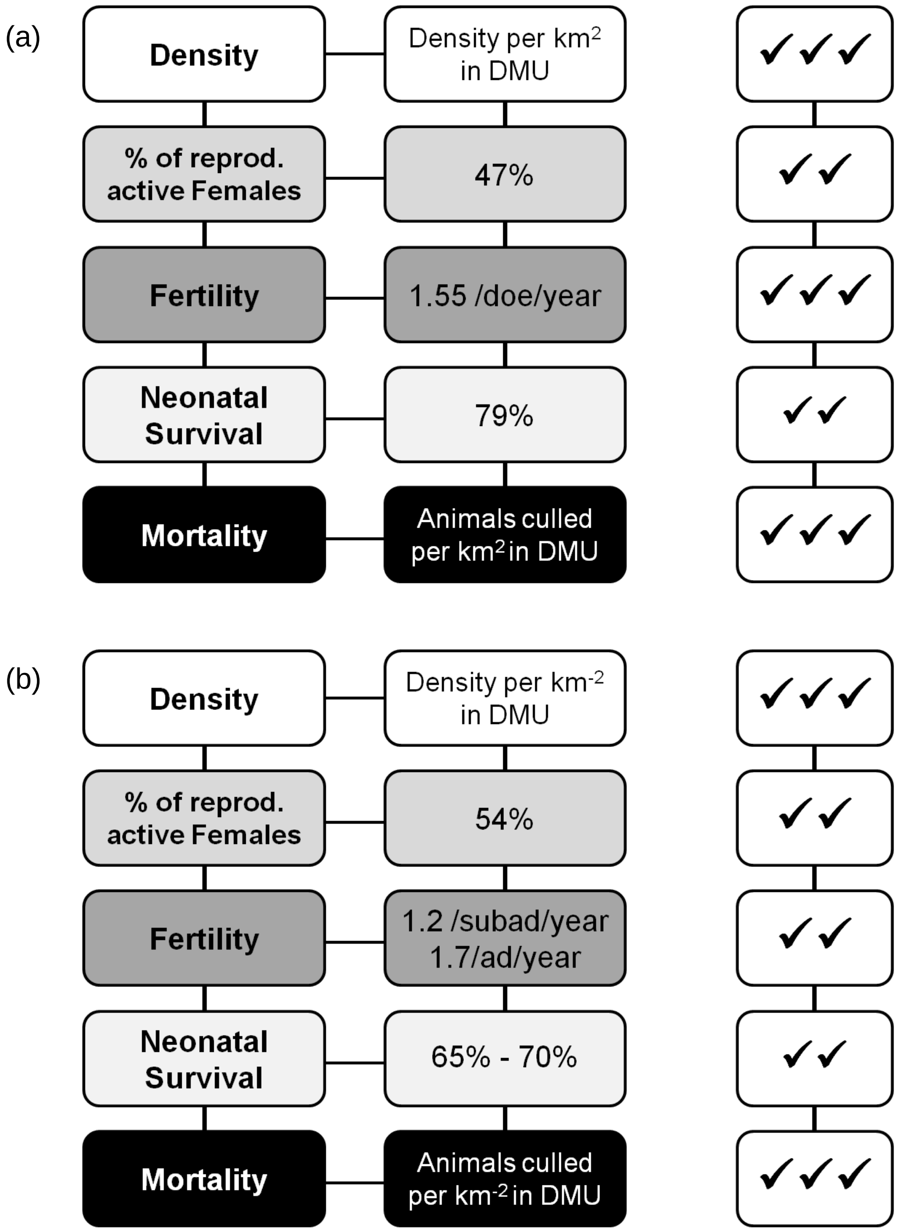

Fig. 5.4. Data summary and evaluation (three ticks = robust, high degree of confidence, narrow error bounds; two ticks = strong knowledge, but some potential uncertainty and wider error bounds) a) roe deer and b) Reeve's muntjac for calculation of source-sink dynamics.

Table 5.2. Overview of roe deer and Reeve's muntjac density, potential population growth and potential number of emigration or immigration individuals in seven forest blocks of Thetford Forest in 2008-2010 estimated from distance sampling thermal imaging data.

Forest block	Density [km^{-2}] (mean ± SE)			Potential population growth [km^{-2}]		Potential no. of emigrations / immigrations		No. of deer culled [% culled of population]		No. of deer culled of annual production [%]	
	2008	2009	2010	2008/09	2009/10	2008/09	2009/10	2008/09	2009/10	2008/09	2009/10
(a) roe deer											
Did	14.0 ± 2.7	12.0 ± 4.1	9.2 ± 2.6	1.2	1.9	32.3	42.3	48.9	41.5	85.0	72.2
Mun	32.0 ± 4.1	34.0 ± 4.8	40.2 ± 8.2	14.2	14.0	291.4	261.4	18.9	21.6	32.8	37.5
Lyn	13.4 ± 2.1	14.8 ± 2.1	18.0 ± 3.5	4.4	6.0	43.2	252.5	21.9	18.7	38.1	32.6
Cro	8.1 ± 1.8	14.2 ± 3.2	13.0 ± 3.0	0.9	4.5	-47.8	72.7	47.5	29.6	82.5	51.4
HiLo	7.2 ± 2.1	3.7 ± 1.1	3.5 ± 1.7	2.6	0.8	217.2	55.6	23.4	36.4	40.7	63.3
Elv	10.2 ± 4.2	4.4 ± 1.0	8.7 ± 3.0	4.5	2.3	139.5	-11.0	8.1	10.9	14.0	19.0
Har	5.8 ± 1.3	5.1 ± 1.8	4.1 ± 1.5	2.8	0.7	50.8	18.5	30.6	44.0	53.2	76.5
(b) Reeve's muntjac (kid survival 65%)											
Did	44.0 ± 5.5	51.2 ± 7.7	47.7 ± 7.4	12.5	15.2	48.6	172.3	26.4	25.1	48.2	45.7
Mun	36.6 ± 3.5	35.3 ± 6.5	33.1 ± 5.3	10.1	8.8	273.7	266.2	27.3	29.7	49.9	54.3
Lyn	22.3 ± 2.8	22.3 ± 2.4	19.9 ± 2.7	7.1	5.5	149.8	167.5	23.0	30.0	41.9	54.7
Cro	22.4 ± 3.4	16.2 ± 3.5	12.9 ± 1.9	4.4	-2.7	75.2	4.5	35.2	71.3	64.3	130.1
HiLo	11.6 ± 1.9	11.5 ± 2.4	10.8 ± 2.3	2.6	3.1	93.0	132.9	32.5	27.6	59.4	50.3
Elv	14.6 ± 3.0	13.7 ± 2.7	12.2 ± 3.5	7.5	6.6	138.9	133.6	3.3	6.6	6.1	12.1
Har	71.2 ± 8.4	50.4 ± 7.0	32.6 ± 6.2	31.8	18.7	515.2	358.1	10.2	17.6	18.6	32.1
(b) Reeve's muntjac (kid survival 70%)											
Did	44.0 ± 5.5	51.2 ± 7.7	47.7 ± 7.4	14.3	17.4	89.6	206.0	26.4	25.1	44.8	42.5
Mun	36.6 ± 3.5	35.3 ± 6.5	33.1 ± 5.3	11.6	10.3	320.5	280.3	27.3	29.7	46.3	50.4
Lyn	22.3 ± 2.8	22.3 ± 2.4	19.9 ± 2.7	8.0	6.5	165.4	166.2	23.0	30.0	38.9	50.8
Cro	22.4 ± 3.4	16.2 ± 3.5	12.9 ± 1.9	5.3	-2.0	86.8	15.7	35.2	71.3	59.7	120.8

Table 5.2.

HiLo	11.6 ± 1.9	11.5 ± 2.4	10.8 ± 2.3	3.1	3.6	141.2	184.5	32.5	27.6	55.2	46.7
Elv	14.6 ± 3.0	13.7 ± 2.7	12.2 ± 3.5	8.1	7.2	121.0	106.8	3.3	6.6	5.6	11.2
Har	71.2 ± 8.4	50.4 ± 7.0	32.6 ± 6.2	34.8	20.9	554.4	385.8	10.2	17.6	17.2	29.8

Results

Roe deer density differed among forest blocks, but within each forest block was mainly stable between years and ranged between 3.0 roe deer km^{-2} and 41.9 km^{-2} in 2008-10 (Table 5.2, Fig. 5.5). In forest block Cro roe deer density increased significantly from 2008 to 2009 (*z*-test: p =0.05) but in forest block HiLo and Did there was a significant decrease in roe deer density (z-test: $p < 0.05$) from 2008 to 2010. Reeve’s muntjac density ranged from 10.8 deer km^{-2} to 71.2 km^{-2} in 2008-10 (Table 5.2, Fig. 5.6). A significant decrease of muntjac density (z-tests: $p < 0.05$) was found in forest block Cro and Har from 2008 to 2010. The observed roe deer and Reeve’s muntjac densities were higher in the North than in the South of the surveyed area in all surveyed years. For roe deer and Reeve’s muntjac an annual cull of about 50% for roe deer and about 60% for muntjac of the population is necessary to harvest the annual production (number of reproductively active females x fertility x kid survival).

Roe deer

The calculated potential population growth rate was positive in 2008/09 and 2009/10 for all seven forest blocks and showed no extreme variations between years (Table 5.2). The potential population growth in 2008/09 ranged from 0.9 to 4.5 roe deer km^{-2} in six out of seven forest blocks in Thetford Forest. Only one forest block in the western part of the forest showed a higher potential population growth of 14.2 roe deer km^{-2} in 2008/09 (Table 5.2, Fig. 5.9). In 2009/10 the potential population growth ranged between 0.7 roe deer km^{-2} and 6.0 roe deer km^{-2}. As in the previous year the forest block in the western part of the forest showed the highest potential population growth (14.0 roe deer km^{-2}).

In 2008/09 six out of seven forest blocks were classified as sources with roe deer potential emigration into the surrounding landscape ranging from 3.5 roe deer per km^{2} of source block (totalling 32 individuals across the block) to 12.1 deer km^{-2} (291 individuals across that block) (Table 5.2, Fig. 5.12). Only one forest block was identified as a sink despite observed positive population growth. Here the actual roe deer density in year 2 was 6.7 deer km^{-2} (48 individuals) higher than the expected deer density for year 2 (Table 5.2, Fig. 5.12).

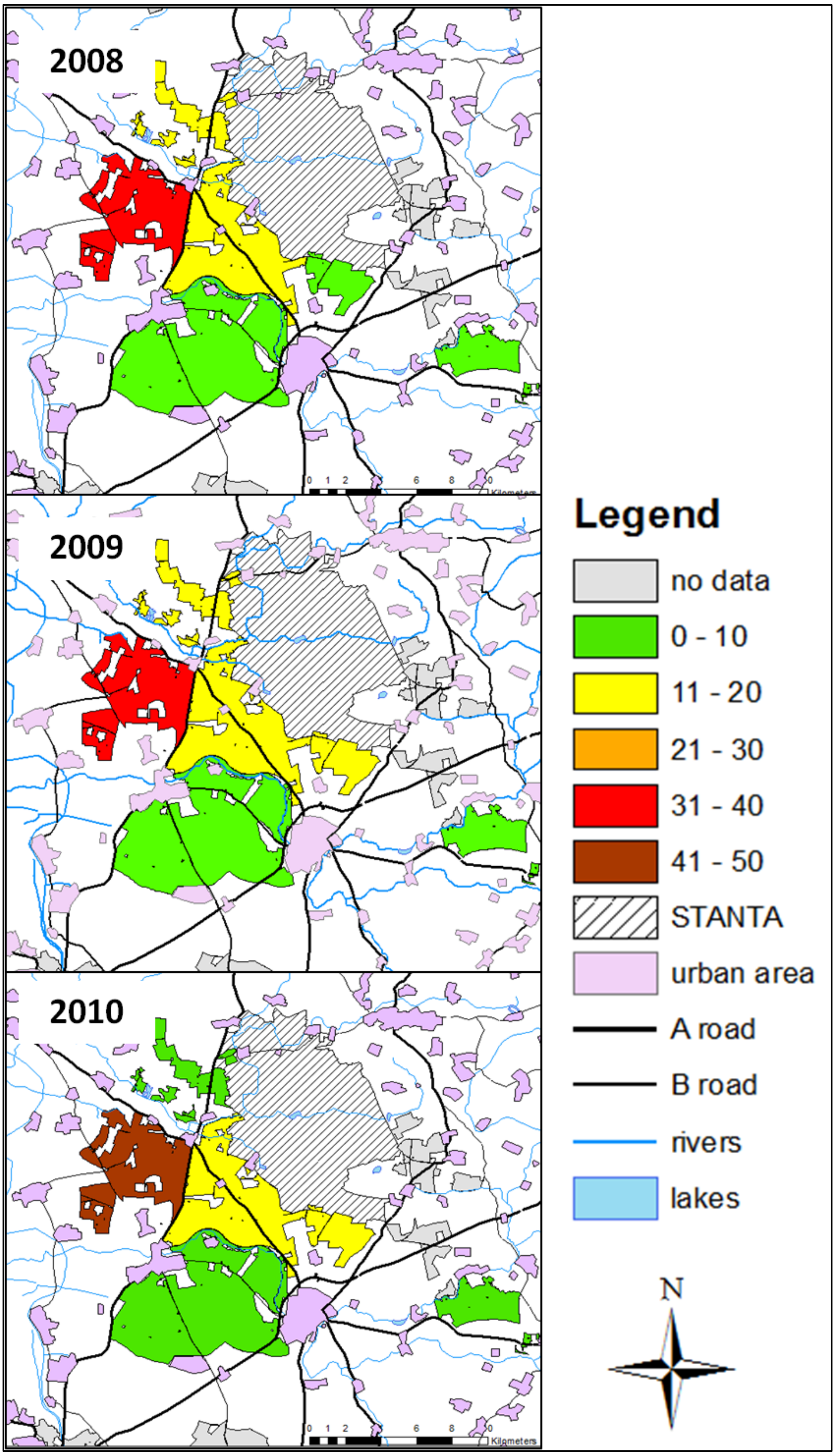

Fig. 5.5. Spatial variation of roe deer density (km^{-2}) in seven forest blocks in Thetford Forest in 2008-10.

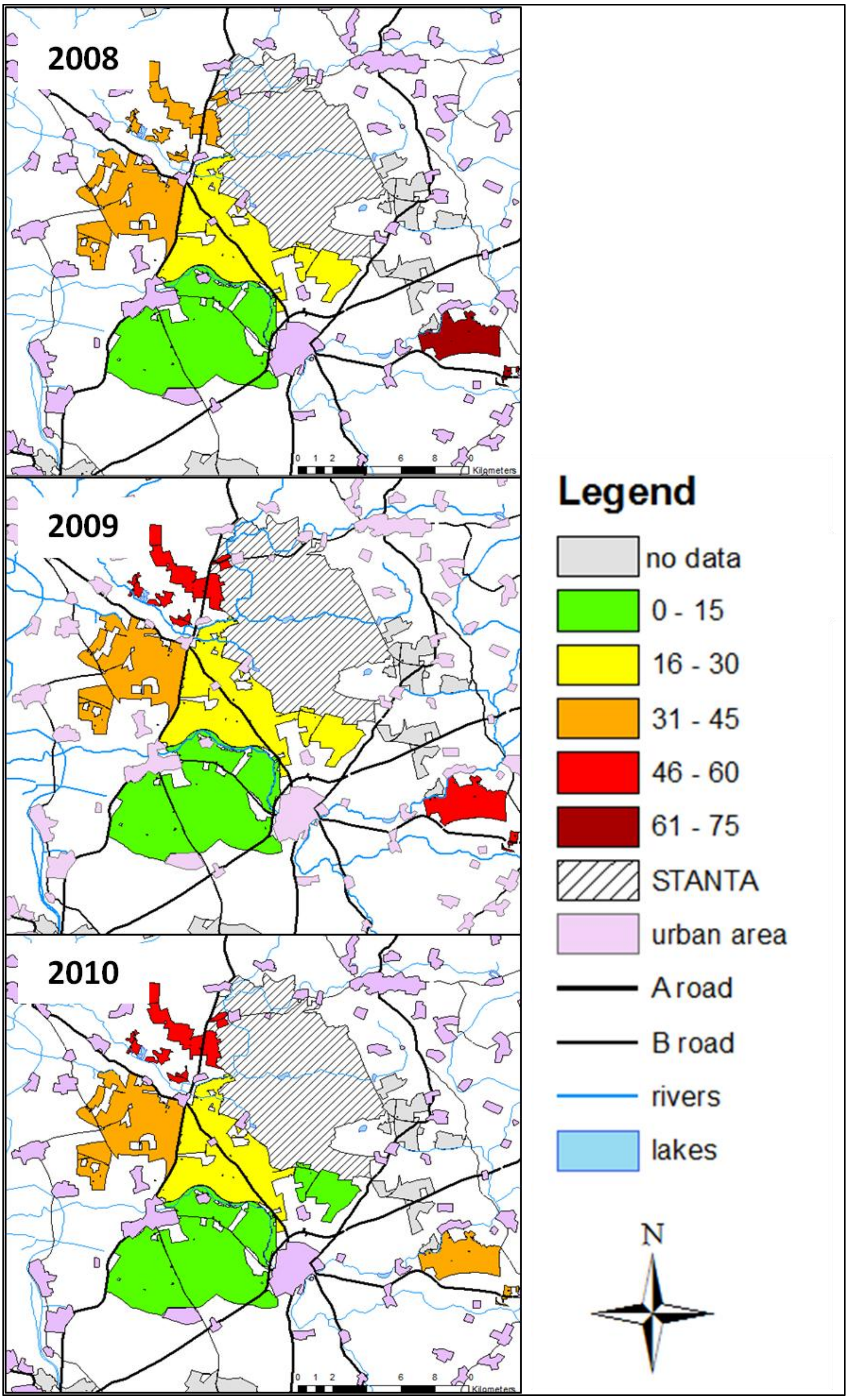

Fig. 5.6. Spatial variation of Reeve’s muntjac density (km^{-2}) in seven forest blocks in Thetford Forest in 2008-10.

