

**The interaction of Sika deer (*Cervus nippon* Temminck 1838)
with lowland heath mosaics**

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The interaction of Sika deer (*Cervus nippon* Temminck 1838) with lowland heath mosaics

Antonio Uzal Fernandez

ABSTRACT

Sika deer (*Cervus nippon*) has become an invasive species in many parts of the world. In the south of England large populations appear to be concentrated in landscapes comprising of mosaics of lowland heath, woodlands and grassland. Despite the association between the distribution of Sika deer and that of lowland heath, little is known regarding the extent to which Sika deer utilize lowland heath and their impacts on its plant and animal communities. The aim of this thesis was to investigate the ecological interaction of Sika deer with lowland heath set in a mosaic of other habitats. Specifically, the main three objectives of this thesis were: i) to investigate the different ecological factors affecting the distribution and habitat use by Sika deer; ii) to explore consistency in Sika deer habitat associations as a potential tool to predict the distribution and abundance of Sika deer; iii) to investigate the ecological impacts of the usage of areas of lowland heath by Sika deer upon plant and animal communities of lowland heath. Results showed that Sika deer distribution and habitat use are affected by the availability of habitats, landscape structure and human disturbance at both the landscape and home range scale (i.e. few hundred of hectares and few dozens of hectares respectively). At the landscape scale, Sika deer seemed to use the requirement for safe access to pastures as the main criteria for their habitat selection. At the home range scale, the criteria of choice in the use of resources by Sika deer seemed to be related to a requirement for an appropriate balance of food and cover as the selection of pastures and cover were inversely related to their availability. However, human disturbance, as a form of perceived risk, was also a limiting factor of habitat use at the home range scale. Consistencies in the habitat selection by Sika deer at the landscape scale between areas with similar landscape were detected, which could potentially be used to develop models to predict the distribution and abundance of Sika deer and their subsequent impacts in areas of lowland heath. This study has found a different response of plant and animal communities between dry and wet heath to levels in usage of areas of heath by Sika deer. The existence of a threshold in the local density of Sika deer on areas of heath above which dry lowland heath showed signs of decline in quality has also been identified.

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CHAPTER 1: INTRODUCTION

Understanding the factors that affect the spatial distribution and abundance of wild large herbivores that are able to modify plant and animal communities is vital for managers aiming to balance the ecological, cultural and economic sustainability of ecosystems. Large herbivores affect plant and animal community composition and ecosystem functioning (e.g. Hobbs and Huenneke, 1992, Hobbs, 1996, Ford and Grace, 1998, Hester *et al.*, 1999, Cote *et al.*, 2004, Gordon *et al.*, 2004, Mysterud, 2006). Consequently, herbivores fall into the group of highly interactive species as defined by Soulé *et al.* (2003) because their absence leads to significant changes in some features of their ecosystem(s). In addition, the interaction of large herbivores with their environment has raised particular interest where the herbivore is a non-native or a reintroduced species (i.e. Clout, 2002, Lau, 2006, Johnson and Cushman, 2007, Petty *et al.*, 2007), as it is critical to understand if and how invasive herbivores affect the structure and composition of invaded ecosystems.

During the 19th and 20th Century Sika deer (*Cervus nippon* Temminck 1838) established as a non-native species in many parts of the world following escapes from private collections with wild-living populations established in different European countries (Austria, Britain, Denmark, France, Germany and Hungary), a number of US states (e.g. Virginia, Texas) and also in New Zealand and Australia (Fraser, 2005, Pitra, 2005, and McCullough *et al.*, 2009 for an updated review of the present worldwide distribution of this species). Sika deer are native to East Asia, with a wide range from eastern Siberia to Korea, Eastern China, and parts of Vietnam and Taiwan (Formosa). Also Sika deer can be found on some Pacific islands (Pitra, 2005). The name ‘Sika’ originates from the Japanese word for deer (Mann, 1982) due to the broad distribution of the species in this country. Nevertheless, “Sika deer” is widely used in the western literature (McCullough *et al.*, 2009, page 1); consequently it is the term used in this thesis.