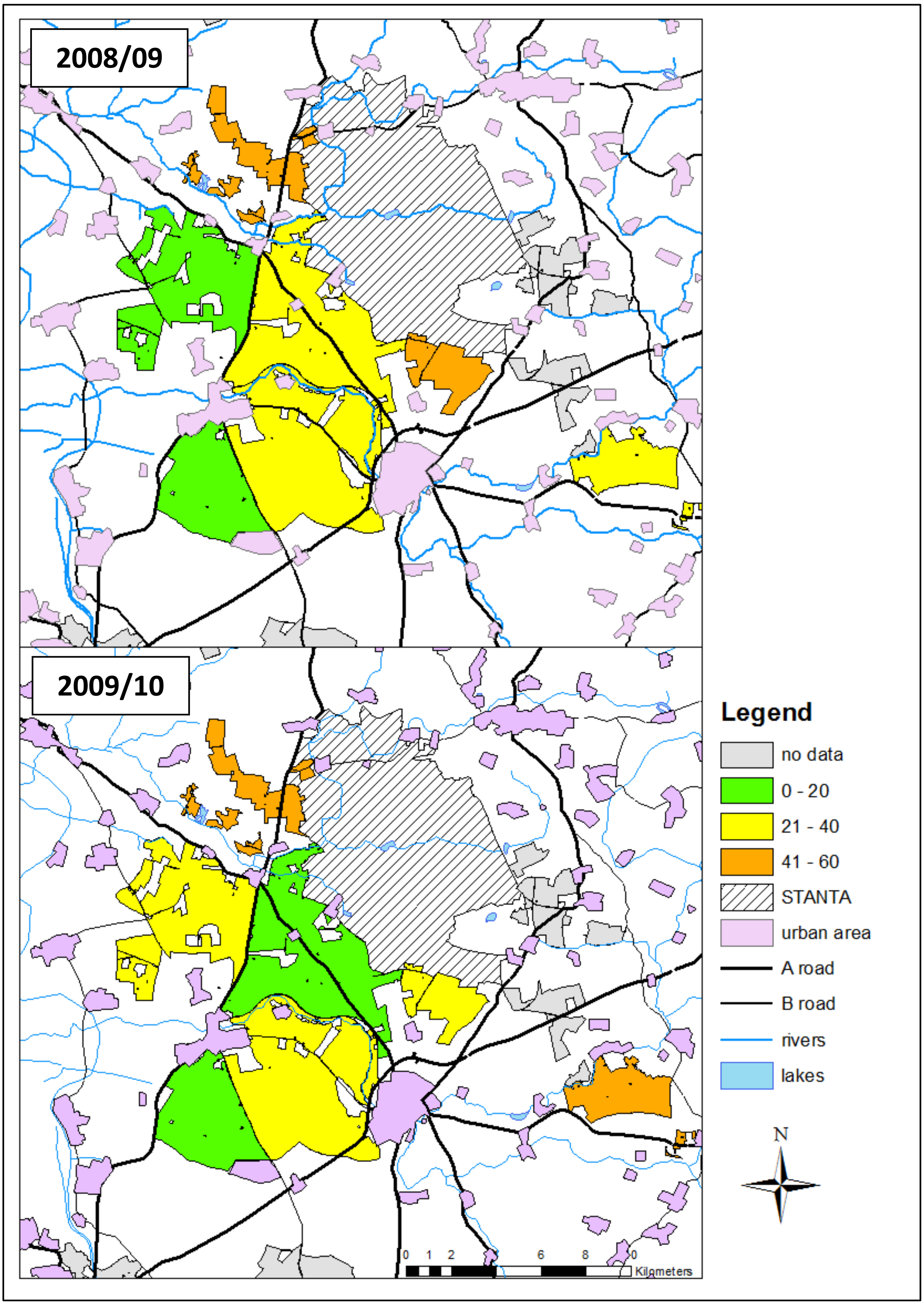

Fig. 5.7. Spatial variation of roe deer cull as percentage of population culled in Thetford Forest in 2008/09 and 2009/10.

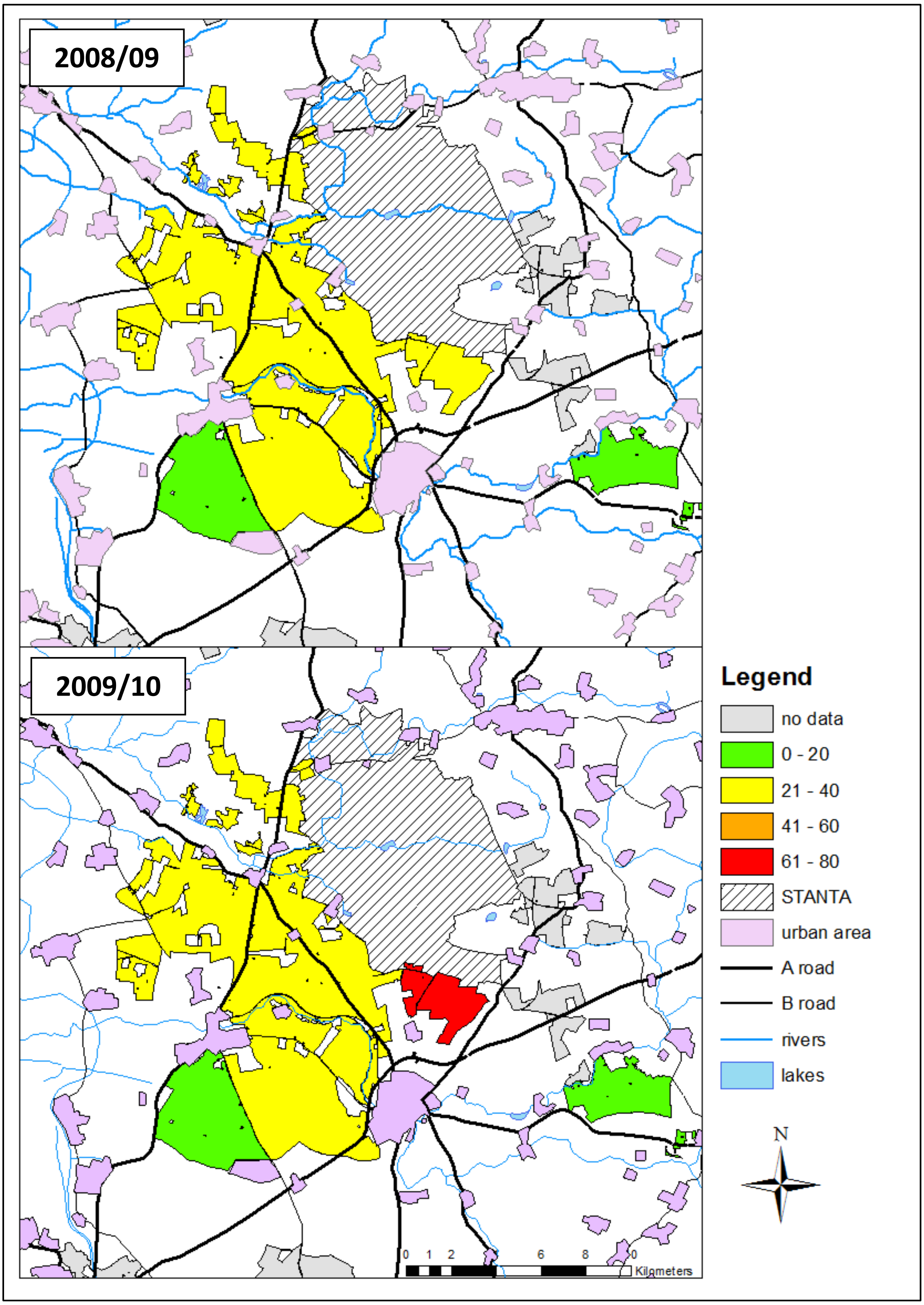

Fig. 5.8. Spatial variation of Reeve's muntjac cull as percentage of population culled in Thetford Forest in 2008/09 and 2009/10.

Similarly, in 2009/10 six out of seven forest blocks may have acted as sources, potentially exporting roe deer into the surrounding landscape, ranging from 1.6 roe deer per km^2 of source block (totalling 56 individuals from the block) to 10.8 deer km^{-2} (261 individuals) (Table 5.2, Fig. 5.12). In forest block Elv I found 0.5 deer km^{-2} (8 individuals) more in year 2 than the expected density for year 2 predicted (Table 5.2, Fig. 5.12).

Overall in 2008/09 and 2009/10 potentially 430 roe individuals and 438 roe individuals emigrated respectively in surrounding areas.

Reeve's muntjac – kid survival 65%

When kid survival is taken to be 65%, then the calculated potential population growth rate of Reeve's muntjac was positive in all seven forest blocks in 2008/09 and in six forest blocks in 2009/10 for. Only in forest block Cro I found a negative population growth of -2-7 muntjac km^{-2} in just one of two years, 2009/10 (Table 5.2, Fig. 5.10). The potential population growth was highest in forest block Har in 2008/09 (31.8 muntjac km^{-2}) and 2009/10 (18.7 muntjac km^{-2}). Within the other forest blocks the potential population growth of muntjac ranged between 2.6 deer km^{-2} and 15.2 deer km^{-2} in 2008/09-2009/10 (Fig. 5.10).

Potential emigration rates of Reeve's muntjac range from 2.7 deer km^{-2} to 52.6 deer km^{-2} in 2008/09, and 0.6 deer km^{-2} to 36.5 deer km^{-2} in 2009/10 (Fig. 5.13). Despite a reduction in potential population growth of 32% from 2008/09 to 2009/10 in forest block Har due to higher cull pressure, 358 individual deer (36.5 km^{-2}) were still potentially emigrating to surrounding areas (Table 5.2, Fig. 5.13).

As a result in 2008/09 potentially 1294 individuals and in 2009/10 potentially 1235 individuals were potentially available to emigrate out of these seven blocks into the surrounding landscape (Table 5.2).

Reeve's muntjac – kid survival 70%

When kid survival is taken to be 70%, then potential population growth was predicted to be negative for just one forest block (Cro) in 2009/10; and was predicted to be positive in all other blocks across both years. Potential population growth ranged from 3.1 muntjac km^{-2} (HiLo) to 34.8 muntjac km^{-2} (Har) in 2008/09 and from -2.0 muntjac km^{-2}

(Cro) to 20.9 muntjac km^{-2} (Har) in 2009/10 (Table 5.2, Fig. 5.11). Again the highest potential emigration rate was found in forest block Har in 2008/09 (554 individuals) and 2009/10 (386 individuals) (Table 5.2). Of the total number of potentially emigrating deer pooling across the 120 km^2 considered here, Har (area = 9.8 km^2) contributed 40% in 2008/09 and 30% 2009/10 (Table 5.2, Fig. 5.14).

Overall in 2008/09 potentially 1479 muntjac and in 2009/10 potentially 1345 muntjac potentially emigrated from these seven forest blocks out into the surrounding landscape (Table 5.2)

Cull data

Roe deer cull varied between 8% and 49% of population density. In most forest blocks the cull ranged between 10% and 30% (Table 5.2, Fig. 5.7). Despite low roe deer numbers (< 10 deer km^{-2}) there was still a high roe deer cull (> 40% of population density) in some forest blocks (Fig. 5.7). Low emigration rates or immigration was observed when the roe deer cull reached about 50% of the population density. For roe deer the annual harvest reached between 14.0% and 85.0% of the annual production (number of reproductively active females x fertility x kid survival) in 2008/09 and 2009/10 (Table 5.2). Thus, in some forest blocks the cull has to be five times higher even just to harvest the annual production.

The Reeve’s muntjac cull varied from 3% to 35% of the population density (Table 5.2, Fig. 5.8). In most forest blocks the cull ranged between 21% and 35% of the population density (Table 5.2, Fig. 5.8). A cull of about 70% of the population density converted the forest block Cro into a sink in 2009/10. Only in forest block Cro for kid survival 65% and 70% the annual cull reached over the annual production by 30% and 20% respectively in 2009/10. In all other forest blocks the percentage shoot of the annual production varied from 6% to 64% for a kid survival of 65% and from 6% to 60% for a kid survival of 70% in 2008/09 and 2009/10 (Table 5.2). Hence, in forest block Elv the cull has to be about 15 times higher to harvest the annual production.

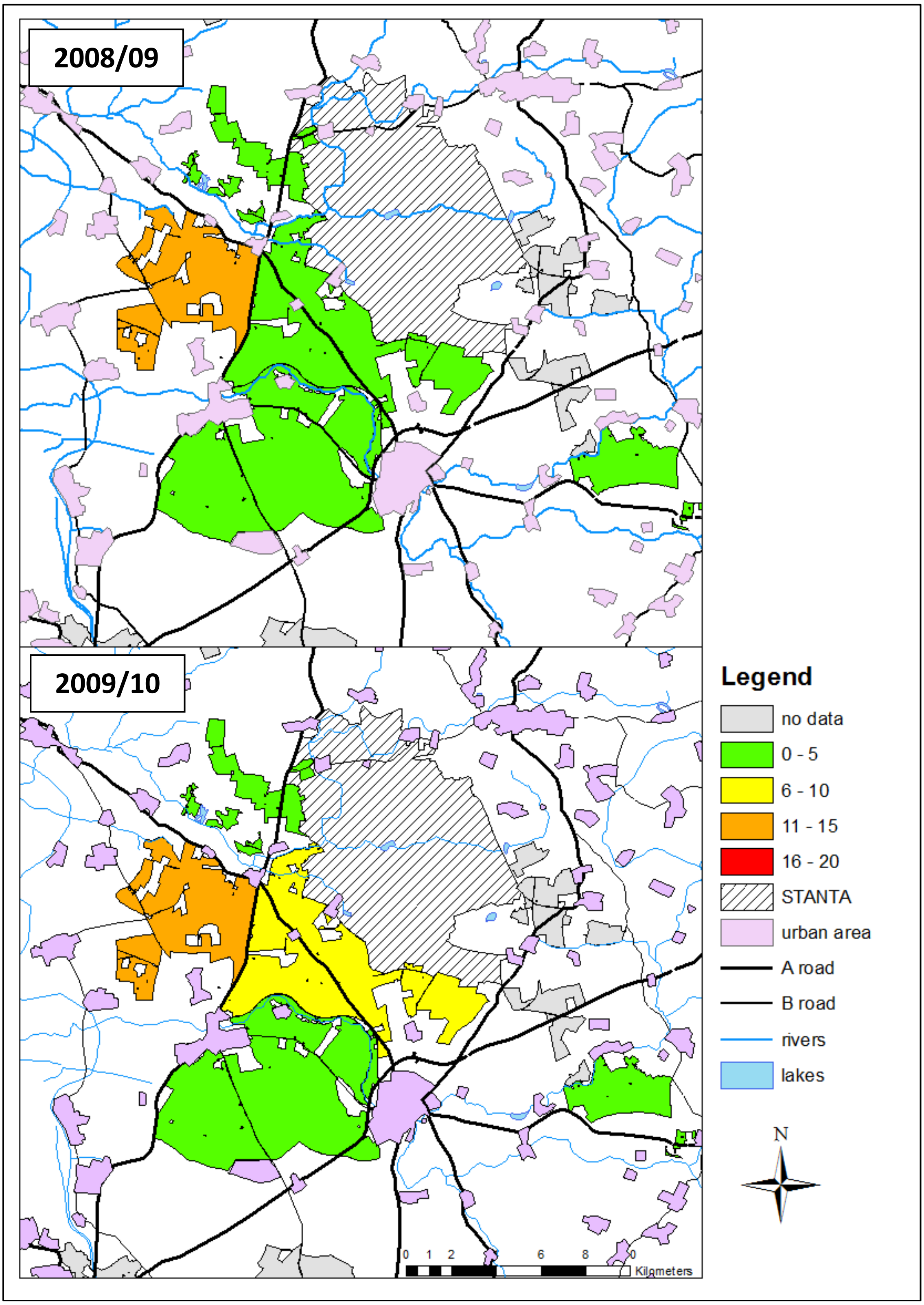

Fig. 5.9. Spatial variation of potential roe deer population growth (km^{-2}) in seven forest blocks of Thetford Forest in 2008/09 and 2009/10.

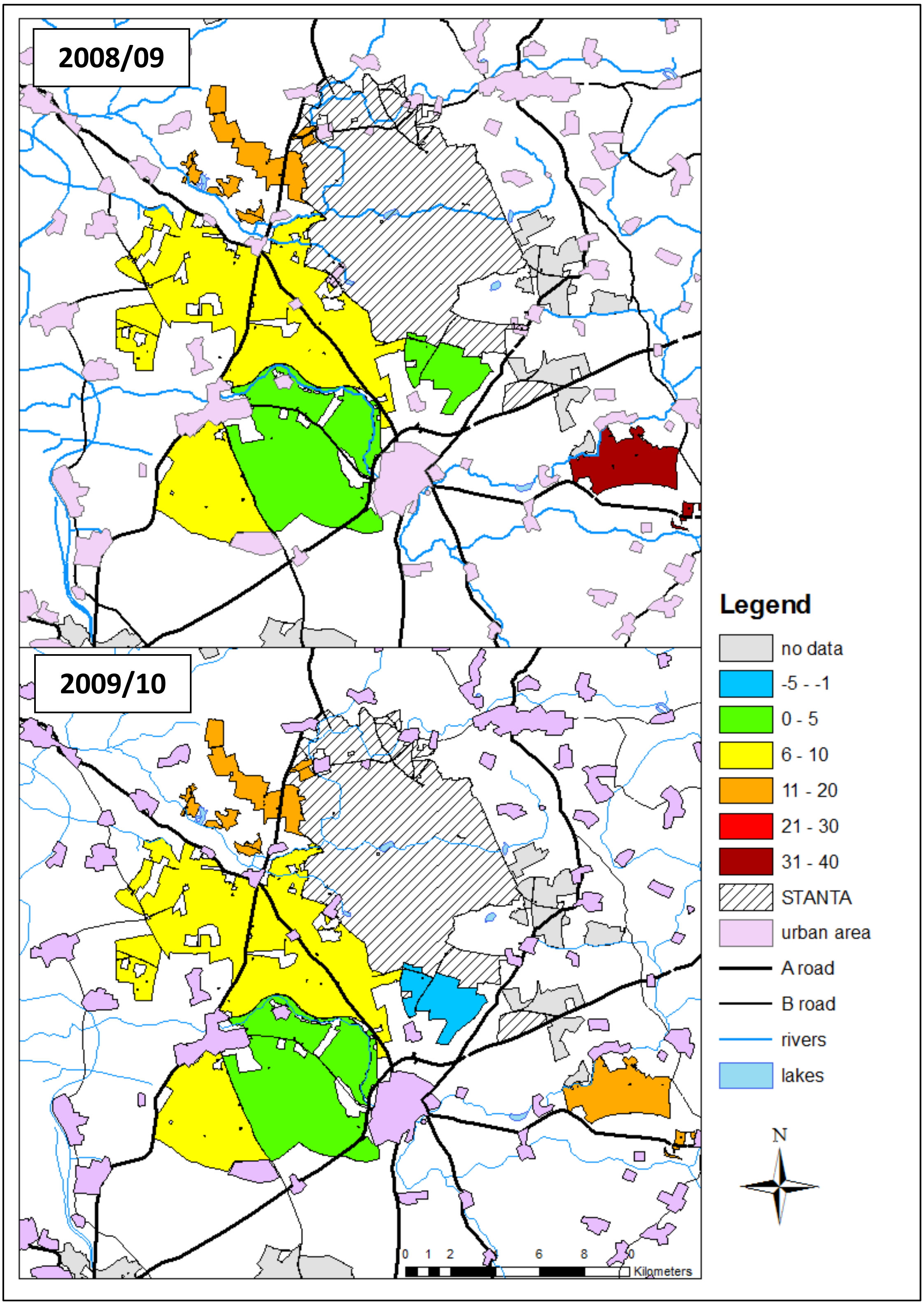

Fig. 5.10. Spatial variation of potential Reeve’s muntjac population growth (km^{-2}) assuming 65% kid survival in seven forest blocks of Thetford Forest in 2008/09 and 2009/10.

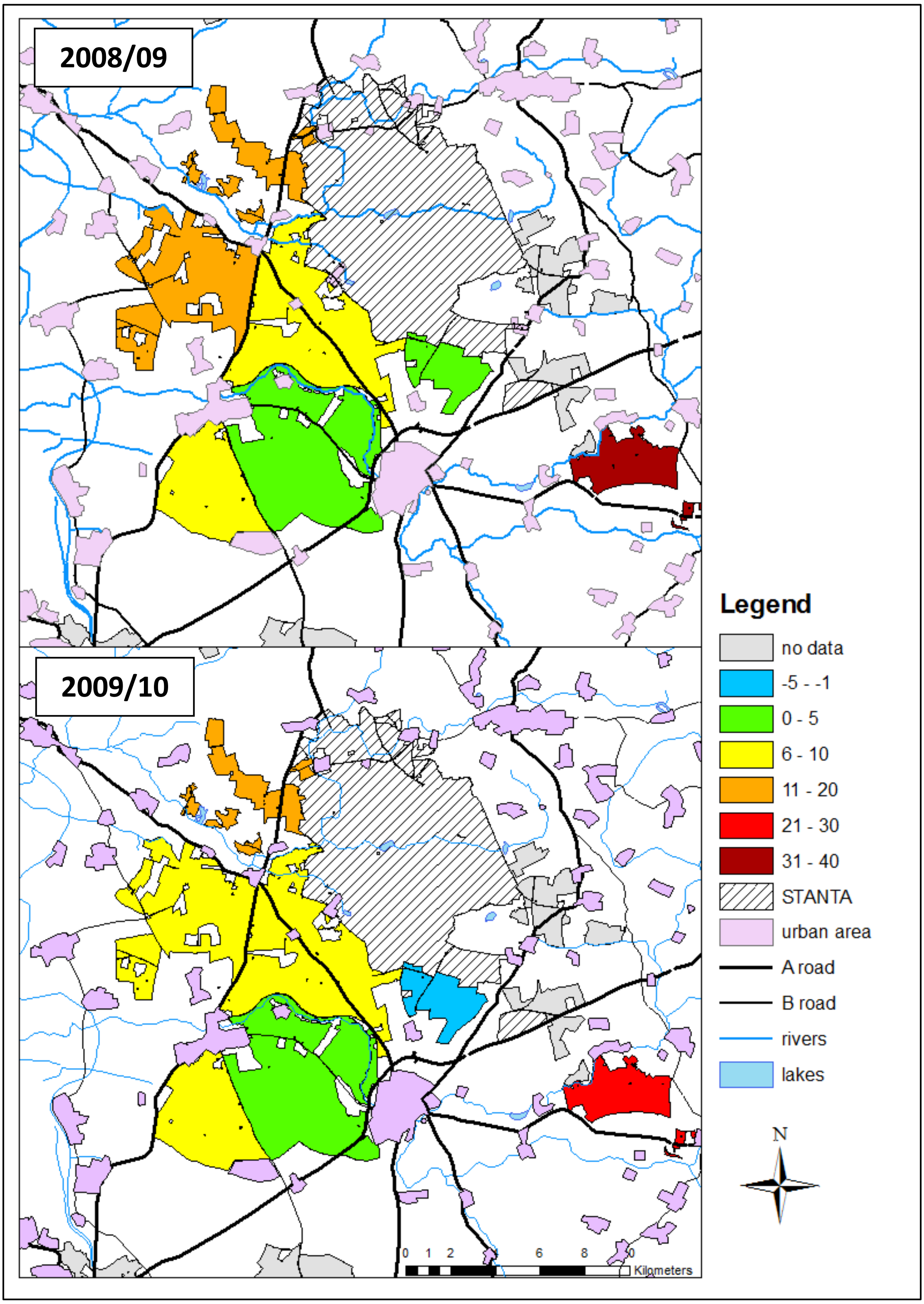

Fig. 5.11. Spatial variation of potential Reeve's muntjac population growth (km^{-2}) assuming 70% kid survival in seven forest blocks of Thetford Forest in 2008/09 and 2009/10.

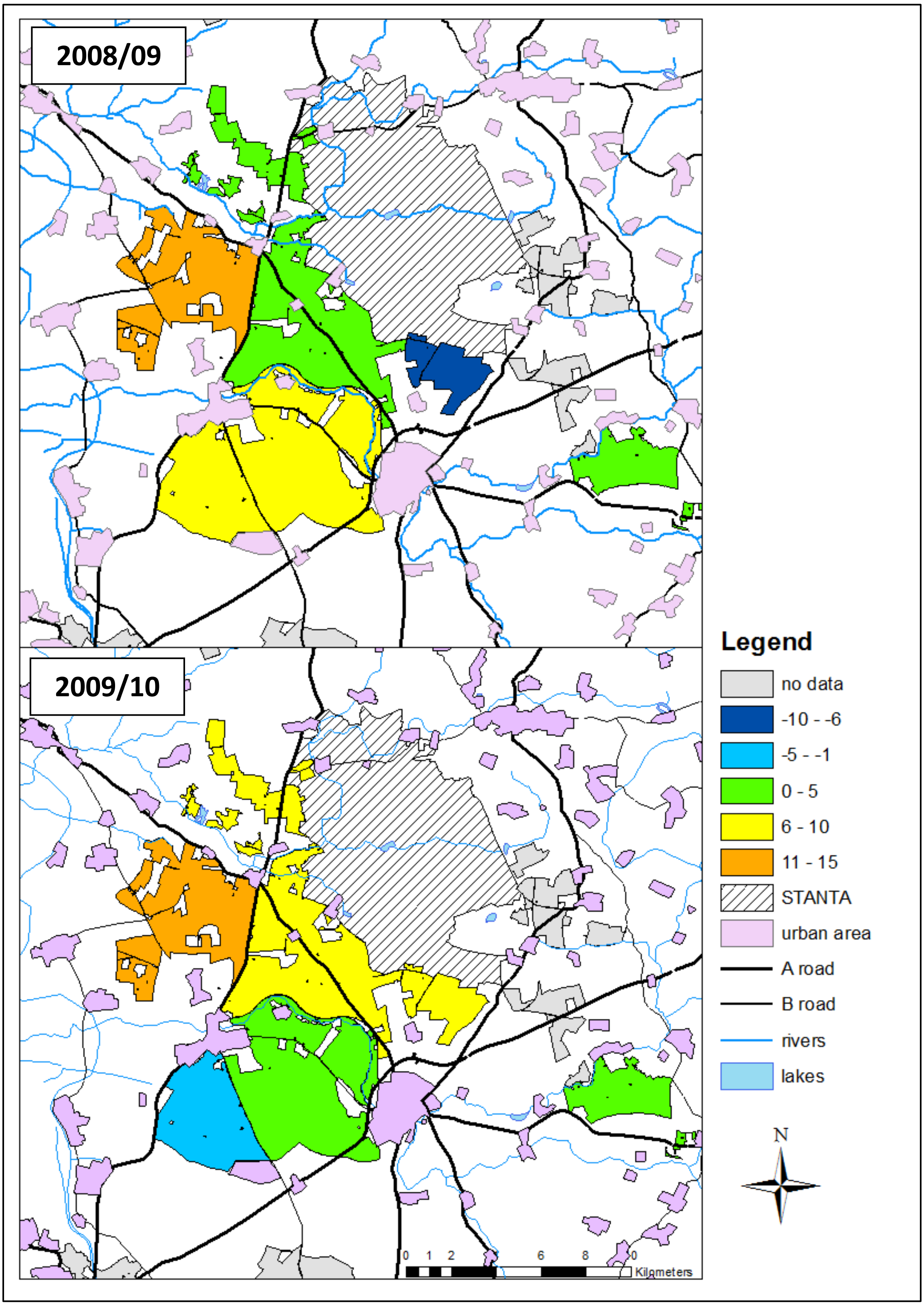

Fig. 5.12. Spatial variation of potential roe deer (km^{-2}) emigrating or immigrating in seven blocks of Thetford Forest in 2008/09 and 2009/10.

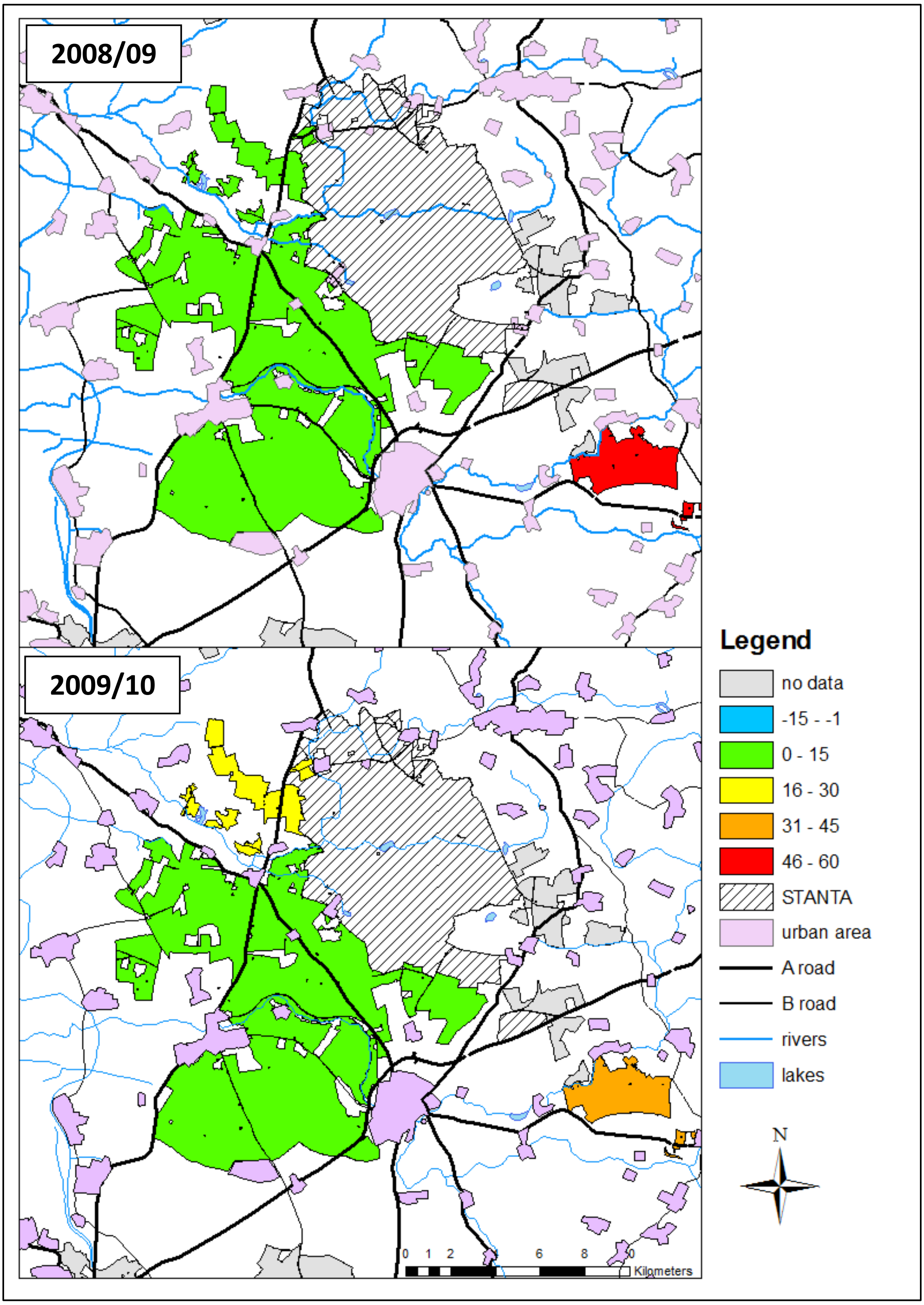

Fig. 5.13. Spatial variation of potential Reeve’s muntjac (km^{-2}) emigrating or immigrating assuming 65% kid survival in seven blocks of Thetford Forest in 2008/09 and 2009/10.

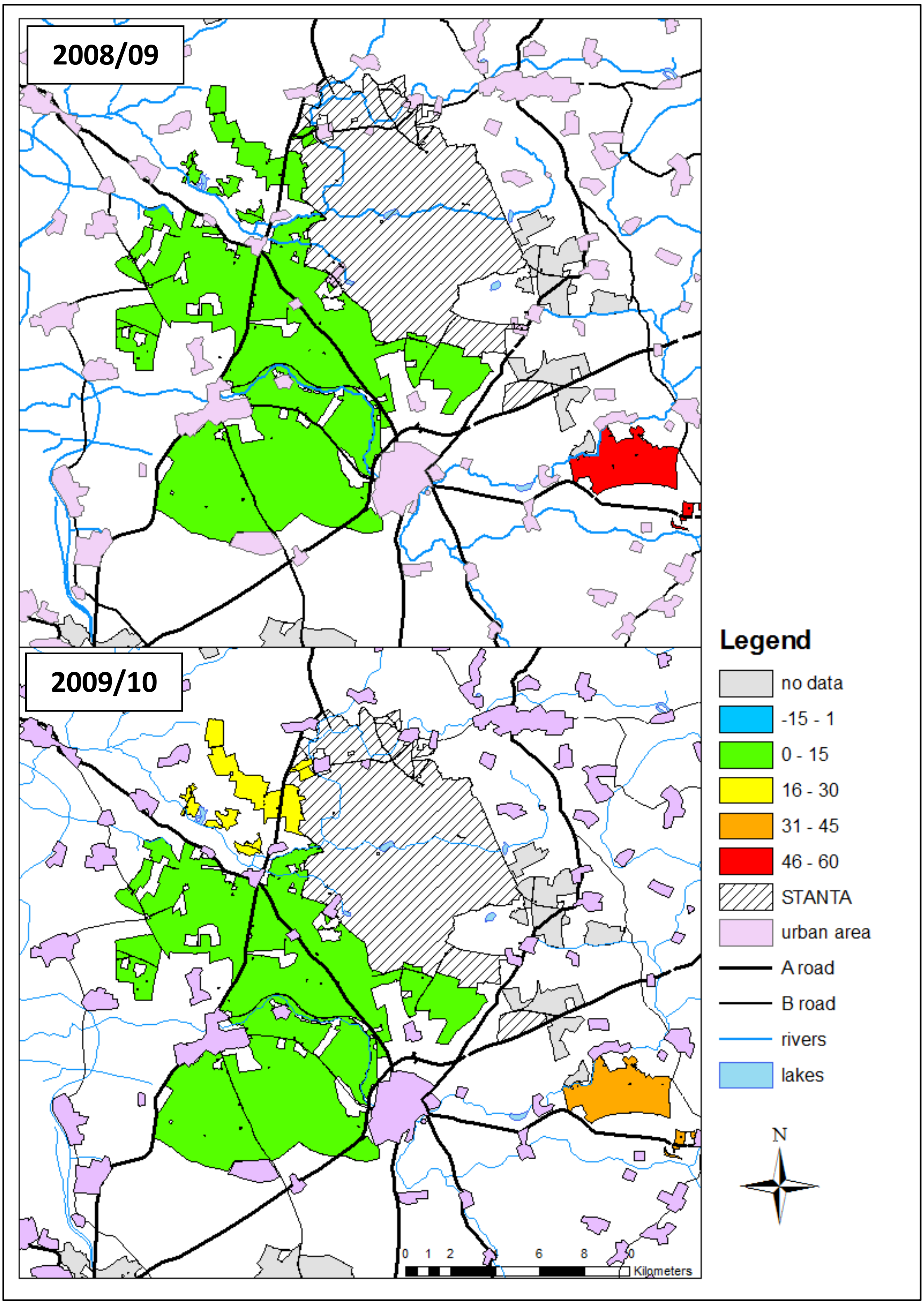

Fig. 5.14. Spatial variation of potential Reeve’s muntjac (km^{-2}) emigrating or immigrating assuming 70% kid survival in seven blocks of Thetford Forest in 2008/09 and 2009/10.

Discussion

Roe deer and Reeve's muntjac densities differed across monitored forest blocks but were stable between years, whereas potential net population growth differed between forest blocks and years. I found potential emigration of roe deer in six out of seven forest blocks in 2008/09 and in 2009/10. For Reeve's muntjac emigration potentially occurred in all forest blocks in both 2008/09 and 2009/10.

Variations in density of large herbivores are typically low from year to year (Morellet et al., 2007) as shown in this study when deer management practice stayed unchanged. Despite positive potential population growth and low variations in deer density from year to year, two forest blocks within this study showed low (potentially 11 individuals) to medium (potentially 48 individuals) immigration rates for roe deer. Pulliam (1988) and Runge et al. (2006) suggested that positive population growth does not necessarily mean deer is emigrating due to increasing numbers and negative population growth not necessarily deer is immigrating. Potential emigration rate differed among forest blocks and ranged from very few individuals to several hundred individuals per block per year and differed also among years for both roe deer and muntjac. Despite low roe deer density (< 10 deer km^{-2}, Mayle (1996)) in three out of seven forest blocks, the observed roe deer density in year 2 was lower than the potential density (deer density in year 1 plus production minus cull). Roe deer and muntjac emigration/immigration rates may annually vary between forest blocks due to carrying capacity, unknown sources of mortality (e.g. RTA's) and/or impacts (interspecific density dependence) of other deer species e.g. fallow deer (Focardi et al., 2006) and Reeve's muntjac (Dolman and Wäber, 2008, Hemami et al., 2005).

In Thetford Forest the number of known RTA's across all twelve forest blocks is about 100 individuals each for roe deer and Reeve's muntjac (T. Banham pers. communication). Yet, the total number of RTA's will be difficult to assess. Langbein (2010) reported that forest rangers believe they were only able to record about 60% of the total RTA's in an area. For Thetford Forest this would imply that the total number of RTA's may be closer to 200 RTA's than 100 RTA's annually. The seven forest blocks in Thetford Forest cover about 62% of the total forest area. Thus, about 100 RTA's involving deer may be observed annually in these seven blocks together suggesting that only 15% of the potential emigrating roe deer and 7% of the potential emigration of Reeve's muntjac may die on the road. Of the remaining 75%-93% some deer may be shot on neighbouring estates, by illegal harvested or killed by diseases. Currently, venison prices are low suggesting that only few individuals may be illegally harvested.

To my knowledge there were no disease outbreaks in Thetford Forest in the last four years, while carcasses or skeletons are very rarely encountered within the forest. But there is still the possibility that net emigration occurred due to local demographic stochasticity, for example if local (block-specific) neonatal mortality was lower than the forest-wide estimated mean used in the model. I tested if a replacement of the mean deer density by the lower 95% CI's of the density would change the predicted source sink dynamics. The 95% CI's of the density estimates were on average 37% for roe deer and 27% for muntjac smaller than the mean density. For roe deer I found that the potential overall emigration for the seven forest blocks was reduced by 46% (total number emigrating: 371 individuals) in 2008/09 and by 33% (469 individuals) in 2009/2010 leaving only three forest blocks where deer emigration in each block was higher than 60 individuals (Mun, Elv, HiLo). The potential overall emigration rate for Reeve's muntjac was reduced by about 20% (65% kid survival: 1049 individuals; 70% kid survival: 1155 individuals) in 2008/09 and by about 50% (65% kid survival: 566 individuals; 70% kid survival: 657 individuals) in 2009/10. Here Mun and Har proved to be the biggest source for net emigration exporting more than 300 individuals each in the wider landscape. Using the lower 95% CI density data and reducing kid survival for roe deer and muntjac to a low level of 50% reduced the predicted potential net emigration for roe by about 88% (total number emigrating: 85 individuals) and for muntjac by 44% (729 individuals) in 2008/09 and for roe by 73% (190 individuals) and for muntjac by 76% (296 individuals) in 2009/10. Thus, if kid survival were reduced to 50%, then emigration and immigration for roe deer was most likely balanced in the seven forest blocks in 2008/09. However, there is strong evidence to support the mean neonatal mortality used in the basic model. In contrast, for muntjac even if neonatal mortality is assumed to be as low as 50%, these forest blocks were still a source. Hereby, the potential emigration rate was still high in block Har (> 20 deer km^{-2}). Thus, for roe deer forest blocks with either high deer density or where only a low percentage of the population was culled (e.g. 10%) were strong sources whereas the other forest blocks may either be weak sources or sinks.