The majority of ecological information about Sika deer comes from their native distribution in Japan, in which Sika deer generally occupy a large ecological range, from subtropical and warm-temperate broad-leaved evergreen forests, deciduous, boreal mixed and coniferous forests to artificial plantations and abandoned crops (Maruyama, 1992). Sika deer are usually considered in Japan neither typical forest dwellers (but see Takatsuki,

2009b) nor adapted for open spaces, usually inhabiting the forest edge (Takatsuki, 1991 in Hannaford et al. 2006, Borkowski, 2000). Studies monitoring radio-tracked Sika deer (mainly females) have shown the existence of migration patterns in Japanese populations (e.g. Takatsuki *et al.*, 2000, Uno and Kaji, 2000, Sakuragi *et al.*, 2003a, Sakuragi *et al.*, 2003b, Igota *et al.*, 2004). There is also evidence of high site fidelity to their seasonal home ranges (Uno and Kaji, 2000, Igota *et al.*, 2004). However, Sika deer feeding behaviour in Japan is highly variable even within populations occupying the same area (e.g. Yokoyama *et al.*, 2000, Takahashi and Kaji, 2001, Campos-Arceiz and Takatsuki, 2005). Sika deer adapt their behaviour to different feeding resources and when resources are limited or have been depleted they are capable of exploiting foods that they have not used in the past (Takahashi and Kaji, 2001, Miyaki and Kaji, 2009). Sika deer show a wide range of feeding behaviour across their Japanese distribution, from specialist grazing to seasonal or continuous browsing (e.g. Jayasekara and Takatsuki, 2000, Ueda *et al.*, 2003, Takatsuki, 2009a), hence Sika deer have been considered as intermediate feeders (i.e. able to graze and browse) due to the contribution of graminoids and woody plants to their diet (see Asada and Ochiai, 1996). In the UK, it has been shown that Sika deer also shift diets to obtain the most nutritious food available through each season and in differing areas (Mann and Putman, 1989a).

In contrast to the abundant research into the food habits and migration movements, studies on the home range of Sika deer (i.e. size and habitat use) are limited (Ito and Takatsuki, 2009). Previous studies have investigated Sika deer habitat preferences (e.g. Mann, 1982, Mann and Putman, 1989b, Borkowski and Furubayashi, 1998a, Borkowski, 2000, Sakuragi *et al.*, 2002, Sakuragi *et al.*, 2003b, Ito and Takatsuki, 2009), the relationship between landscape structure and Sika deer ecology (e.g. Miyashita *et al.*, 2007, Miyashita *et al.*, 2008), and to a limited extent, the effects of disturbance on Sika deer behaviour (e.g. fleeing behaviour, Borkowski, 2001). However, in a humanized biosphere (*sensu* Vitousek *et al.*, 1997), the habitat availability, landscape structure and human disturbance are likely to interact and produce combined responses in the distribution and habitat use of wild mammals such as Sika deer. Morrison (2001) suggests that wildlife-habitat relationship studies should focus on resources as the basic currency for the survival and reproduction of individuals. Therefore, the present study has considered the spatial distribution of key resources (i.e. food and cover) and the environmental constraints that limit the exploitation of those resources (i.e. human disturbance). Moreover, as the selection of habitats can

occur at different hierarchical levels (Johnson, 1980, Aebischer *et al.*, 1993) it has been suggested that analyses of habitat selection should follow a multi-scale approach (e.g. Mysterud and Ims, 1998, Dussault *et al.*, 2005, Herfindal *et al.*, 2009, Zweifel-Schielly *et al.*, 2009). Still, no studies have explicitly considered the combined effects of habitat availability, landscape structure and disturbance on the distribution and habitat use of Sika deer at different spatial scales.

As large herbivores, Sika deer might affect both plant and animal communities of the habitats they use. The majority of the information about Sika deer impacts on animal and plant communities comes from Japan (e.g. Kaji and Yajima, 1992, Shimoda *et al.*, 1994, Takatsuki *et al.*, 1994, Takatsuki and Hirabuki, 1998, Akashi and Nakashizuka, 1999, Yokoyama *et al.*, 2001, Nagaike and Hayashi, 2003). However, Japanese studies are mostly concentrated on the effects upon different plant communities of forests such as coniferous, mixed and deciduous broad-leaved forests (e.g. Kaji and Yajima, 1992, Takatsuki and Gorai, 1994, Takatsuki and Hirabuki, 1998, Oi and Suzuki, 2001); much less on open or mixed habitats (but see Takada *et al.*, 2002). The same appears true elsewhere, where Sika deer impacts have been mainly reported within woodland ecosystems in countries such as UK (Lowe and Gardiner, 1975, Ratcliffe, 1987, Chadwick, 1996, Putman and Moore, 1998), New Zealand (Husheer *et al.*, 2006) and Russia (reviewed in Aramilev, 2009). An exception is a study by Hannaford *et al.* (2006) that documented changes to saltmarshes and fenland communities in Poole Harbour in England.