Differences in roe deer and Reeve's muntjac emigration and immigration in 2008/09 and 2009/10 may be due to winter weather effects such as cold temperature. In 2009/10 mean monthly winter temperature were lower and the period of snow covering the ground longer (Santon Downham weather station) than in 2008/09. Also due to prolonged frost from December to February in 2009/10 the farmland could not be cultivated and food availability for deer was low. Therefore areas with lower deer density and higher carrying capacity may have acted as sinks into which dispersing deer recruited, whereas areas with high deer density could no longer support these high numbers of deer. In 2009/10 the net emigration/immigration (per km^2) was positively correlated to deer density (per km^2) for roe deer ($n = 7$, $r = 0.82$, $p = 0.03$) and muntjac ($n = 7$, $r = 0.85$, $p = 0.02$) but not in 2008/09 (roe deer: $n = 7$, $r = 0.60$, $p = 0.16$; muntjac: $n = 7$, $r = 0.56$, $p = 0.19$). Forest block Did is a small island block surrounded by farmland. Here emigration rate may have increased due to less available food in the farmland. In contrast, Lyn and HiLo are core blocks with restricted access to farmland, however food availability in the block may not have supported the same number of deer as the year before. In island forest blocks Har and Cro the impact of an increased cull and the decreased food availability in the surrounding farmland may have reduced emigration rates.

Radio telemetry studies show that there is some support for the hypothesis that roe deer may disperse across landscapes. In southern Norway Mysterud (1999) observed that radio collared roe deer migrated to low quality areas in higher evaluations during summer although roe deer density was low (3-5 roe km^{-2}). He suggested that density dependent habitat selection may be one possible explanation of these movements and speculated that sub-dominant animals may be forced to higher evaluations by dominant animals. Here migration distances were greater for females (range 0.7-45.7 km) than for males (range 2.5-7.1 km). In Sweden, however, observed dispersal of radio collard roe deer under high population density was mainly over short distances (< 10 km) (Wahlstrom and Liberg, 1995). Investigating fine-scale natal dispersal in two roe populations in France and one roe population in Sweden Gaillard et al. (2008) found no differences in proportion or dispersal distances between male and female roe deer and in relation to population density. They suggested that habitat quality may act as driver for fine-scale natal dispersal. Thus, movements over several kilometres are not uncommon across the European range of this species, and the source sink dynamics postulated for Thetford Forest are highly feasible.

For Reeve’s muntjac Chapman et al. (1994) suggested that the natural rate of spread is 1 km per year and similar to dispersal rates of other deer species living in Britain whilst Ward (2005) suggested that muntjac has the highest range expansion (expansion at a compound rate of 8.2% of occupied 10 km squares per year) of all six deer species in Britain. However, if an area is acting as a source there will be a shift in distribution in the wider landscape and deer at the periphery of the distribution may be forced to colonise new areas due to a wave initiated by the core subpopulation acting as a source. Distribution maps by Ward (2005) showing that roe deer and Reeve’s muntjac have expanded greatly in range from 1972 to 2002, with a spreading range in Eastern England from the initial Thetford Forest nucleus, support my findings that

Thetford Forest has mainly acted as a source and has contributed to spreading roe deer and Reeve's muntjac into the wider landscape. Though, Thetford Forest will not be the only source in the wider landscape. Possible net emigration from one landscape into the wider landscape will have consequences for deer management and nature conservation issues.

The ability to measure deer densities, fertility, kid survival, and cull levels allowed the planning of strategic deer management. In Europe deer numbers have been underestimated in the past leading to their expansion in the wider landscape. The lack of knowledge of Reeve's muntjac biology (e.g. kid survival rates, migration distances) has undermined effective deer management in Thetford Forest in the past. Calculating source-sink dynamics for red deer and fallow deer will be more complicated. Much larger areas have to be considered stretching over entire deer management groups. Here, acquiring and collating comprehensive cull numbers and fertility may be more difficult.

These results emphasise the extent to which local effects of management may be offset by inward migration and recruitment from neighbouring, possible unmanaged, parts of the landscape. The understanding of possible source sink dynamics will help to understand how the cull relates to the size of the population, the magnitude of possible productivity or the potential for recruitment from neighbouring areas and therefore allows to predict appropriate management targets. For example, the knowledge of such sources of deer emigration may enable deer managers to focus their cull effort in source areas. The artificial creation of source-sink dynamics may be helpful in management areas where culling is difficult e.g. in areas with high public access or inaccessible areas. More research is needed investigating deer densities across management boundaries and across deer species to improve our knowledge about source-sink dynamics, deer impacts on biodiversity and how source-sink dynamics may be influenced by inter-specific competition.

References

Aitken, R. J. (1974) Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility,* **39,** 225-233.

Allombert, S., Stockton, S. & Martin, J. L. (2005) A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology,* **19,** 1917-1929.

Barrett, M. A. & Stiling, P. (2006) Effects of Key deer herbivory on forest communities in the lower Florida Keys. *Biological Conservation,* **129,** 100-108.

Bruinderink, G. & Hazebroek, E. (1996) Ungulate traffic collisions in Europe. *Conservation Biology,* **10,** 1059-1067.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. (2001) *Introduction to Distance Sampling - Estimating abundance of biological populations,* Oxford University Press, Oxford.

Chapman, N., Harris, S. & Stanford, A. (1994) Reeves muntjac *Muntiacus reevesi* in Britain - Their history, spread, habitat selection, and the role of human iintervention in accelerating their dispersal. *Mammal Review,* **24,** 113-160.

Chapman, N. G. (1991) Chinese muntjac *Muntiacus reevesi*. *The handbook of British mammals* (eds G. B. Corbet & S. Harris), pp. 526-532. Blackwell Scientific, 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.

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 Theriologica,* **30,** 287-303.

Chapman, N. G., Furlong, M. & Harris, S. (1997) Reproductive strategies and the influence of date of birth on growth and sexual development of an aseasonally-breeding ungulate: Reeves' muntjac (*Muntiacus reevesi*). *Journal of Zoology,* **241,** 551-570.

Cote, 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 (2009) Rural development programme - Questions and Answers: Section G.

Dolman, P. M. & Sutherland, W. J. (1992) The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* **29,** 402-413.

Dolman, P. M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research,* **35,** 202-214.

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.

Feber, R. E., Brereton, T. M., Warren, M. S. & Oates, M. (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. *Forestry,* **74,** 271-276.

Flowerdew, J. R. & Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry,* **74,** 277-287.

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.

Fuller, R. J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. *Forestry,* **74,** 289-298.

Fuller, R. J., Smith, K. W., Grice, P. V., Currie, F. A. & Quine, C. P. (2007) Habitat change and woodland birds in Britain: implications for management and future research. *Ibis,* **149,** 261-268.

Gaillard, J.-M., Hewison, A. J. M., Kjellander, P., Pettorelli, N., Bonenfant, C., van Moorter, B., Liberg, O., Andren, H., van Laere, G., Klein, F., Angibault, J.-M., Coulon, A. & Vanpé, C. (2008) Population density and sex do not influence fine-scale natal dispersal in roe deer. *Proceedings of the Royal Society B,* **275,** 2025-2030.

Gill, R. M. A. & Beardall, V. (2001) The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry,* **74,** 209-218.

Gordon, I. J., Hester, A. J. & Festa-Bianchet, M. (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology,* **41,** 1021-1031.

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, Norwich.

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.

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.

Kjellander, P., Gaillard, J. M. & Hewison, A. J. M. (2006) Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia,* **146,** 521-530.

Langbein, J. (2008) Urban deer vehicle collisions - A risky life for deer. *Urban deer conference*. Linnean Society / British Deer Society, London.

Langbein, J. (2010) Collison course. *DEER: The journal of the British Deer Society,* **15,** 10-12.

Mayle, B. A. (1996) Progress in predictive management of deer populations in British woodlands. *Forest Ecology and Management,* **88,** 187-198.

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. *Journal of Applied Ecology,* **44,** 634-643.

Mysterud, A. (1999) Seasonal migration pattern and home range of roe deer (Capreolus capreolus) in an altitudinal gradient in southern Norway. *Journal of Zoology,* **247,** 479-486.

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

Pulliam, H. R. (1988) Sources, sinks, and population regulation. *American Naturalist,* **132,** 652-661.

Putman, R. J. & Moore, N. P. (1998) Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. *Mammal Review,* **28,** 141-163.

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

Runge, J. P., Runge, M. C. & Nichols, J. D. (2006) The role of local populations within a landscape context: Defining and classifying sources and sinks. *American Naturalist,* **167,** 925-938.

Scott, D., Welch, D. & Elston, D. A. (2009) Long-term effects of leader browsing by deer on the growth of Sitka spruce (*Picea sitchensis*). *Forestry,* **82,** 387-401.

Sempéré, A. J., Mauget, R. & Mauget, C. (1998) Reproductive physiology of roe deer. *The European roe deer: the biology of success* (eds R. Andersen, P. Duncan & J. D. C. Linnell), pp. 161-188. Scandinavian University Press, Oslo.

Suominen, O. & Danell, K. (2006) Effects of large herbivores on other fauna. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (eds K. Danell, R. Bergstrom, P. Duncan & J. Pastor), pp. 383-412. Cambridge University Press, Cambridge.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. & Burnham, K. P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology,* **47,** 5-14.

Wahlstrom, L. K. & Liberg, O. (1995) Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). *Journal of Zoology,* **235,** 455-467.

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

Wilson, C. J. (2003) A preliminary estimate of the cost of damage caused by deer to agriculture in England. *Rural Development Service* (ed DEFRA).

Chapter Six

Consequences of heterogeneity in deer abundance and composition: response of vegetation structure and woodland birds

Abstract

The effects of increasing deer populations on vegetation have been widely reported in Europe and North America. There is mounting evidence from North America that structural changes to vegetation caused by deer reduce the abundance and alter the community composition of forest bird assemblages and there is some evidence of similar effects in the UK. However, effects of different deer species within multi-species assemblages have not been examined previously. Here I examine the impacts of deer density and distribution on vegetation and birds at the landscape scale (120 km^2) in a lowland pine forest in East Anglia, UK. Percentage cover of shrubs, grass, bramble and bracken as well as the bird species assemblage were assessed in seven forest blocks in the summers of 2007 and 2008. Deer biomass per forest block was calculated from deer densities estimated in 2008-10. Four deer species (Reeve's muntjac, roe, fallow and red deer) were present in the study area but varied in density among blocks. Total deer biomass varied between forest blocks and was mainly dominated by the combined biomass of roe deer and Reeve's muntjac, with the combined biomass of red and fallow deer dominant in two of the seven forest blocks. I predicted that the percentage cover of shrubs and bramble would be reduced, and that the percentage grass cover would be greater, in areas with higher deer biomass. Thus, due to reduced shrub understorey foliage density in areas with high deer biomass, abundances of understorey dependent bird species were predicted to be lower whereas abundances of understorey independent bird species should not vary among forest blocks. However, no direct relationship between deer biomass and either vegetation or birds could be established. Percentage of vegetation cover and the abundance of understorey independent birds varied more widely among plantation growth stages than among the seven forest blocks. Forest blocks are a complex ecological system varying in many factors, for example in soil composition. I suggest that due to different carrying capacity among forest blocks and long term browsing effects, it is difficult to establish differences in vegetation cover and in bird abundances in response to contemporary differences in deer densities. However, the abundance of understorey dependent birds varied more widely among forest blocks than growth stages. To further investigate this finding I suggest further research should not only concentrate on the abundance of birds (bird/ha) but also on the number of species. It would also be useful for further analysis to concentrate on bird species that are known to be sensitive to deer browsing such as Garden Warbler *Sylvia borin* or Dunnock *Prunella modularis*.

Introduction

It is a well-known phenomenon that herbivores modify their habitat through browsing and grazing (Cote et al., 2004, Dolman and Wäber, 2008). There is increasing evidence that high and still increasing deer densities (Ward, 2005, Dolman and Wäber, 2008) affect habitat suitability for woodland birds, especially through reducing the foliage density of shrub layer and sub-canopy vegetation (e.g. below 1.5 m) (Gill and Morgan, 2010, Fuller and Gill, 2001, Gill and Fuller, 2007, Amar et al., 2006).

Exclosures studies (Putman and Moore, 1998, Cooke and Farrell, 2001, Morecroft et al., 2001), comparing complete deer exclusion to a usually unquantified deer density, show clearly and graphically how deer can affect vegetation structure and composition. Evidence that deer browsing affects Common Nightingale *Luscinia megarhynchos* by reducing dense understorey at fine-scale habitat selection and habitat use has been provided by Holt et al. (2010). Using radio telemetry and territory mapping they found that density of territories was 15 times greater in exclosures than in grazed controls, suggesting that increased deer populations have contributed to the decline in Nightingales in Britain (Holt et al., 2010). But the understanding that these experiments provide is incomplete, when the relationship between ungulate density and the dependent biodiversity responses are non-linear (Rooney and Waller, 2003) and differ between features (e.g. birds, plants).

Very few studies have investigated the impacts of different levels of deer density on bird abundance at landscape scale (e.g. Zipkin, et al. (2010), Allombert et al. (2005a)). Zipkin et al. (2010) compared bird communities in two geographically similar study areas which differed in density of white-tailed deer *Odocoileus virginianus* (hunted versus not hunted) in the US. Here, they found no differences in the overall bird communities between the two study areas but lower estimated densities for some understorey species in the area with no hunting. In British Columbia, Canada, bird assemblages were compared on six islands that had either no deer, had white-tailed deer present for less than 20 years or more than 50 years (Allombert et al., 2005a). Songbird abundance was 55-70% lower on islands with a browsing history of more than 50 years compared with deer free islands. Allombert et al. (2005a) found that species with the highest dependence on understorey declined by 93% on islands where deer had been present for more than 50 years.

In the UK an unusual multi-species deer assemblage exists, consisting of three introduced species (Reeve’s muntjac *Muntiacus reevesi*, Chinese water deer

Hydropotes inermis and sika deer *Cervus nippon*), one naturalised species (fallow deer *Dama dama*) and two native species (roe deer *Capreolus capreolus* and red deer *Cervus elaphus*). Although, deer impacts on biodiversity have been investigated in many areas of the world (Barrett and Stiling, 2006, Palmer et al., 2003) the focus has been on the impact of either one species (e.g. for North America: white-tailed deer *Odocoileus virginianus* in Rooney and Waller (2003)) or the combined impacts of different deer species (e.g. for the UK: Reeve's muntjac, roe and fallow deer in Holt et al. (2010)). However, deer differ in their feeding habits, ranging behaviour, height and browse line. Previous studies have shown differences in impacts of Reeve's muntjac and fallow deer on ground flora (Cooke, 2006). No previous study has attempted to contrast the impacts of different deer species.

In this study we related bird abundance sampled across 126 plots, to deer biomass, and vegetation cover of the shrub layer, grass layer, bramble (*Rubus* spp.) and bracken (*n* = 189 plots) in a 195 km^2 conifer plantation in the UK. Data were collected in seven forest blocks (120 km^2) during 2007-08. The indirect effects of herbivory on birds, arising from deer grazing and browsing impacts on woodland structure were explored. My hypotheses are that (1) varying deer densities and species distribution within the forest will be reflected in differences in vegetation structure and composition as well as bird abundance; (2) deer impacts on vegetation in forest blocks with greater densities of red deer and fallow deer are expected, compared to areas with greater densities of roe deer and Reeve's muntjac.

Methods

(a) Study area

Thetford Forest, the largest lowland conifer forest (195 km^2) in the UK, is located in Breckland, a biogeographical region in eastern England (52°30´N, 0°60´W). The region is characterised by semi-continental climate and sandy, nutrient-poor soils (Dolman and Sutherland, 1992). Corsican pine (*Pinus nigra*) (59 %) and Scots pine (*Pinus sylvestris*) (15 %) dominating the forest in a mosaic of growth stages with other conifers taking up 5% and deciduous tree species 10% of the area. Thetford Forest is subdivided into twelve deer management units (DMU's) (mean area = 15.6 ± 10.2 km^2 SD, range 4.5 km^2 to 34.7 km^2) by roads. The data presented in this Chapter were obtained from seven (120 km^2) of these DMU's; however one DMU was sub-divided to provide two sampling blocks, while a further two DMU’s were combined into a single sampling block (see below). As a result, sampling covered a total of seven forest blocks.

Thetford Forest is managed by rotational clear-felling, creating a mosaic of even aged growth stages (sub-compartments) (mean area = 3.1 ha ± 3.1 SD) subdivided by a ride network (Eycott et al., 2006). Detailed information (crops species, planting year, area and soil type) of each management sub-compartment are available from a GIS database maintained by Forestry Commission (FC).

Four deer species are present in the study area: native roe deer and red deer and the introduced Reeve’s muntjac and fallow deer. The two smaller deer species, roe deer and Reeve’s muntjac, are widespread at low to high densities (range: 3 km^{-2} to 40 km^{-2} and 11 km^{-2} to 81 km^{-2} respectively) throughout the study area. Red deer are widespread at low numbers (density < 5 km^{-2}) with herds being larger in the southern than in the northern forest blocks. Fallow deer are well established in the southern forest blocks at densities between 5 km^{-2} and 10 km^{-2}, but are still scarce in the northern forest blocks (density < 2 km^{-2}).

(b) Overview of study design

Deer density and species distribution differs spatially across the forest and thus differs among DMU’s. Within this study seven out of the twelve forest DMU’s were sampled: Croxton, Didlington, Harling, Mundford, High Lodge, Elveden and Lynford. However, the last was split between Lynford North and Lynford South for vegetation and bird surveys as access was limited in Lynford North in the first year of the project due to timber management, whereas Elveden and High Lodge were pooled as vegetation structure and deer species composition were similar to increase sample size. Thus for the purpose of study design, sampling and analysis, a total of seven sampling units (hereafter referred to as blocks) were considered (Cro, Did, Lyn S, Har, Mun, HiLo+Elv, Lyn N). Forest block (n = 7) is therefore considered as a higher landscape-scale level of sampling structure, that relates to differences in deer biomass or deer composition. Within forest blocks, both birds and vegetation were sampled in replicate coupes (even-aged planting areas, hereafter referred to as plots) that were stratified by growth stage and soil type. An inevitable weakness of the experimental design is the low number of forest blocks that could be sampled. This limits the power of the analyses to detect clear relationships with deer. However, given the interest in examining differing effects of deer species, and non-linear relationships with deer density, it is nevertheless informative to examine any responses that can be observed.

Bird and vegetation surveys were stratified among growth stages as both vegetation and bird species composition differ with stand development. Areas with dense undergrowth are particularly susceptible to deer grazing and browsing. Therefore sampling effort was concentrated on those growth stages that support dense undergrowth (i.e. pre-thicket, thicket and mature stages, excluding young restocks or shaded pole stages) as they were considered to contain bird populations likely to be impacted by deer browsing. Although, some restock (age: 1-3 years after planting) and pole stage (21-45 years) plots were sampled they were excluded from analyses as they have little undergrowth, and therefore were considered to be unlikely to contain bird populations that may potentially be impacted by deer browsing.

Pre-thicket plots (age: 5-10 years after planting), after establishment of the young trees but before canopy closure, comprise encroaching tree crop and dense herb and shrub layer vegetation. Thicket plots (11-20 years) were those in the initial stages of canopy closure before the relatively dense field and shrub layers associated with the open conditions of earlier growth stages had been shaded out. Mature pine plots (> 45 years) contained large trees at a low density following regular thinning management (conducted at five year intervals after 25 years growth) and also where the canopy had thinned in places due to competitive self-thinning of trees, often leading to understorey regeneration and dense bramble, grass or bracken. Soil type reflected whether compartments had been de-stumped (DS) at the time of the previous harvest or not (non-destumped; NDS). De-stumping profoundly affects habitat suitability for some bird species as the regular rows of upturned stumps that are created are initially exploited by species such as pied wagtail *Motacilla alba* and robin *Erithacus rubecula*, and later as scrub develops along and within the stump row they may be colonised by species such as whitethroat *Sylvia communis* and wren *Troglodytes troglodytes*.

Sampling intensity (in terms of the number of replicate plots per block) for vegetation and bird surveys was not equal among blocks. It varied in respect of a planned before-after case-control experiment to examine responses to deer management. Blocks were divided between one high intensity survey block (Cro: that provides the base line prior to subsequent experimentally enhanced deer management), medium sampling replication in three control blocks (Did, Lyn S, Har that form the controls for the subsequent deer management experiment) and lower sampling intensity in each of three wider landscape blocks (Lyn N, HiLo + Elv, Mun) in which fewer replicate plots were sampled (see Table 6.1a and 6.1b). Results presented here relate to baseline monitoring prior to imposition of experimental deer management.

For bird surveys, where-ever possible, for each growth stage and soil type class, three replicate plots were sampled in the intensive block (Cro), two replicate plots were sampled in each of the three control blocks (Did, Lyn S, Har), two replicate plots in the pooled wider landscape block (Elv + Hi Lo), and just one replicate in each of the remaining wider landscape blocks (Lyn N, Mun) (see Table 6.1a). For vegetation surveys, where-ever possible, for each growth stage and soil type class, three replicate plots were sampled in each of the four intensitve and control blocks (Cro, Did, Lyn S, Har) and two in each of the wider study blocks (Lyn N, Elv, Hi Lo, Mun) (Table 6.1b and 6.3), which therefore provided four replicates per strata in the pooled Elv + Hi Lo wider landscape block. There were minor differences in growth stage classes sampled for birds, and for vegetation. Although efforts were made to sample vegetation in all bird-survey plots, a small number of these (early thicket aged) were not sampled for vegetation structure. In addition to the growth stages sampled for birds (pre-thicket, early thicket, mature) restock aged plots were also sampled for vegetation, while younger (late pole age 35 years+) stands were also sampled in addition to mature plots (>40 years). The growth stage definition (age classes) was the same for birds and vegetation.

Roe deer and Reeve’s muntjac are both characterised as browsers (i.e. concentrate selectors) and are of similar height (though roe are slightly taller) (Corbet and Harris, 1991). Thus, the impacts of these two deer species on shrub layer vegetation are expected to be similar but are predicted to be different from the impacts of the taller red and fallow deer which are characterised as grazers (Clauss et al., 2003). Grazers unlike browsers have a large rumen which enables them to tolerate lower quality forage (Clauss et al., 2003); thus they may persist on grass dominated vegetation after shrubs have been suppressed by browsing. The structure of vegetation and of bird communities was therefore related separately to the combined biomass of roe and muntjac, and to that of red and fallow deer. Finally, I pooled the biomass of all deer species to examine the overall effect of deer browsing and grazing on vegetation cover and birds.

Table 6.1. Number of coupes surveyed for a) birds (*n* = 126) and b) vegetation structure plots (2008: *n* = 143; 2009: *n* = 172) in each growth stage (restock: 1-3 years after planting, pre-thicket: 5-10 years, thicket: 11-20 years, pole: 21-45 years, pre-fell: > 45 years) and soil type (Non-destumped NDS vs. destumped DS) in each forest block in 2007 and 2008 in Thetford Forest. Birds were not surveyed in restock or pole stages.

a) coupes sampled for birds

Block	Year	Pre-thicket		Thicket		Pre-fell	
		NDS	DS	NDS	DS	NDS	DS
Croxton	2007	3	3	3	3	3	3
	2008	3	4	4	3	2	2
Didlington	2007	2	2	2	2	2	2
	2008	2	3	2	2	2	1
Harling	2007	-*	-*	2	2	2	2
	2008	3	2	2	2	1	2
Lynford South	2007	2	2	2	2	2	2
	2008	3	2	2	2	1	2
Lynford North	2007	1	1	1	1	1	1
	2008	2	1	1	1	1	-
Elveden	2007	1	1	1	1	1	1
	2008	1	2	1	1	-	1
High Lodge	2007	1	1	1	1	1	1
	2008	2	1	1	1	1	-
Mundford	2007	1	1	1	1	1	1
	2008	2	1	1	1	-	1
Total		29	27	27	26	21	22

*no pre-thicket available in 2007

b) coupes sampled for vegetation

Block	Year	Restock		Pre-thicket		Thicket		Pole		Pre-fell	
		NDS	DS	NDS	DS	NDS	DS	NDS	DS	NDS	DS
Croxton	2007	-	-	2	2	3	3	3	-	3	4
	2008	4	-	3	3	3	3	3	-	3	3
Didlington	2007	-	-	1	3	3	3	3	3	3	4
	2008	2	3	1	3	3	3	3	3	2	3
Harling	2007	-	-	-*	-*	3	3	-	3	3	3
	2008	1	3	-*	-*	3	3	-	2	3	3
Lynford South	2007	-	-	3	3	3	3	3	3	3	3
	2008	3	3	3	3	3	3	3	3	3	3
Lynford North	2007	-	-	-	2	2	2	2	-	2	2
	2008	2	-	-	2	2	2	2	-	2	2
Elveden	2007	-	-	2	2	1	2	2	2	2	2
	2008	2	2	2	1	2	2	2	2	2	2
High Lodge	2007	-	-	2	2	2	2	2	2	2	1
	2008	2	2	2	2	2	2	2	2	2	1
Mundford	2007	-	-	2	1	2	2	2	2	1	2
	2008	2	2	2	2	2	2	2	2	1	1
Total		18	15	25	31	39	40	34	29	37	39

*no pre-thicket available in 2007 and 2008

(c) Deer density and biomass estimates

The density of each of the four deer species was measured by nocturnal thermal imaging distance sampling, carried out in each forest block (Cro, Did, Elv, Har, HiLo, Lyn, Mun) between January and March from 8pm to 4am in each of three years 2008-2010. Estimated deer densities for Lynford were used for both Lynford South and Lynford North. Details of field methodology and data collection are provided in Chapter four.

To obtain robust density estimates for roe deer and Reeve's muntjac the detection function was stratified by blocks and years, but pooled across growth stages. Density was estimated following the procedure described by (Buckland et al., 2001) with the computer software DISTANCE 6.0 release 2 (Thomas et al., 2010). As roe deer density stayed stable in four and Reeve's muntjac density stayed stable in five out of seven forest blocks (z-test: n.s.) (see Chapter 4, Fig. 4.8 and 4.9) the density estimates for 2008 were used for further analysis in this Chapter. For further technical details of density analyses see Chapter four.

Home ranges of red deer and fallow deer are larger than those of the two smaller deer species and can exceed the extent of forest block areas. However, to calculate the biomass for red and fallow deer for each forest block I decided to calculate block-specific densities for each of the two species. Distance sampling data for red and fallow deer were analysed separately by pooling the detection function across all seven forest blocks and across years (2008-2010) as I observed fewer than 90 deer groups in each year or forest block. This did provide species specific density estimates per forest block.

Red deer (n = 77; mean group size = 5.8 ± 4.1 SD; range: 1-21 individuals per group) and fallow deer (n = 97; mean group size = 4.3 ± 2.9 SD; range: 1-12 individuals per group) are mainly observed in herds which vary in group size (Fig. 6.1). Therefore group size may affect density estimates as smaller clusters may be missed at greater distances or cluster size may be underestimated at larger distances (Buckland et al., 2001). Using General Linear Models with poisson error I tested whether the observed group size for red and fallow deer was affected by distance after 5% right truncation of the most distant observations.

For red deer I found that group size (dependent; n = 74 groups) was not affected by distance (continuous; Wald $\chi^2_{(1)} = 2.77$, $p = 0.10$) whilst controlling for year (categorical; Wald $\chi^2_{(2)} = 0.12$, $p = 0.99$). However, the detection of fallow deer group size (dependent; n = 92 groups) was affected by distance (continuous; Wald $\chi^2_{(1)}$ = 21.18, $p < 0.001$, B = 0.004 groups/m ± 0.001 *SE*) whilst controlling for year (categorical; Wald $\chi^2_{(2)}$ = 1.21, p = 0.55). Thus, for further deer density calculations for red deer I used the observed mean group size and for fallow deer the size bias regression method provided within the software Distance. I pooled group size across blocks and years. As for roe deer and Reeve's muntjac, density was calculated following the procedure described by (Buckland et al., 2001).

Total deer biomass for each forest block was calculated from the species-specific density estimates from the thermal imaging distance sampling surveys. The mean living body mass (The Deer Initiative, 2010) for each deer species (approximately: roe deer = 20 kg; Reeve's muntjac = 12 kg; red deer = 130 kg; fallow deer = 55 kg) was used to calculate the species-specific biomass, and pooled biomasses, for each block.

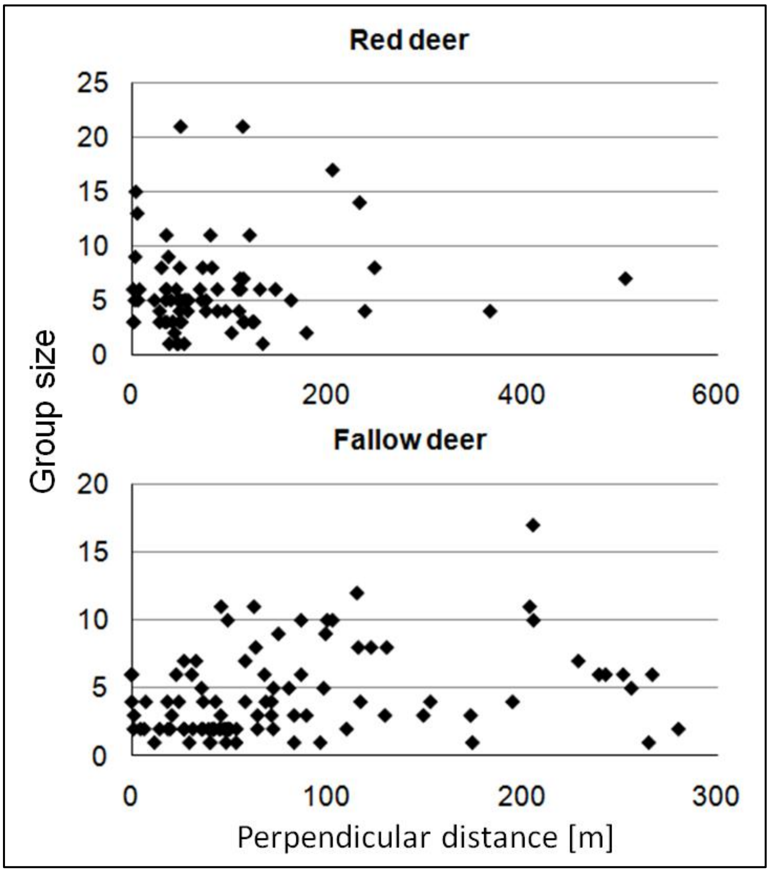

Fig. 6.1. Relationship between observed group size of red deer (n = 77) and fallow deer (n = 97) and perpendicular distance [m] from the line transect.

(c) Bird survey

Bird surveys were carried out in the same forest blocks as the thermal imaging distance sampling. All avian survey fieldwork was conducted by the British Trust for Ornithology.

In 2007 and 2008 a total of 74 and 78 coupes were surveyed respectively (Table 6.1a and 6.2). Of those 30 plots were surveyed in both years, 44 plots were unique to 2007, and 48 plots were unique to 2008.

Table 6.2. Summary of bird survey plots showing mean age ± *SD*, range years for each growth stage and soil type (NDS versus DS).

		2007				2008			
Habitat		*n*	mean	*SD*	range	*n*	mean	*SD*	range
Restock	NDS	-				3	2.3	1.2	1-3
	DS	-				1	1		1
Pre-thicket	NDS	11	7.6	1.6	5-10	12	7.9	1.5	5-10
	DS	11	7.2	1.3	6-9	18	7.2	1.4	5-10
Thicket	NDS	13	15.3	2.9	11-19	12	12.8	1.1	11-15
	DS	13	13.9	3.1	11-19	12	12.8	1.4	11-15
Pole	NDS	-				-			
	DS	1	42.0		42	-			
Mature	NDS	14	66.6	11.0	48-80	8	66.8	11.5	48-79
	DS	12	64.8	11.0	47-79	9	68.7	10.5	52-81
Total		75				78			

*restock: 1-3 years; pre-thicket: 4-10; thicket: 11-20; pole: 21-45; mature: > 45 years.

Table 6.3. Summary of vegetation plots showing mean age (± *SD*) and range of years growth, for each growth stage and soil type (NDS versus DS).

		2007				2008			
Habitat		*n*	mean	*SD*	range	*n*	mean	*SD*	range
Restock	NDS	-				12	2.1	0.8	1-3
	DS	-				9	1.9	0.8	1-3
Pre-thicket	NDS	16	7.5	1.6	5-10	19	6.7	2.1	4-10
	DS	17	7.3	1.5	5-10	22	7.2	1.9	4-10
Thicket	NDS	17	15.0	2.9	11-19	20	15.9	3.0	11-20
	DS	20	14.2	2.8	11-19	20	14.7	3.0	11-20
Pole	NDS	20	38.0	4.9	23-45	18	37.9	4.7	24-44
	DS	13	36.3	5.7	22-45	16	36.9	6.4	23-45
Mature	NDS	20	65.5	10.3	48-80	20	67.1	11.3	48-81
	DS	20	68.2	10.3	47-81	16	68.4	12.3	46-83
Total		143				172			

*restock: 1-3 years; pre-thicket: 4-10; thicket: 11-20; pole: 21-45; mature: > 45 years.

Each plot (coupe) was surveyed during two separate visits in each year. The first field surveys took place between mid-April and mid-May and the second from mid-May to mid-June, in both 2007 and 2008. In each coupe two transect lines where walked where possible, a minimum of 150 meters apart. For each bird heard or seen the location of first detection was marked on a 1:2,500 map and activity was recorded (e.g. singing, flying).

The number of all recorded birds and the number of singing birds within 0-25 m, 25-50 m and 50-75 m of each transect line were extracted for each species from the maps. The total area surveyed within 25, 50 and 70 metres of the transect lines within each plot was calculated by overlaying buffers around the transect lines onto the plot boundaries using ArcView 9.1 GIS. Where the buffers overlapped the plot boundaries, only the area inside the plot was included since birds were not recorded outside these boundaries. Where the buffers from adjacent transect lines within the plot overlapped (where transect lines were slightly less than 150 metres apart), the buffers were dissolved within the area of overlap so that the actual area surveyed could be calculated. For further analysis we used the number of recorded singing birds within 0-50 m of the transect line divided by the actual surveyed area.

Table 6.4. Number of plots for each growth stage sampled for both vegetation and birds in Thetford Forest in 2007 and 2008.

Habitat		2007	2008
Restock	NDS	-	2
	DS	-	1
Pre-thicket	NDS	11	10
	DS	11	12
Thicket	NDS	11	6
	DS	13	6
Pole	NDS	-	-
	DS	-	-
Mature	NDS	14	4
	DS	12	6
Total		72	47

Birds which are likely to be affected by deer browsing mostly depend on rich undergrowth in forested landscapes. Browsing of overabundant deer should therefore reduce understorey structure and suitable habitat for understorey dependent bird species. To analyse the bird species survey data I therefore pooled the recorded bird species in two bird guilds: (1) understorey dependent birds and (2) understorey independent birds (Table 6.5). Birds were classified as understorey dependent when they either nest or feed in the shrub or field layer. For each guild I pooled the number of singing birds/ha within 0-50 m of the line transect by plot (*n* = 126) for each visit (*n* = 2) in each year (*n* = 2).

Table 6.5. Bird species composition in two bird guilds: (1) understorey dependent and (2) understorey independent bird species in Thetford Forest. Bird data have been recorded in surveys in 2007 and 2008. Species in paranetheses are doubtfully associated with understorey vegetation, while those marked with an asterisk may benefit from enhanced deer browsing intensity as they are negatively associated with understorey shrub layers or positively associated with ground layer grass.

Understorey dependent species (*n*)	Understorey independent species (*n*)
[Willow Warbler *Phylloscopus trochilus*] (754)	Robin *Erithacus rubecula* (514)
Wren *Troglodytes troglodytes* (598)	Chaffinch *Fringilla coelebs* (440)
Whitethroat *Sylvia communis* (206)	Goldcrest *Regulus regulus* (349)
Blackcap *Sylvia atricapilla* (191)	Coal tit *Periparus ater* (269)
Yellowhammer *Emberiza citrinella* (140)	Chiffchaff *Phylloscopus collybita* (266)
Dunnock *Prunella modularis* (125)	Tree pipit *Anthus trivialis* (109)
Garden Warbler *Sylvia borin* (56)	Great tit *Parus major* (71)
[Song Thrush *Turdus philomelos*] (55)	Tree creeper *Certhia familiaris* (39)
[Black Bird *Turdus merula*] (18)	Blue tit *Cyanistes caeruleus* (26)
[Greenfinch *Carduelis chloris*] (12)	[Linnet *Carduelis cannabina*] (15)
Marsh Tit *Poecile palustris* (8)	Skylark *Alauda arvensis* * (15)
Grasshopper Warbler *Locustella naevia* (6)	Woodlark *Lullula arborea* * (9)
Long-tailed Tit *Aegithalos caudatus* (4)	Siskin *Carduelis spinus* (8)
Bullfinch *Pyrrhula pyrrhula* (2)	Goldfinch *Carduelis carduelis* (4)
[Lesser Redpoll *Carduelis cabaret*] (2)	Nuthatch *Sitta europaea* (4)
Stonechat *Saxicola torquatus* (1)	Common crossbill *Loxia curvirostra* (1)
	Mistle thrush *Turdus viscivorus* (1)
	Pied wagtail *Motacilla alba* (1)
	Spotted flycatcher *Muscicapa striata* (1)

(d) Vegetation survey

Structure and composition of vegetation were monitored in most of the plots in which bird surveys had been carried out and in additional stands (Table 6.4), from 9 July to 7 August in 2007, and between 30 June and 7 August in 2008. In 2007 and 2008 a total of 143 plots and 172 plots were sampled respectively. Of those 126 plots were surveyed in both years, 17 plots were unique to 2007 and 46 plots to 2008. Thus all vegetation surveys took place after vegetation growth was complete and before autumn leaf drop or vegetation die back. Surveys rotated among blocks, returning to blocks each week, so that blocks were not confounded by date.