In Britain, the majority of populations of Sika deer are found in areas of coniferous plantations and surrounding heath (Putman 2000). Despite the extensive use by Sika deer of heath and the fact that lowland and upland heaths (moorlands) are international priority conservation areas (Habitats Directive 92/43/EEC), still very little is known about the effects of Sika deer upon these communities. Moreover, the majority of available information with regard to impacts of large herbivores on heath mosaics is restricted to sheep and Red deer (*Cervus elaphus*) in the Scottish moorlands upland heath (e.g. Gimingham, 1972, Clarke *et al.*, 1995b, Welch and Scott, 1995, Palmer, 1997, Hester and Baillie, 1998, Stewart and Hester, 1998, Hester *et al.*, 1999, Palmer *et al.*, 2003) and north-western European heaths (i.e. Bakker *et al.*, 1983, Achermann, 2000). Much less substantial work has been conducted on the impacts of other domestic grazers such as

cattle, ponies and goats (but see Putman, 1986, Bokdam and Gleichman, 2000, Jauregui *et al.*, 2008) and other deer species upon plant and animal communities of heath.

Large populations of Sika deer occur in parts of the south of England (Swanson and Putman, 2009), and they overlap in distribution with mosaics of lowland heath, woodlands and grassland. This link between Sika deer distribution and lowland heath suggests that Sika deer, through grazing and trampling might be affecting vegetation structure, plant community composition and the abundance of plant species. Lowland heaths are not only important because of their rare plant communities, they also support breeding populations of species of invertebrates, rare reptiles, amphibians and birds that have long been UK Biodiversity Action Plan priorities (DOE, 1995). The responses of both the vegetation and animal communities of lowland heath to the level of heath usage by Sika deer are currently unknown.

Two gaps in the scientific knowledge about the interaction of Sika deer with lowland heath mosaics have been identified during the literature review related to this topic. The first is related to the combined role of habitat availability, landscape structure and human disturbance in the distribution and habitat use of Sika deer. The second gap in the scientific knowledge is related to the effects of Sika deer on animal and plant communities of lowland heath. For ecosystem managers who wish to meet environmental and economic objectives to manage protected areas, the prediction of the distribution, abundance and potential impacts of Sika deer might be more important than reacting once that deer have been established in such density that the management objectives are compromised. Making such predictions requires three stages. The first step is to determine the factors affecting the distribution and habitat use by Sika deer in mosaics of lowland heaths, woodlands and grassland. The second step is to establish the ecological impacts of Sika deer at different densities on lowland heath. Finally, the third step is identifying behaviour consistency in the distribution and habitat associations of Sika deer across different areas as a potential tool to predict the distribution and abundance of Sika deer and abundance and the subsequent ecological impacts on protected areas.

The aim of this thesis is to investigate the ecological interaction of Sika deer with lowland heath mosaics to better understand the factors that affect the habitat selection and distribution of Sika deer and the processes through which Sika deer might be affecting

plant and animal communities of lowland heath. Specifically, the main three objectives of this research were:

- i) investigate the different ecological factors affecting the distribution and habitat use by Sika deer;
- ii) explore consistency in Sika deer habitat associations as a potential tool to predict the distribution and abundance of Sika deer and the subsequent impacts on plant and animal communities of protected habitats.
- iii) investigate the ecological impacts of the usage of areas of lowland heath by Sika deer upon plant and animal communities of lowland heath;

The second chapter of this thesis describes the methods used to address the objectives of this research. The third chapter investigates the ecological factors affecting Sika deer distribution and habitat use in lowland heath mosaics, in particular the availability of habitat, the landscape structure and disturbance by humans. The fourth chapter compares the habitat associations of Sika deer between different study areas to identify behaviour-site consistency in the distribution and habitat use by Sika deer. Finally, the fifth chapter studies the ecological impacts of Sika deer activity upon plant and animal communities of lowland heath. In particular, different levels of local density of Sika deer in areas of lowland heath are related to differences in the communities of plant and surface-active invertebrates of lowland heath. The general discussion of the thesis (sixth chapter) integrates the findings of the individual papers, discusses them in terms of the new ecological knowledge acquired by this thesis, highlights the usefulness of this knowledge for the management of Sika deer populations and the conservation of lowland heath and suggests further work to improve the understanding of the interaction of Sika deer with lowland heath mosaics.

CHAPTER 2: METHODS

2.1 STUDY AREA

This research has been carried out in Purbeck, which is a rural district covering around 40,000 hectares in the South West of England (Figure 2.1) that contains over 40 Sites of Special Interest (SSSI), accounting for 23% of the total area. It includes 30 habitats and 200 plant and animal species of national and local concern, with Special Protection Areas, Special Areas of Conservation and RAMSAR sites. It also contains 5% of the UK's reed beds and heathlands and over 1% of the UK's neutral, acid and calcareous grasslands (Purbeck, 1998).

The landscape of Purbeck is composed of a mosaic of areas of different sizes of heath, grasses, woods, reed-beds, saltmarshes and other habitats. Purbeck has one of the largest groups of feral Sika deer in England, with numbers that have been estimated in the region of 2,000 individuals (Putman, 2008). During the season 2006-2007 an estimated total of 1,350 Sika deer were harvested in the land managed by some of the main stakeholders in Purbeck (The Royal Society for the Protection of Birds, The National Trust and The Ministry of Defence). This number suggests that Sika deer population in Purbeck might have been underestimated and/or the population has increased during this decade. Numbers of Roe deer (*Capreolus capreolus*) are much lower, while observations of wild Muntjac deer (*Muntiacus reevesi*), Red deer (*Cervus elaphus*) and Fallow deer (*Dama dama*) are anecdotal.

For this thesis three study areas that represent the diversity of habitats contained in Purbeck have been selected: Arne, Hartland and Studland (Figure 2.1).