Within each plot, habitat measurements were taken at a minimum of 10 intervals along each transect line following compass bearings across the longest diagonal of each sampled patch or coupe. Sampling intensity therefore scaled with stand area, with analysis based on stand means. At each point the following measurements were collected foliage density (classed as 1-5 after training with a chequer-board, according to the distance class at which at least 50% of the board was obscured by vegetation; where 1 = 50% board visible at >20m; 2 = 50% board visible at 10-20m; 3 = 6-10m; 4 = 2-6m; 5 < 2m) with measurements taken at a 90° angle from the transect line on both sides, with separate measurements take within the herb layer (0.5 m) and low shrub layer (1.5m), visually estimated percentage ground cover of the following vegetation classes (<1.5m) in 1 m x 1 m quadrate: bramble *Rubus spp*., broom *Cytisus scoparius*, gorse *Ulex europaeus*, birch *Betula* spp., hawthorn *Crataegus* spp., holly *Ilex aquifolium*, oak *Quercus* spp., pine *Pinus* spp., nettle *Urtica dioica*, *Deschampsia flexuosa*, *Holcus lanatus*, *Dactylorhiza glomerata*, *Calamagrostis epigejos*, and the combined percentage cover of other grass and sedge species, and combined cover of other herbs. Field work was carried out by two surveyors each year whereupon one surveyor was present in both years. Before the surveyors independently measured structure and composition of vegetation they trained for consistency.

(e) Analysis

Growth stage may have a major influence on the percentage cover of the vegetation variables and the bird species distribution. Thus, it is important to understand the effect of growth stage on vegetation and birds. Therefore, I compared the fit of models for each vegetation variable including only growth stage as a predictor with models including forest block and growth stage, or including biomass and growth stage, as predictors. For bird guilds I compared the fit of models including growth stage, visit and year as predictors with models including block, growth stage, visit and year; or vegetation cover (%), growth stage, visit and year; or deer biomass, growth stage, visit and year.

Deer-vegetation relationship

The forest blocks in Thetford Forest are characterised by complex ecological factors including conifer growth stage distribution and deer species distribution. By using General Linear Models with normal error we examined the differences in vegetation structure (per plot, dependent variables) across forest blocks (categorical factor) whilst controlling for plot growth stage (categorical factor - pre-thicket: DS and NDS; thicket: DS and NDS; mature pine) as vegetation structure differs between growth stages.

Finally, we tested if vegetation structure (dependent) was related to deer biomass (continuous variable, per block) whilst controlling for forest growth stage (categorical factor - pre-thicket: DS and NDS; thicket: DS and NDS; mature pine) using General Linear Models.

Vegetation structure and composition was surveyed in 143 plots in 2007 and 172 plots in 2008 whereas deer densities were estimated at the forest block level. Therefore we calculated the mean percentage cover of each vegetation category, in each growth stage for each block, pooling across surveyed years for the following vegetation variables: percentage cover of bramble, percentage cover of shrub layer (excluding pine and bramble), percentage cover of grass layer (total grass and sedge cover including *Dactylorhiza glomerata* and *Calamagrostis epigejos*) and percentage cover of bracken. I than used the mean percentage cover per growth stage per block of each vegetation variable as a dependent variable for further analysis.

Vegetation structure was related to:

a) The combined biomass of roe and muntjac (combined as concentrate selector or browsing species)

b) The combined biomass of red and fallow deer (combined as larger bodied grazers, able to subsist on low quality forage after browse has been removed)

c) Total combined deer biomass (all four species)

Bird-vegetation and bird-deer relationship

I tested if bird guilds (dependent; singing birds per ha) differ among forest blocks (categorical factor) using General Linear Models with normal error, while controlling for growth stage (categorical factor), visit (categorical factor) and year (categorical factor). Last, I examined if any direct relationship between bird guilds and deer biomass can be found using General Linear Models whilst controlling for growth stage, visit and year.

Results

Deer biomass among forest blocks

Total deer biomass (kg/km^{-2}) varied markedly between blocks but was correlated with the biomass of roe deer and Reeve's muntjac combined (r = 0.77, p = 0.04) and not correlated to the combined biomass of red and fallow deer (r = 0.09, p = 0.43). The biomass of roe deer and Reeve's muntjac dominated the overall biomass in the blocks Did, Mun, Lyn and Har (Fig. 6.2). The combined biomass of roe deer and muntjac contributed more than 80% to the overall deer biomass in these four blocks. The biomass of the smaller deer species contributed 67% in block Har and 36% in HiEl to the overall biomass. Thus, the biomass of red and fallow deer dominated the overall biomass only in forest block HiEl (64%) (Fig. 6.2).

The highest total deer biomass was found in block Mun (1360 kg/km^{-2}) which is dominated by roe deer and Reeve's muntjac biomass. Forest blocks Cro (660 kg/km^{-2}) and Lyn (672 kg/km^{-2}) had the lowest biomass. The total deer biomass was 51% lower in Cro and Lyn than in block Mun and 37% lower in Did (860 kg/km^{-2}) and Har (856 kg/km^{-2}) than in block Mun (Fig 6.2).

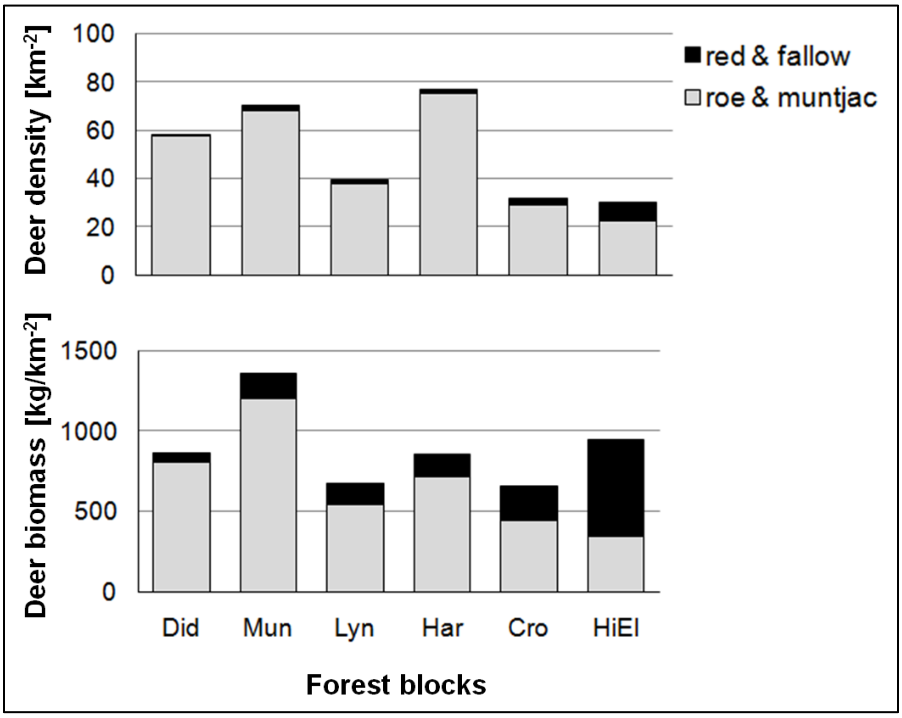

Fig. 6.2. Combined deer density [km^{-2}] and biomass [kg/km^{-2}] in six forest blocks (HiLo and Elv combined as HiEl) in Thetford Forest. Density data are established using distance sampling thermal imaging data from 2008-10.

The combined body mass of roe deer and Reeve's muntjac was highest in block Mun (1200 kg/km^{-2}). In block Mun the biomass of roe deer and muntjac was about 72% higher than in the block with the lowest biomass HiEl (341 kg/km^{-2}), about 40%-60% higher than in Lyn, Har, Cro and about 33% higher than in Did (Fig. 6.2). The highest biomass for red and fallow deer was found in block HiEl (608 kg/km^{-2}). In this block the biomass was 90% higher than in the block with the lowest biomass Did (56 kg/km^{-2}) and about 65%-80% higher than in the other forest blocks (Fig. 6.2).

Table 6.6. Overview of General Linear Models, showing the effects of growth stage and forest block on the percentage cover of the shrub layer, grass layer, bramble and bracken in Thetford Forest in 2007-08. Sample size *n* represents for growth stage as predictor the number of the pooled means for each block and for block as predictor the number of pooled means for each growth stage. Tukey test[1] significance comparing growth stage effects and block effects are shown with superscripts, periods that do not share a superscript differ significantly ($p < 0.05$).

Model	Model predictors	*n*	*B* ± *SE*	*F*	*p*	R^2	df
Effect of growth stage							
1	*Shrub layer cover*					0.34	
	Growth stage	7		3.83	0.01		4
2	*Grass layer cover*					0.37	
	Growth stage	7		4.30	0.01		4
3	*Bramble cover*					0.26	
	Growth stage	7		2.60	0.06		4
	Bracken cover					0.60	
	Growth stage	7		11.35	< 0.001		4
Effects of block and growth stage							
4	*Shrub layer cover*			2.58	0.03	0.52	10
	Block	5		1.49	0.23		6
	Growth stage[1]			4.21	0.01		4
	Mature pine	7	0.93 ± 2.02^{a,b}				
	Pre-thicket NDS	7	5.71 ± 2.02^{a}				
	Pre-thicket DS	7	1.66 ± 2.02^{a,b}				
	Thicket NDS	7	-2.30 ± 2.02^{b}				
	Thicket DS	7	-^{a,b}				
5	*Grass layer cover*			4.09	0.002	0.63	10
	Block (HiEl)[1]	5	-^{a}	2.88	0.03		6
	Did	5	-15.14 ± 9.56^{a}				
	Mun	5	-13.74 ± 9.56^{a}				
	Lyn S	5	11.58 ± 9.56^{a}				
	Lyn N	5	-5.86 ± 9.56^{a}				
	Cro	5	10.74 ± 9.56^{a}				
	Har	5	10.18 ± 9.56^{a}				
	Growth stage[1]			5.92	0.002		4
	Mature pine	7	-19.54 ± 8.16^{b}				
	Pre-thicket NDS	7	-2.90 ± 8.16^{a,b}				
	Pre-thicket DS	7	16.09± 8.16^{a}				
	Thicket NDS	7	-15.23 ± 8.16^{b}				
	Thicket DS	7	-^{a,b}				

Table 6.6.

6	*Bramble cover*			2.38	0.04	0.50	10
	Block	5		1.91	0.12		6
	Growth stage[1]			3.08	0.04		4
	Mature pine	7	6.30 ± 2.43^{a}				
	Pre-thicket NDS	7	$1.99 \pm 2.43^{a,b}$				
	Pre-thicket DS	7	$3.56 \pm 2.43^{a,b}$				
	Thicket NDS	7	-1.39 ± 2.43^{b}				
	Thicket DS	7	$-^{a,b}$				
7	*Bracken cover*			4.72	0.001	0.66	10
	Block	5		0.72	0.64		6
	Growth stage[1]			10.71	< 0.001		4
	Mature pine	7	22.0 ± 3.88^{a}				
	Pre-thicket NDS	7	5.13 ± 3.88^{a}				
	Pre-thicket DS	7	0.51 ± 3.88^{a}				
	Thicket NDS	7	5.07 ± 3.88^{a}				
	Thicket DS	7	-				

Deer-vegetation relationship

Generally, percentage cover of the shrub layer, grass layer, bramble and bracken varied more widely among growth stages (pre-thicket: DS and NDS; thicket: DS and NDS; mature pine) than among forest blocks or in relation to deer biomass (Table 6.6, Fig. 6.3 and 6.4). Hereby, the extent of the shrub layer was 92% greater in pre-thicket (NDS) than in thicket (NDS) (mean difference = 8.01% ± 2.02 *SD*); the cover of the grass layer was 64% greater in pre-thicket (DS) than in mature pine (mean difference = 35.63% ± 8.16 *SD*); the cover of bramble was 85% higher in mature pine than in thicket (NDS) (mean difference = 7.69% ± 2.43 *SD*); and the cover of bracken was 79% higher in mature pine than in thicket (DS) (mean difference = 22.0% ± 3.88 *SD*).

In all models vegetation variables were significantly related to growth stage, that explained most of the variation in percentage cover (Table 6.6). Adding block in the existing model with growth stage and plant cover significantly improved the overall fit for the grass layer cover (AIC of growth stage only model minus AIC growth stage and block model: Δ AIC = -6.98) but not for the shrub layer cover (Δ AIC = -0.98) and bramble cover (Δ AIC = -1.65). However, only for grass layer I found a significant effect of forest blocks overall, but no significant differences between individual pairs of forest blocks (Tukey test: *n.s.*) (Table 6.6). However, the extent of the grass layer in Lyn S (highest cover) was 26.7% higher than in Did (lowest cover). The highest percentage cover of about 46% was found in blocks Lyn S, Cro and Har and the lowest of about 20% in forest blocks Did and Mun. The two other blocks Lyn N and HiEl had a percentage cover of grass of 30% and 36% respectively. The largest mean difference in percentage cover of the shrub layer and bramble between forest blocks was < 7%.

Contrary to expectation, the percentage cover of the shrub layer exluding bramble was weakly positively related to the pooled biomass of roe deer and Reeve's muntjac, but showed no relation to the pooled biomass of red and fallow deer, or of all deer species combined (Table 6.7). However, although non-significant, the effect of the pooled biomass of all deer species (B = 0.01 % per kg ± 0.004 SE) was greater than that of the combined biomass of roe deer and muntjac (Table 6.7). The shrub cover was 7% greater in extent in the block with the greatest overall biomass for all deer species (1360 kg/km^{-2}) compared to the block with the lowest biomass (660 kg/km^{-2}). Hereby, the block with highest overall biomass was also the block with the highest roe deer and muntjac biomass combined (1200 kg/km^{-2}). The block with the lowest overall biomass consisted of 33% biomass of red and fallow deer and 67% biomass of the two smaller species.

A similar relationship between blocks was established for the percentage bramble cover which was 7% greater in the block with the highest biomass of all deer species pooled (1360 kg/km^{-2}) compared to the block with the lowest biomass of all deer species (660 kg/km^{-2}); thus total deer biomass was greater in blocks with greater bramble browse resource. However, examining the relationship of red and fallow deer biomass combined to the percentage cover of bramble I found a result contrasted with that for combined deer biomass (Table 6.7). In the forest block with the lowest total deer biomass (660 kg/km^{-2}) which is composed of 33% red and fallow deer biomass and 67% roe deer and muntjac biomass, the percentage bramble cover was 7% greater than in the block with the greatest biomass of the smaller species (1360 kg/km^{-2}).

For bracken nearly all of the variation in percentage cover was already explained by the simplest model including only growth stage (Table 6.6). Percentage cover of bracken was not related to forest block or deer biomass (Table 6.6 and 6.7, Fig. 6.4).

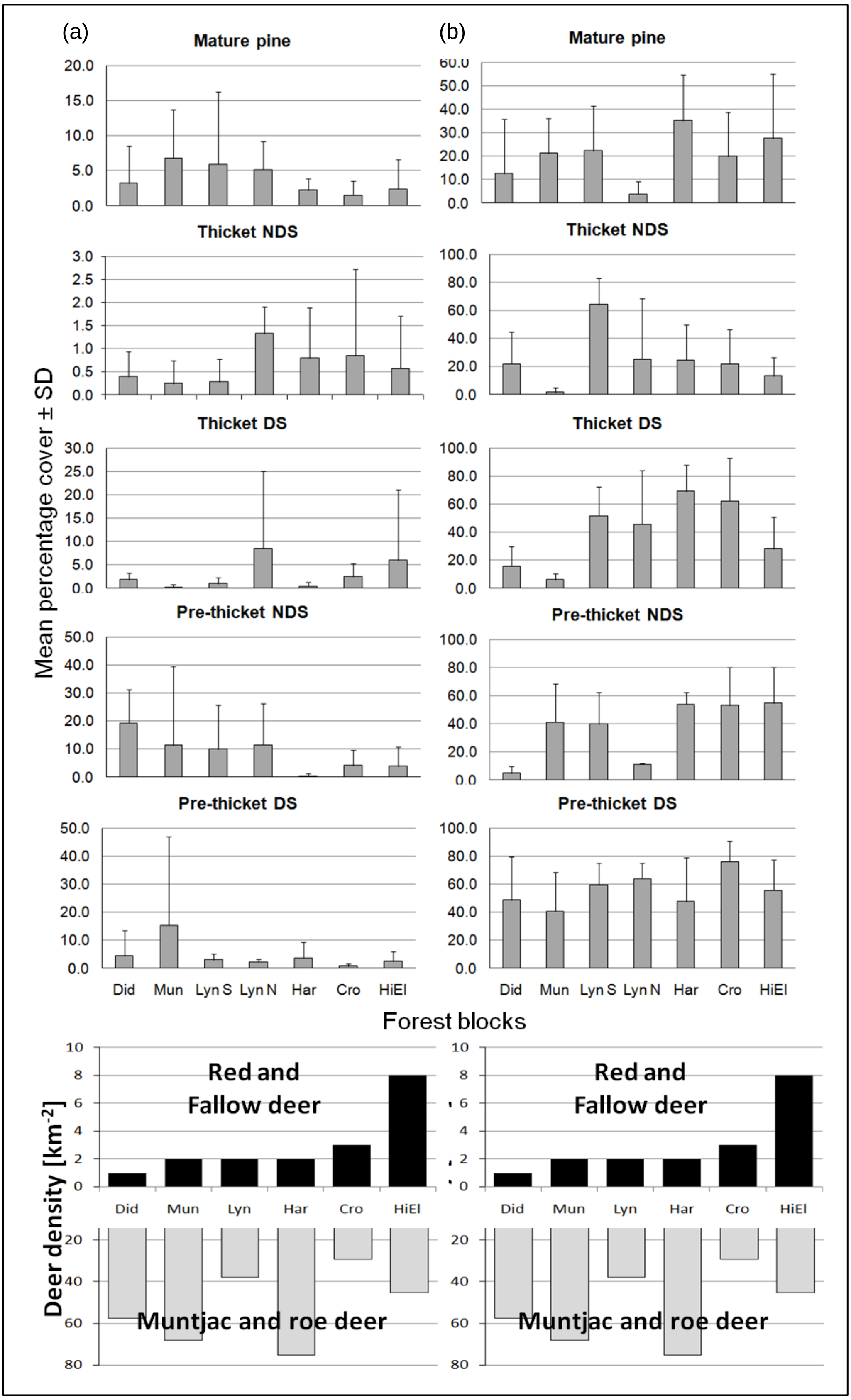

Fig. 6.3. Mean percentage cover ± *SD* of (a) shrub layer (excluding bramble) and (b) grass layer in six forest blocks in Thetford Forest in 2007-08 and deer density in six forest blocks in Thetford Forest in 2008.