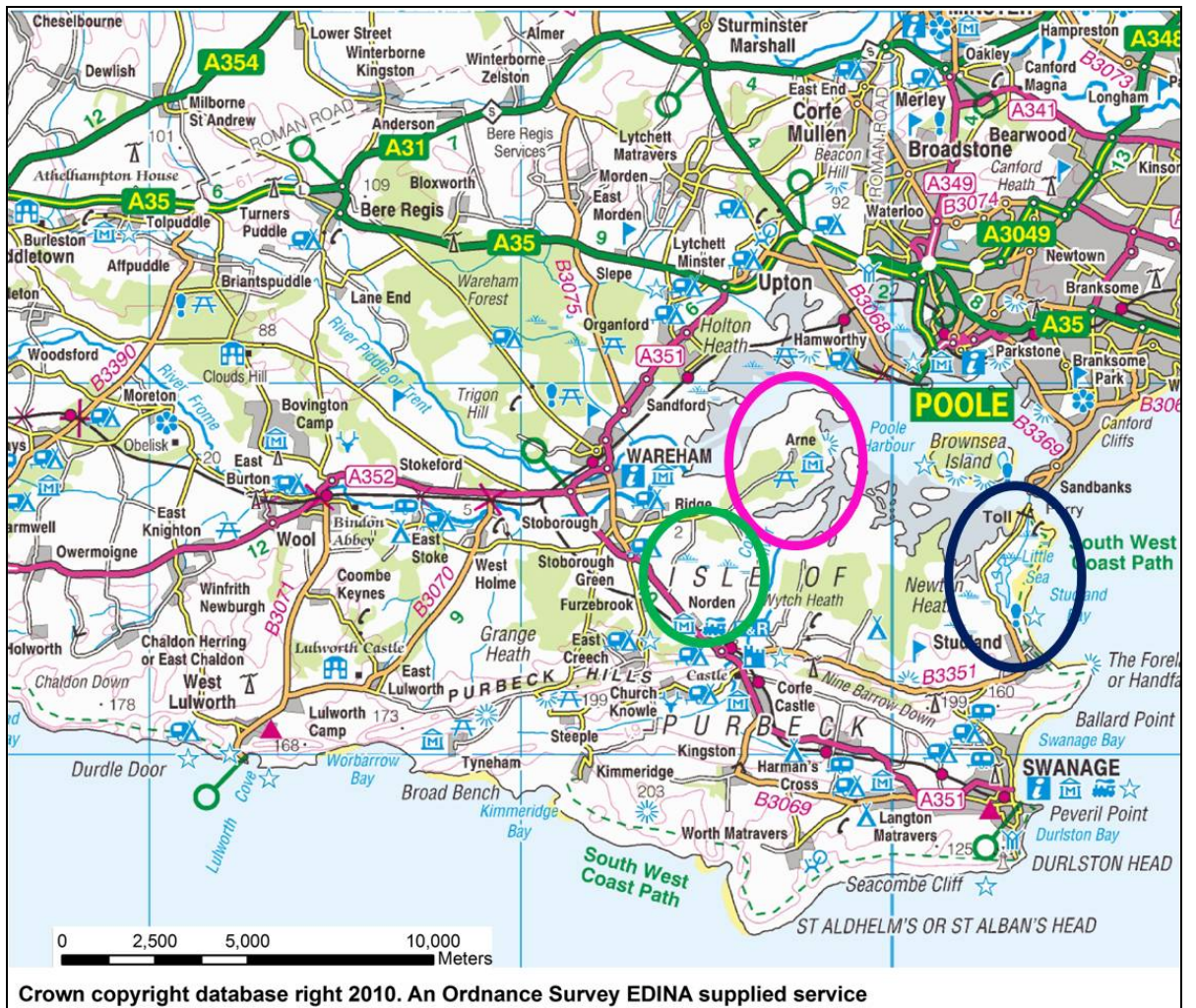


Figure 2.1: Location of The Purbeck district and surroundings and the three study areas. The pink circle indicates the location of Arne, the green circle indicates the location of Hartland and the blue circle indicates the location of Studland.

2.1.1 Arne

Arne Reserve (‘Arne’), is an area of 608 hectares (50° 41' 20" N, 2° 2' 20" W, Figure 2.2). Arne is managed by The Royal Society for the Protection of Birds (RSPB). Poole Harbour, adjoining Arne, is recognised as an important area for wildlife, with many designations including Special Site of Scientific Interest (SSSI), Special Protection Area (SPA), and a RAMSAR site. Arne Reserve for itself is a SSSI and a National Nature Reserve (NNR).

Arne attracts a large number of visitors every year (85,000 in 2008-2009, source: RSPB). It contains a mosaic of coniferous and deciduous woodland, lowland heath, pastures and wetland habitats such as saltmarshes. At Arne, the most abundant habitat was heathland (33% cover) followed by saltmarshes (14% cover) and coniferous woodland (13% cover). Arne also contains highly diverse plant and animal communities, with over 250 species of vascular plants, a rich invertebrate fauna and numerous species of protected birds

Two species of deer are present, Sika deer in large numbers and Roe deer in small numbers. Population densities of Sika deer in Arne were estimated at 118 deer/km² by a deer count conducted in October 2007. Culling management occurs from October to April. During the 2007-2008 hunting season, 33% the annual estimated population in Arne was harvested. Apart from deer grazing, cattle also graze in the grass fields of Arne Farm.

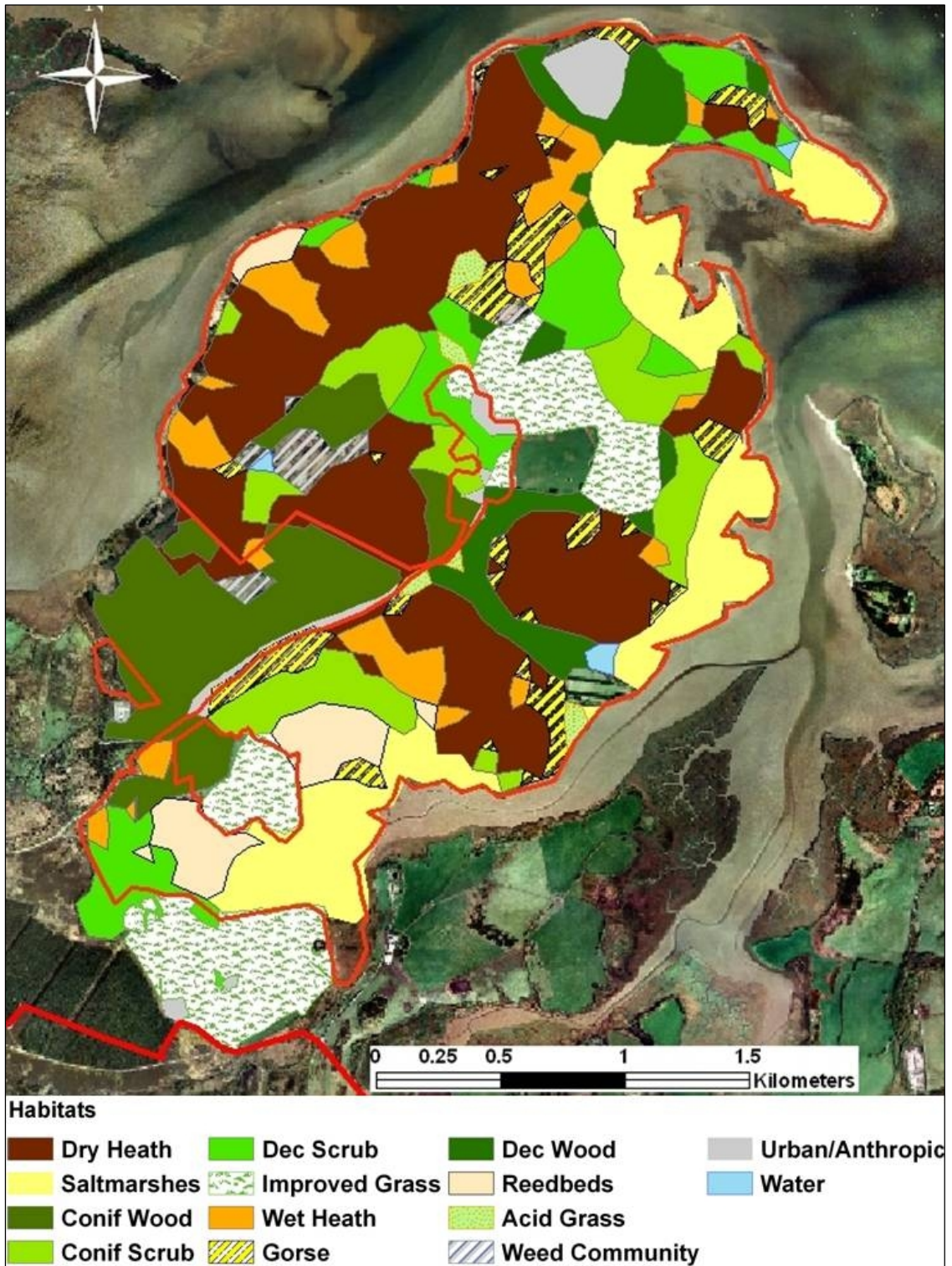


Figure 2.2: Habitats map of Arne. The red line indicates the limits of the study area. The red line on the south west corner indicates the northern limits of Hartland (see below).

2.1.2 Hartland

Hartland Moor and Middlebere Heath ('Hartland', 50° 39' 58" N, 2° 4' 26" W, Figure 2.3) are protected areas (National Nature Reserve and Site of Special Scientific Interest) managed by The National Trust (NT) and Natural England (NE). The total size of the study area is around 550 hectares.

The area is visited regularly by dog walkers and large numbers of tourists (far fewer compared to Arne, although reliable numbers are not available), many attracted by the possibilities of watching Sika deer and lowland heath birds. Hartland contains a mosaic of grasslands, lowland heaths, crops and patches of semi natural broadleaved woodlands and reed beds. At Hartland the most abundant habitat is improved grassland (35% cover) followed by heathland (33% cover) and mires (11% cover). The north part of this area is dominated by an extensive patch of dry heath, wet heath and mire, whilst the south is dominated by patches of grassland with a lower proportion of dry heath and patches of deciduous woodland and scrub.

Population densities of Sika deer were estimated in October 2007 by a deer count at 26.5 deer/km². During the 2007-2008 hunting season 17% of the annual estimated population in Hartland were culled. Numbers of Roe deer, the only other deer species in the area, were extremely low.