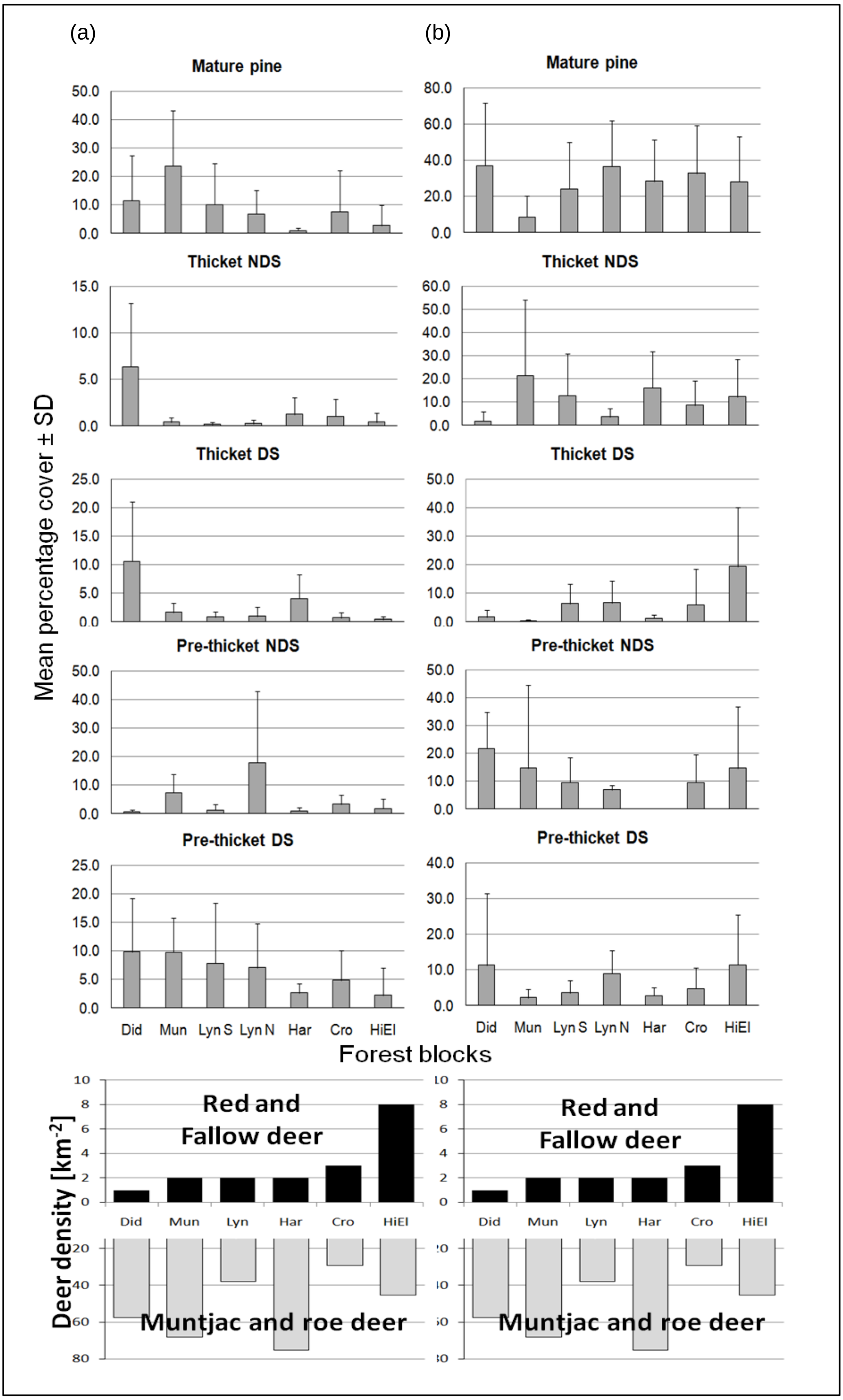

Fig. 6.4. Mean percentage cover ± *SD* of (a) bramble and (b) bracken in six forest blocks in Thetford Forest in 2007-08 and deer density in six forest blocks in Thetford Forest in 2008.

Table 6.7. Model overview (General Linear Models) showing the relation between the percentage cover of the shrub layer, grass layer, bramble and bracken and effects of growth stage and deer biomass [considered as (a) pooled roe deer and Reeve's muntjac biomass, (b) pooled red and fallow deer biomass and (c) combined biomass of all deer species], in Thetford Forest in 2007-08. Sample size *n* represents for growth stage as predictor the number of the pooled means for each block and for block as predictor the number of pooled means for each growth stage.

Model	Model predictors	*n*	B ± SE	*F*	*p*	R^2	df
(a) Roe deer and muntjac biomass							
5	*Shrub layer cover*			4.16	0.006	0.42	5
	Deer biomass	7	0.004 ± 0.002	3.95	0.06		1
	Growth stage			4.21	0.01		4
6	*Grass layer cover*			4.96	0.002	0.46	5
	Deer biomass		-0.02 ± 0.01	5.19	0.03		1
	Growth stage	7		4.90	0.004		4
7	*Bramble cover*			4.03	0.007	0.41	5
	Deer biomass		0.01 ± 0.003	7.49	0.01		1
	Growth stage	7		3.17	0.03		4
8	*Bracken cover*			9.80	< 0.001	0.63	5
	Deer biomass		-0.006 ± 0.004	2.04	0.16		1
	Growth stage	7		11.74	< 0.001		4
(*b) Red and fallow deer biomass*							
5	*Shrub layer cover*			3.26	0.02	0.36	5
	Deer biomass		-0.004 ± 0.004	0.98	0.33		1
	Growth stage	7		3.83	0.01		4
6	*Grass layer cover*			3.42	0.02	0.37	5
	Deer biomass		0.01 ± 0.02	0.28	0.60		1
	Growth stage	7		4.20	0.01		4
7	*Bramble cover*			3.05	0.03	0.34	5
	Deer biomass		-0.01 ± 0.01	3.84	0.06		1
	Growth stage	7		2.85	0.04		4
8	*Bracken cover*			9.76	< 0.001	0.63	5
	Deer biomass		0.01 ± 0.01	1.96	0.17		1
	Growth stage	7		11.71	< 0.001		4
(c) Biomass of all deer species combined							
9	*Shrub layer cover*			3.89	0.01	0.40	5
	Deer biomass		0.01 ± 0.003	3.05	0.09		1
	Growth stage	7		4.10	0.01		4
10	*Grass layer cover*			5.39	0.001	0.48	5
	Deer biomass		-0.03 ± 0.01	6.57	0.02		1
	Growth stage	7		5.10	0.003		4

Table 6.7.

11	*Bramble cover*			2.91	0.03	0.33	5
	Deer biomass		0.01 ± 0.004	3.34	0.08		1
	Growth stage	7		2.81	0.04		4
12	*Bracken cover*			9.05	< 0.001	0.61	5
	Deer biomass		-0.004 ± 0.006	0.55	0.47		1
	Growth stage	7		11.18	< 0.001		4

Bird-vegetation and bird-deer relationship

The abundance (recorded singing birds/ha) of understorey dependent bird species varied more widely among forest blocks (difference between the block with the highest and lowest abundance of understorey dependent birds: difference = 0.86 birds/ha ± 0.25 *SE*; 44%) than growth stages (difference = 0.48 birds/ha ± 0.20 *SE*; 30%) whereas the abundance of understorey independent species varied more widely among growth stages (mean difference = 1.25 birds/ha ± 0.13 *SE*; 74%) than forest blocks (mean difference = 0.25 birds/ha ± 0.14 *SE*; 20%) (Table 6.8 and 6.9, Fig. 6.5).

The best fitting model (R^2 = 0.11) for the abundance of understorey dependent birds included effects of both forest block and growth stage (Table 6.8). Here, I found a significant effect of forest block on the abundance of understorey dependent birds: bird abundance was 44% greater in Lyn S than in Har (highest muntjac density) (mean difference = 0.86 birds/ha ± 0.25 *SE*) and 43% greater in Lyn S than in Cro (mean difference = 0.85 birds/ha ± 0.21 *SE*).

All other models analysing effects on understorey dependent birds including as predictors plant cover/deer biomass and growth stage, visit and year did not improve the model fit (R^2 = 0.05). No direct effects of percentage cover or deer biomass could be detected in these models (Table 6.8 and 6.9).

All fitted models investigating the effects of forest blocks, growth stages and deer biomass on understorey independent bird species showed a considerable fit (about R^2 = 0.34) which was due to the effect of growth stage (Table 6.10 and 6.11). As expected no difference in the abundance of understorey independent birds between forest blocks was established.

Table 6.8. Model overview (General Linear Models) relating the abundance of understorey dependent birds to effects of growth stage, forest block, and vegetation cover in Thetford Forest in 2007-08. Tukey test[1] significance comparing growth stage effects and block effects are shown with superscripts, periods that do not share a superscript differ significantly ($p < 0.05$).

Model	Model predictors	*n*	*B ± SE*	*F*	*p*	R^2	df
1	*Model*	310		2.58	0.02	0.05	6
	Growth stage			2.10	0.08		4
	Visit			6.67	0.01		1
	Year			0.85	0.36		1
2	*Model*	310		3.08	< 0.001	0.11	12
	Block[1] (HiEl)	48	- ^{a,b}	3.45	0.003		6
	Did	48	-0.06 ± 0.24 ^{a,b}				
	Mun	26	-0.27 ± 0.28 ^{a,b}				
	Lyn S	50	0.37 ± 0.24 ^{b}				
	Lyn N	24	-0.37 ± 0.29 ^{a,b}				
	Cro	74	-0.49 ± 0.22 ^{a}				
	Har	40	-0.46 ± 0.25 ^{a}				
	Growth stage[1]			2.18	0.07		4
	Mature pine	88	-0.47 ± 0.20				
	Pre-thicket NDS	54	0.02 ± 0.23				
	Pre-thicket DS	62	-0.21 ± 0.22				
	Thicket NDS	52	-0.07 ± 0.23				
	Thicket DS	54	-				
	Visit			6.99	0.01		1
	Year			0.75	0.39		1
3	*Model*	310		2.23	0.03	0.05	7
	Shrub layer cover		0.01 ± 0.02	0.19	0.67		1
	Growth stage			2.09	0.08		4
	Visit			6.65	0.01		1
	Year			0.79	0.38		1
4	*Model*	310		2.43	0.02	0.05	7
	Grass layer cover		0.004 ± 0.003	1.50	0.22		1
	Growth stage			2.19	0.07		4
	Visit			6.68	0.01		1
	Year			1.27	0.26		1
5	*Model*	310		2.27	0.03	0.05	7
	Bramble cover		0.01 ± 0.01	0.45	0.50		1
	Growth stage			1.98	0.10		4
	Visit			6.65	0.01		1
	Year			0.82	0.38		1
6	*Model*	310		2.38	0.02	0.05	7
	Bracken cover		-0.01 ± 0.01	1.19	0.28		1
	Growth stage			2.16	0.07		4
	Visit			6.67	0.01		1
	Year			1.03	0.31		1

Table 6.9. Model overview (General Linear Models) relating the abundance of understorey dependent birds to effects of growth stage, deer biomass [considered as (a) pooled roe deer and Reeve's muntjac biomass, (b) pooled red and fallow deer biomass and (c) combined biomass of all deer species], controlling for visit and year in Thetford Forest in 2007-08.

Model	Model predictors	*n*	*B* ± *SE*	*F*	*p*	R^2	df
(a) Roe deer and muntjac biomass							
6	*Model*	310		2.21	0.03	0.05	7
	Biomass		0	0.08	0.78		1
	Growth stage			2.10	0.08		4
	Visit			6.64	0.01		1
	Year			0.81	0.37		1
(b) Red and fallow deer biomass							
7	*Model*	310		2.20	0.03	0.05	7
	Biomass		0	0.01	0.93		1
	Growth stage			2.09	0.08		4
	Visit			6.64	0.01		1
	Year			0.83	0.36		1
(c) Biomass of all deer species combined							
8	*Model*	310		2.21	0.03	0.05	7
	Biomass		0	0.08	0.78		1
	Growth stage			2.09	0.08		4
	Visit			6.64	0.01		1
	Year			0.84	0.36		1

Surprisingly, I found a negative relation with the percentage cover of bramble and a positive relation with the percentage cover of bracken for the abundance of understorey independent bird species (Table 6.10). The abundance of understorey independent birds in the block with the least bramble cover (HiEl: mean = 1.69% ± 0.97 SD, n = 48) was 86% higher than in the block with the greatest extent of bramble cover (Mun: mean = 10.79% ± 9.29 *SD*, *n* = 26). I found 45% higher bird abundance in the block with the greatest extent of bracken cover (HiEl: mean = 17.59% ± 6.68 SD, n = 48) than in the block with the least cover (Mun: mean = 9.72% ± 7.21 *SD*, *n* = 26). These results may relate to underlying relationships between bramble, bracken, soil fertility or pH, and forest stand productivity and canopy composition. Bird abundance of understorey independent birds was not related to the percentage cover of the shrub layer, grass layer or deer biomass (Table 6.10, Fig. 6.5).

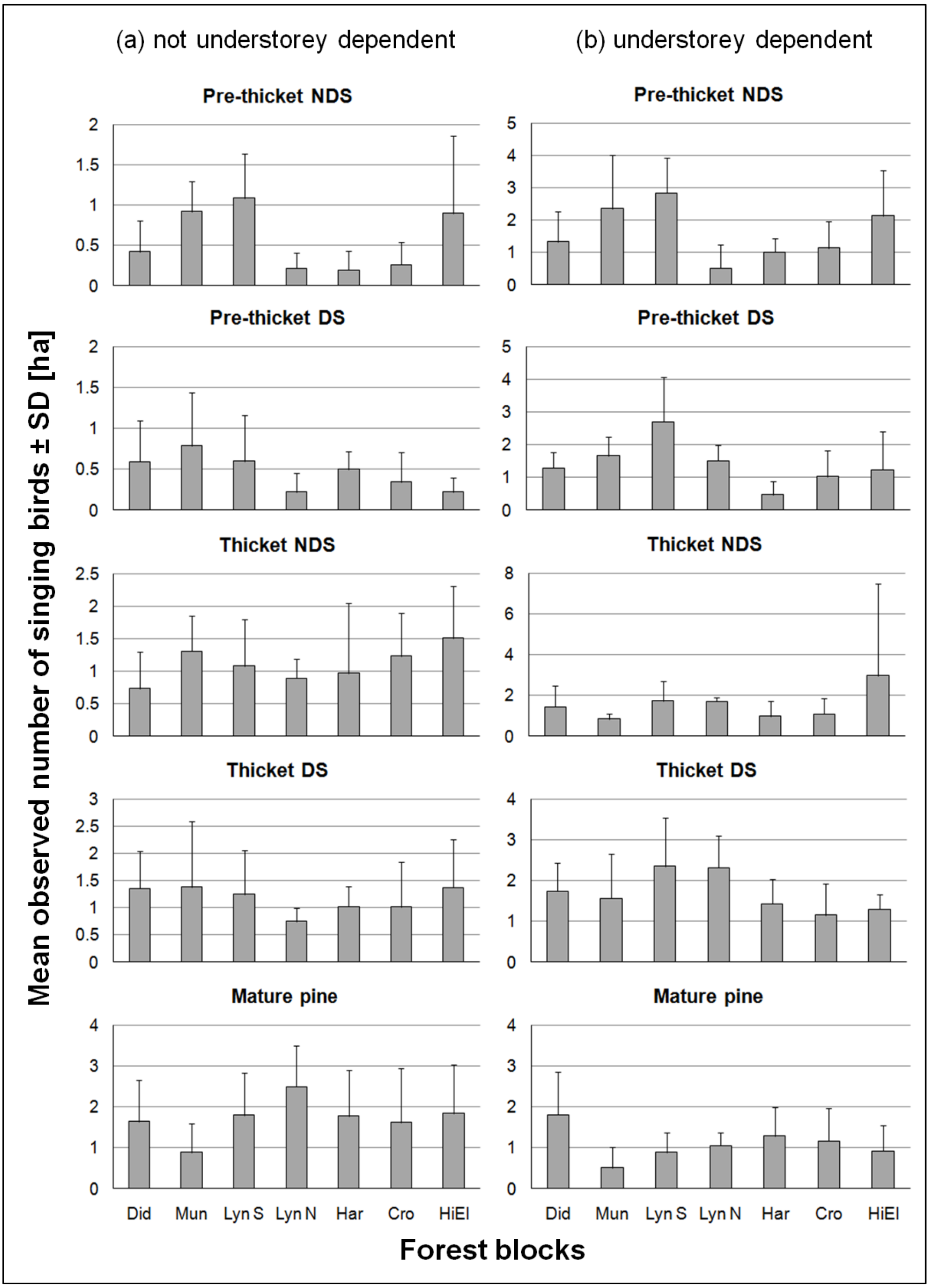

Fig. 6.5. Bird abundance [ha] ± *SD* of (a) not understorey dependent and (b) understorey independent bird species in six forest blocks (arranged in order of increasing density of red and fallow deer, see Fig. 4) in Thetford Forest in 2007-08.

Table 6.10. Model overview (General Linear Models) relating the abundance of understorey independent birds to effects of growth stage, forest block and vegetation in Thetford Forest in 2007-08. Tukey test[1] significance comparing growth stage effects are shown with superscripts, periods that do not share a superscript differ significantly ($p < 0.05$).

Model	Model predictors	*n*	*B* ± *SE*	*F*	*p*	R^2	df
1	*Model*	310		25.13	< 0.001	0.33	6
	Growth stage[1]			24.85	< 0.001		4
	Mature pine	88	0.54 ± 0.13^{a}				
	Pre-thicket NDS	54	-0.51 ± 0.15^{c}				
	Pre-thicket DS	62	-0.61 ± 0.15^{c}				
	Thicket NDS	52	-0.01 ± 0.15^{b}				
	Thicket DS	54	$-^{b}$				
	Visit			4.33	0.04		1
	Year			24.62	< 0.001		1
2	*Model*	310		12.98	< 0.001	0.34	12
	Block			0.88	0.51		
	Growth stage			24.56	< 0.001		6
	Visit			4.18	0.04		1
	Year			24.91	< 0.001		1
3	*Model*	310		21.50	< 0.001	0.33	7
	Shrub layer cover		0.01 ± 0.01	0.14	0.71		1
	Growth stage			23.47	< 0.001		4
	Visit			4.32	0.04		1
	Year			24.56	< 0.001		1
4	*Model*	310		21.75	< 0.001	0.34	7
	Grass layer cover		-0.003 ± 0.003	1.30	0.26		1
	Growth stage			15.86	< 0.001		4
	Visit			4.32	0.04		1
	Year			24.50	< 0.001		1
5	*Model*	310		22.48	< 0.001	0.34	7
	Bramble cover		-0.02 ± 0.01	4.72	0.03		1
	Growth stage			26.33	< 0.001		4
	Visit			4.33	0.04		1
	Year			24.82	< 0.001		1
6	*Model*	310		22.76	< 0.001	0.35	7
	Bracken cover		0.02 ± 0.01	6.01	0.02		1
	Growth stage			10.24	< 0.001		4
	Visit			4.41	0.04		1
	Year			24.67	< 0.001		1

Table 6.11. Model overview (General Linear Models) relating the abundance of understorey independent birds to growth stage, deer biomass [considered as (a) pooled roe deer and Reeve's muntjac biomass, (b) pooled red and fallow deer biomass and (c) combined biomass of all deer species], controlling for visit and year in Thetford Forest in 2007-08.

Model	Model predictors	*n*	*B* ± *SE*	*F*	*p*	R^2	df
(a) Roe deer and muntjac biomass							
7	*Model*	310		21.54	< 0.001	0.33	7
	Biomass		0	0.34	0.56		1
	Growth stage			24.74	< 0.001		4
	Visit			4.32	0.04		1
	Year			24.56	< 0.001		1
(b) Red and fallow deer biomass							
8	*Model*	310		21.65	< 0.001	0.33	7
	Biomass		0	0.83	0.36		1
	Growth stage			24.96	< 0.001		4
	Visit			4.27	0.04		1
	Year			24.42	< 0.001		1
(c) Biomass of all deer species combined							
9	*Model*	310		21.47	< 0.001	0.33	7
	Biomass		0	0.004	0.95		1
	Growth stage			24.77	< 0.001		4
	Visit			4.31	0.04		1
	Year			24.54	< 0.001		1

Discussion

Despite differences in deer biomass and distribution among forest blocks the plant cover and the abundance of shrub independent birds varied more widely among growth stages than it did among forest blocks. This has been also reported in other studies investigating the relationship between deer, vegetation and birds (McShea and Rappole, 2000, Zipkin et al., 2010, DeCalesta, 1994). In North America McShea and Rappole (2000) investigated the deer impacts on birds and the structure of forest understorey by comparing deer exclosures with unfenced areas. Density and diversity of understorey woody plants increase following deer exclusion (McShea and Rappole, 2000). The change in abundance and diversity of bird populations was related to the change in understorey vegetation (McShea and Rappole, 2000). DeCalesta (1994) tested the effect of four different deer densities in enclosures on songbirds and vegetation in Pennsylvania, USA. They observed a decline in species richness (27%) and abundance (37%) of intermediate canopy-nesting songbirds between lowest (3.7 deer km^{-2}) and highest (24.9 deer km^{-2}) deer densities (DeCalesta, 1994).

Although, the abundance of shrub dependent bird species varied more widely among forest blocks than it did among growth stages, no clear direction for this effect was found. Thus, no significant difference between the impact of roe deer and muntjac versus red and fallow deer was detected. One possible reason for the lack of differences between roe deer and muntjac versus red and fallow deer may be the long term browsing pressure of all deer species in Thetford Forest. During the 1970s deer numbers increased rapidly in Thetford Forest and stayed at higher levels during the 1980s and 1990s. Only from the beginning of the 21st century did deer cull levels increase, but overall deer numbers are still high. This suggests that the browsing pressure in Thetford Forest has been high for about 30 years. In New Zealand Tanentzap et al. (2009) only observed limited vegetation recovery after 40 years following red deer density reduction to < 6 deer km^{-2} which is comparing the biomass of both studies assuming a mean living body mass of 130 kg for each red deer (780 kg/km^{-2}) similar to the total deer biomass (mean = 893 kg/km^{-2} ± 256 *SD*) in my study. Islands in British Columbia, Canada, which have been exposed to white-tailed deer *Odocoileus virginianus* browsing for more than 50 years showed a 55-70% lower songbird abundance than islands with no deer present (Allombert et al., 2005a). For Thetford Forest, there is some historic information on bird communities from quantitative bird surveys conducted prior to the establishment of high density deer populations (Lack, 1933). However, the structure and composition of the forest vegetation has changed considerably in the intervening period, from a closed canopy young (thicket stage) pine forest to a diverse heterogeneous mixed forest with a full range of growth stages and complex sub-canopy structures, and enhanced deciduous shrub elements. Therefore, no simple before / after comparison of the effects of deer browsing is possible.

Forest blocks are a complex ecological network consisting of a variety of biological processes influencing the carrying capacity for deer and therefore affecting deer impacts. A high deer carrying capacity for example due to high soil fertility and plant growth may support higher deer densities. Thus, in such forest blocks, the impacts of high deer density, may be less than impacts of lower densities, in blocks of lower intrinsic soil fertility, vegetation productivity and deer carrying capacity that have less food availability for deer and thus greater browsing pressure on the forage that is available. This is suggested by the positive relation between roe deer and muntjac biomass combined and the percentage of bramble cover. Here the bramble cover was greater in areas with greater roe deer and muntjac density. In these areas it is possible that the soil fertility is enhancing vegetation growth and therefore the availability of food for deer, leading to greater deer density as deer aggregate on or achieve higher density on areas with greater resource. Alternatively, bramble cover may be suppressed in areas that have experienced a longer history of elevated deer density, while roe and muntjac densities are currently greater in those areas that currently have greater availability of preferred browse. Similarly, Hemami et al. (2005) found a positive relation between the density of roe and muntjac and cover of bramble, across 12 forest blocks. On the other hand I found a weakly negative relation between the combined red and fallow deer biomass and the percentage cover of bramble, implying that where red and fallow deer densities are higher less bramble cover is existent. At present highest red and fallow densities were found in the southern blocks. Historically, these blocks have had higher deer densities in the past than the northern forest blocks as for example fallow deer and muntjac colonisation started from the South. These blocks currently have higher fallow density than the northern blocks.

Bird species which do not depend on dense understorey may either prefer open ground and grass layer or the canopy cover for feeding and/or nesting. I found a negative association between bramble cover on the abundance of understorey independent birds. However, this may be due to a soil effect as bramble cover is greater in de-stumped areas than not de-stumped areas. Also I did not find a relationship between percentage of bramble cover and the percentage of the canopy cover (r = -0.01, p = 0.91, df = 253). For the percentage cover of bracken I found the opposite effect compared to bramble. Here, bracken cover is greater in not de-stumped areas. This suggests a soil effect as bracken prefers to grow on acid soil.

Investigating the overall abundance of all understorey dependent species may ignore the fact that the abundance of birds between blocks may be similar, but the number of bird species between blocks may vary. Although I did not find an effect of deer on the overall abundance of all understorey bird species, the aggregated guilds are coarse and combine species that may be expected to show a strong response to browsing (e.g. Garden Warbler and Dunnock may show lower occurrence in areas with less understorey shrub; Chas Holt, unpublished data) with others that are doubtfully understorey dependent (e.g. Willow Warbler, that was the most abundantly recorded species in this guild). Therefore examining the abundance of individual bird species which are sensitive to deer browsing among forest blocks may be useful to further investigate the impacts of deer on birds, as also suggested by Allombert et al. (2005a).

References

Allombert, S., Gaston, A. J. & Martin, J. L. (2005) A natural experiment on the impact of overabundant deer on songbird populations. *Biological Conservation,* **126,** 1-13.

Amar, A., Hewson, C. M., Thewlis, R. M., Smith, K. W., Fuller, R. J., Lindsell, J. A., Conway, G., Butler, S. & McDonald, M. (2006) What's Happening to our Woodland Birds? Long-term changes in the populations of woodland birds. *RSPB Research Report Number 19*.

Barrett, M. A. & Stiling, P. (2006) Effects of Key deer herbivory on forest communities in the lower Florida Keys. *Biological Conservation,* **129,** 100-108.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. (2001) *Introduction to Distance Sampling - Estimating abundance of biological populations,* Oxford University Press, Oxford.

Clauss, M., Lechner-Doll, M. & Streich, W. J. (2003) Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A reevaluation of an old debate and a new hypothesis. *Oikos,* **102,** 253-262.

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

Cooke, A. S. C. (2006) Monitoring muntjac deer *Munticacus reevesi* and their impacts in Monks Wood National Nature Reserve. pp. pp. 172. English Nature, Peterborough.

Corbet, G. B. & Harris, S. (1991) *Handbook of British Mammals,* Blackwell Scientific, Oxford, UK.

Cote, 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.

DeCalesta, D. S. (1994) Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management,* **58,** 711-718.

Dolman, P. M. & Sutherland, W. J. (1992) The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* **29,** 402-413.

Dolman, P. M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research,* **35,** 202-214.

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.

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. & Fuller, R. J. (2007) The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis,* **149,** 119-127.

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.

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.

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.

Lack, D. (1933) Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. *Journal of Animal Ecology,* **2,** 239-262.

McShea, W. J. & Rappole, J. H. (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology,* **14,** 1161-1170.

Morecroft, M. D., Taylor, M. E., Ellwood, S. A. & Quinn, S. A. (2001) Impacts of deer herbivory on ground vegetation at Wytham Woods, central England. *Forestry,* **74,** 251-257.

Palmer, S. C. F., Hester, A. J., Elston, D. A., Gordon, I. J. & Hartley, S. E. (2003) The perils of having tasty neighbors: Grazing impacts of large herbivores at vegetation boundaries. *Ecology,* **84,** 2877-2890.

Putman, R. J. & Moore, N. P. (1998) Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. *Mammal Review,* **28,** 141-163.

Rooney, T. P. & Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management,* **181,** 165-176.

Tanentzap, A. J., Burrows, L. E., Lee, W. G., Nugent, G., Maxwell, J. M. & Coomes, D. A. (2009) Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. *Journal of Applied Ecology,* **46,** 1064-1072.

The Deer Initiative (2010) Best Practice Guides. *http://www.thedeerinitiative.co.uk/html/bestpractice.htm*.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. & Burnham, K. P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology,* **47,** 5-14.

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

Zipkin, E. F., Royle, J. A., Dawson, D. K. & Bates, S. (2010) Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation,* **143,** 479-484.

Chapter Seven

Conclusion

Conclusion

This thesis has examined a range of aspects of deer density, demography and responses to management at a landscape scale in a heterogeneous forest and open habitat mosaic in Eastern England. It is one of the first studies to attempt to quantify deer densities across large contiguous landscapes and offers the first assessment of potential source sink dynamics across management boundaries. A particular focus of the thesis has been to examine in detail the demographic performance of the roe deer population. An additional aim has been to investigate the biodiversity impacts of mixed species deer assemblages in this forest, though this has proved more problematic.

The roe deer population in Thetford Forest

Since the re-establishment of roe deer to Eastern England in 1884 (Chapman and Whitta, 1996), a large and thriving population has developed, at least partly facilitated by the large extent of forest land offered by Thetford Forest. Roe deer body mass and fertility decreased over the period 1966-2009. Body mass and fertility declined about 25% from the phase of colonisation of Thetford Forest (1960s) to the period with the maximal density in the 1980s and 1990s, suggesting the operation of intra-specific density dependence. Within the last decade (2000-2009) cull pressure on roe deer and all other deer species (red deer, fallow deer, Reeve’s muntjac) in Thetford Forest has increased; this may be the cause of an increase in overall roe performance, suggesting a decrease in intra-specific density dependence. However, it is difficult to judge the impact of inter-species density dependence on the roe deer performance. Generally, the roe population should profit from a population reduction of the two big grazers, red and fallow deer, and the second browsing species, the muntjac. However, the increase in fertility and condition in the recent period of reducing numbers, despite ongoing high numbers of muntjac and an expanding fallow population, suggests that intra-specific competition may be stronger than the effects of other ungulate species.

Compared to other areas of Britain roe deer fertility in Thetford Forest was high (Ratcliffe and Mayle, 1992) in 2006-09. No significant differences in roe deer fertility was found among forest blocks implying that even in core blocks where access to nutritious farmland is reduced, roe deer condition was high. The roe deer population was therefore not limited by food availability. However, emigration rates in 2009/10 suggest that under long periods of frost and snow when food is limited in the farmland carrying capacity of single forest blocks may not support current densities. It has also been suggested that long periods of snow cover will reduce roe deer performance (Mysterud and Ostbye, 2006) but winters during the period of 2007-09 have generally been mild with snow cover persisting only for short time periods. Although, winter weather may affect roe deer condition the effects may be limited and the population will continue to increase in the absence of management. As a result the increasing roe numbers will impose further impacts on habitat and biodiversity.

Thetford Forest is mainly surrounded by nutritious farmland and smaller woodlands. Roe deer fertility and body mass were about 11% (0.2 foetuses/female) and 8% (1.2 kg), respectively, higher in the farmland (Chapter 1). Although, differences in roe deer condition between landscapes exist, these are subtle and will make only a minor contribution to any source sink dynamics. Thus, it is more likely that the varying level of deer control across boundaries either generates or amplifies source-sink dynamics.

The findings for roe deer in this study may also apply to Reeve's muntjac, red and fallow deer in Thetford Forest. Due to the availability of food in high quality and quantity in the farmland as well as the timber management which creates a mosaic of growth stages in the forest, none of these populations will be food limited. They are therefore all expected to show a high potential for potential population growth, in the absence of management. This is strongly supported by the analysis of potential reproductive parameters in the culled muntjac, which strongly suggest fertilisation immediately following parturition.

Deer impacts on biodiversity

Due to insufficient variation in deer density among forest blocks, combined with the long term browsing history of Thetford Forest, it is difficult to experimentally compare high to low impact areas. My results suggest that deer densities, though reduced compared to 1990s, were high in Thetford Forest, and therefore no or very limited recovery of biodiversity or habitat from deer impacts has yet taken place. Thus, deer are having a profound effect on vegetation structure and probably also on birds.

Increased levels of deer browsing change the habitat structure and thus, reduce understorey (Fuller et al., 2007, Gill and Beardall, 2001). Bramble is an important structural element in the forest, for example providing nesting and foraging opportunities for birds, and offering browse for deer especially in winter. The current extent of the bramble cover and distribution was lower in the southern blocks of the forest, than in the northern blocks that have lower densities of red and fallow deer. In 2006/07 and 2007/08 I also undertook work to investigate over winter browsing pressure of deer on bramble, although results have not been collated and presented in this thesis. Tagging of bramble shoots and scoring deer browsing intensity on a verg large sample of bramble leaves, suggests that deer browsing levels were high throughout Thetford Forest (K. Wäber, unpublished). It is notable that the most browsing sensitive bird species (e.g. dunnock) had generally low abundance in the forest.

Further research

Roe deer has been reported to be susceptible to competition with other species like the native red deer, introduced fallow deer and invasive Reeve's muntjac (Dolman and Wäber, 2008, Hemami et al., 2004). In this study I could not detect inter-specific influences on roe deer performance (Chapter 1). However, especially in winter when food is limited, Hemami et al. (2004) found considerable overlap in habitat use and aggregation on key forage resources such as bramble. Bramble is depleted in many parts of the forest (Hemami (2003), K. Wäber, unpublished data) suggesting inter-specific competition for forage may occur. High diet overlap between roe deer and muntjac have been reported by Forde (1989). Further, the introduced muntjac outnumbers the native roe deer two- to three-fold across Thetford Forest. This implies that the roe deer densities may increase when Reeve's muntjac density is reduced and that overall performance (fertility and body mass) of roe deer may also be further improved. To test this hypotheses an experimental reduction of high muntjac densities to a minimum in single forest blocks is needed whilst the roe deer management stays unchanged.

Deer browsing and its effects on biodiversity have been the focus of many research studies (e.g. Gill and Fuller (2007), Fuller and Gill (2001)). Although, deer impacts have been mainly studied in exclosure experiments (e.g. Holt et al (2010), Morecroft et al (2001)), few studies exist that have examined deer impacts on biodiversity at landscape scale (e.g. Tanentzap et al. (2009), Zipkin et al. (2010)). Hereby, studies have mainly focused on the impact of one deer species (e.g. white tailed deer by Rooney and Waller (2003)) or the assemblage of several deer species (e.g. Reeve's muntjac, roe deer and fallow deer by Holt et al. (2010)). More research is needed focusing on how different deer species affect vegetation structures across a range of habitat types. In most areas of Europe a multi species deer assemblage exists. Distinguishing between impacts of different species may, however, be difficult. Therefore, further investigation of species specific habitat use is necessary to understand habitat impacts as suggested by Gill and Morgan (2010). It is of importance to examine deer impacts in a range of woodlands which differ in deer species composition and density; it will require extensive replication to assess this independently across different woodland types. This will help to understand how impacts differ between deer species assemblages and densities and possible help to identify the significance that single deer species have on a change in habitat structure. Another way to compare different types of impacts of different species may be the selective reduction of deer density through increased cull within an area, for example in a forest block. This may be particularly useful when comparing possible different effects of roe deer and Reeve's muntjac, as both species have small home ranges which do not exceed the extent of several forest blocks as home ranges for red and fallow deer.

Management recommendations

Estimating deer numbers is crucial for evidence based deer management. However, estimating deer densities in woodlands with dense understorey has proven to be difficult. Most direct observation techniques are compromised by dense vegetation. Other method such as drive counts or mark-resighting are too labour-intensive to be applied at larger scales. Faecal pellet group methods are depending on uncertain estimates of parameters such as decay and defecation rate (Hemami and Dolman, 2005, Campbell et al., 2004). Although, it has been questioned if distance sampling thermal imaging is a useful method to establish deer numbers (Smart et al., 2004) this study proved that it is a robust method to estimate especially roe deer and Reeve's muntjac density at a landscape level (Chapter 4). In conifer plantation transect routes designed along tree planting rows offer improved detectability of deer and increase the ESW. Also it is possible to detect changes in numbers over a small number of years. For example changes in population density due to increased cull or habitat changes ranging between 21% and 47% have been detected in this study. The cost of expensive thermal imaging equipment may be shared by several landowners or equipment may be borrowed, for example from the Deer Initiative.

For a successful reduction of deer numbers it is necessary to understand the impact the deer cull has on the population size; this in turn requires understanding the magnitude of productivity or potential recruitment from neighbouring areas (Chapter 5). Thus, the knowledge of deer density, fertility, kid survival and culled numbers across landowner boundaries is necessary to predict appropriate management targets for evidence based deer management.

Landscapes are heterogeneous mosaics of habitat patches which may influence deer performance (Pettorelli et al., 2005, Pettorelli et al., 2001). Variation in deer performance in combination with varying level of deer management may lead to source sink dynamics. The knowledge of potential sources and sinks within or across landscapes may improve the effectiveness of deer management. Managing sink areas with low deer density where deer is emigrating from neighbouring areas may result in fewer culled deer, per day effort. Thus, concentrating cull efforts in source areas may increase the number of deer culled per day effort and simultaneously reduce deer numbers in the wider landscape.

More landscape-scale deer management research is to be done.

References

Campbell, D., Swanson, G. M. & Sales, J. (2004) Comparing the precision and cost-effectiveness of faecal pellet group count methods. *Journal of Applied Ecology,* **41,** 1185-1196.

Chapman, N. & Whitta, R. (1996) The history of the deer of Thetford Forest. *Thetford Forest Park - The ecology of a pine forest* (eds P. R. Ratcliffe & J. Claridge), pp. 141-149. Forestry Commission, Thetford.

Dolman, P. M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research,* **35,** 202-214.

Forde, P. G. (1989) Comparative ecology of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a commercial coniferous forest. Ph.D. thesis, University Bristol.

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

Fuller, R. J., Smith, K. W., Grice, P. V., Currie, F. A. & Quine, C. P. (2007) Habitat change and woodland birds in Britain: implications for management and future research. *Ibis,* **149,** 261-268.

Gill, R. M. A. & Beardall, V. (2001) The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry,* **74,** 209-218.

Gill, R. M. A. & Fuller, R. J. (2007) The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis,* **149,** 119-127.

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.

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, Norwich.

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. *European Journal of Wildlife Research,* **51,** 19-24.

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.

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.

Morecroft, M. D., Taylor, M. E., Ellwood, S. A. & Quinn, S. A. (2001) Impacts of deer herbivory on ground vegetation at Wytham Woods, central England. *Forestry,* **74,** 251-257.

Mysterud, A. & Ostbye, E. (2006) Effect of climate and density on individual and population growth of roe deer Capreolus capreolus at northern latitudes: the Lier valley, Norway. *Wildlife Biology,* **12,** 321-329.

Pettorelli, N., Gaillard, J.-M., Duncan, P., Ouellet, J.-P. & van Laere, G. (2001) Spatial variations in habitat quality, local density and phenotypic quality in roe deer. *Oecologia,* **128,** 400-405.

Pettorelli, N., Gaillard, J.-M., Yoccoz, N. G., Duncan, P., Maillard, D., Delorme, D., van Laere, G. & Toigo, C. (2005) The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. *Journal of Animal Ecology,* **74,** 972-981.

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

Rooney, T. P. & Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management,* **181,** 165-176.

Smart, J. C. R., Ward, A. I. & White, P. C. L. (2004) Monitoring woodland deer populations in the UK: an imprecise science. *Mammal Review,* **34,** 99-114.

Tanentzap, A. J., Burrows, L. E., Lee, W. G., Nugent, G., Maxwell, J. M. & Coomes, D. A. (2009) Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. *Journal of Applied Ecology,* **46,** 1064-1072.

Zipkin, E. F., Royle, J. A., Dawson, D. K. & Bates, S. (2010) Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation,* **143,** 479-484.