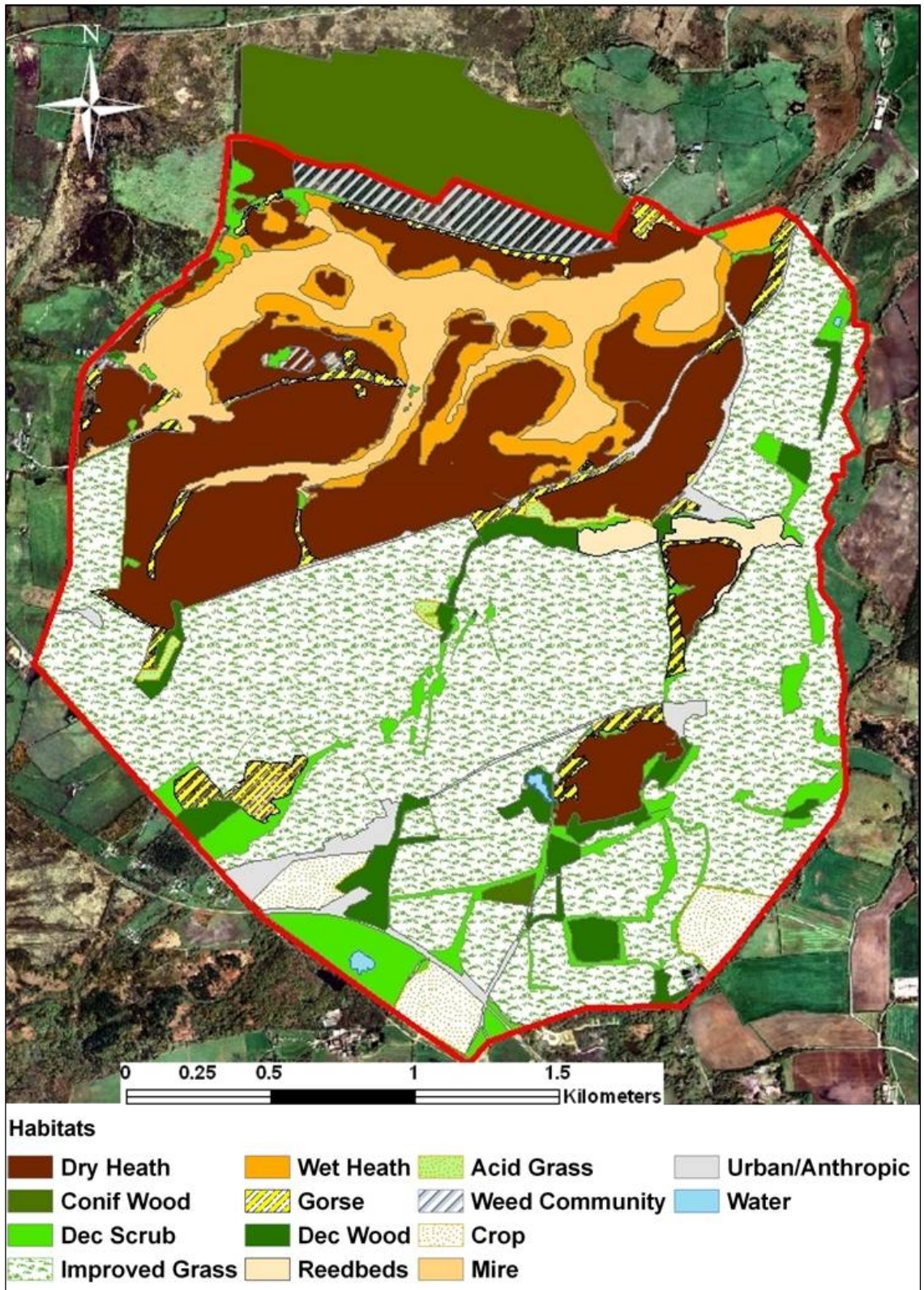


Figure 2.3: Habitats map of Hartland. The red line indicates the limits of the study area.

2.1.3 Studland

Studland and Godlingston Heaths ('Studland', 50° 39' 17" N, 1° 57' 56" W, Figure 2.4) is a protected area (National Nature Reserve and Site of Special Scientific Interest) managed by The National Trust (NT). The total size of this study area is around 792 hectares. Studland contains a mosaic of lowland heaths, mires, pastures and patches of semi natural broadleaved woodlands and sand dunes. Studland is dominated by heath (50% cover), followed by mire (14% cover) and deciduous woodland (10% cover). The area receives an extremely large number of visitors especially during the summer when hundreds of thousands of visitors use the beach facilities.

Two species of deer are present; Sika deer are abundant while Roe deer are found in small numbers. Population densities of Sika deer were estimated at 16.9 deer/km² by a deer count in October 2007. During the 2007-2008 hunting season 27% of the annual estimated population in Studland were culled.

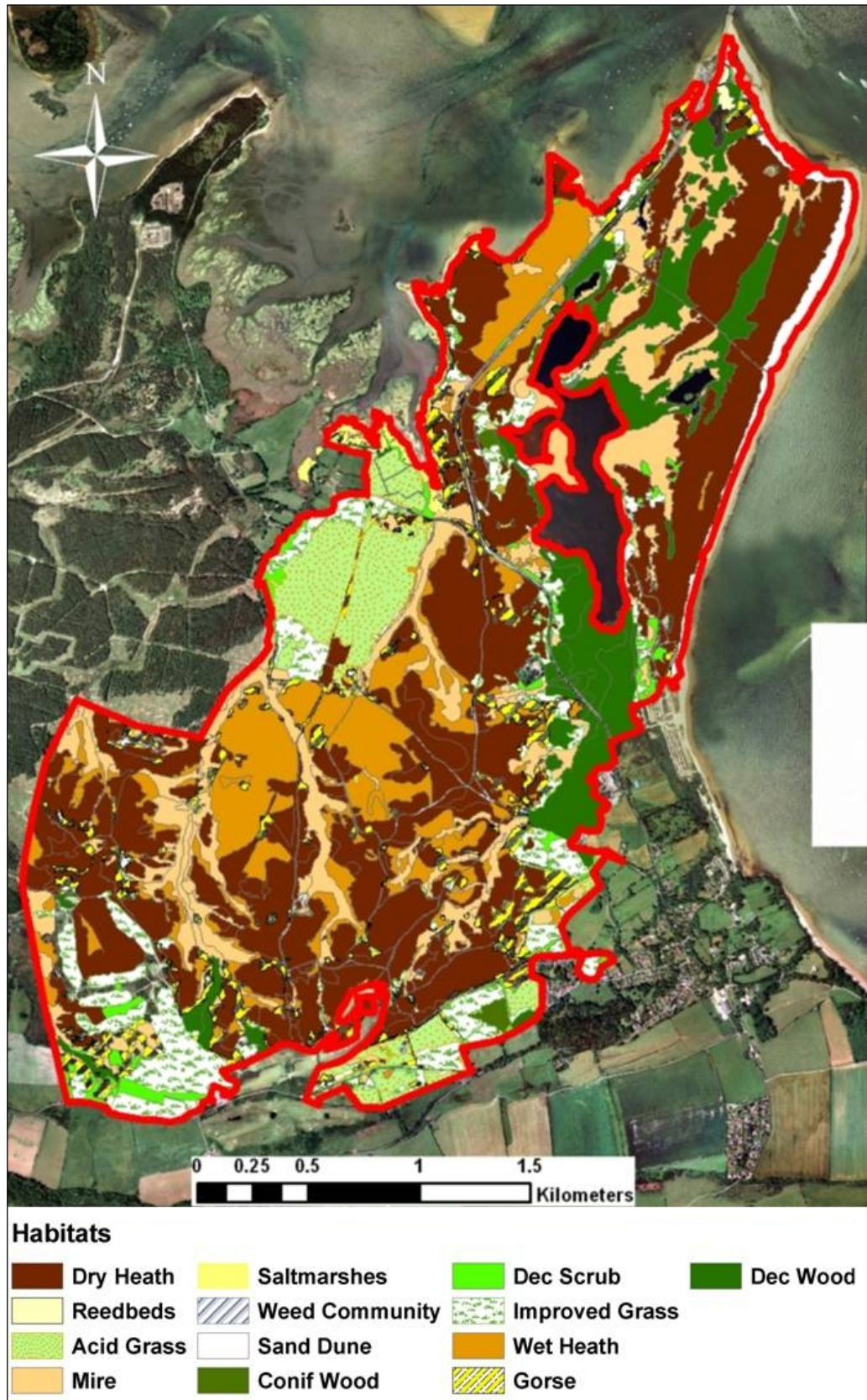


Figure 2.4: Habitats map of Studland. The red line indicates the limits of the study area.

2.1.3 Landscape structure of the study areas

Two of the study areas (Studland and Arne) have similar landscape structure: higher area of cover than pasture, in particular improved grassland (Table 2.1). Both study areas also have a similar distribution of habitats, with patches of grassland scattered across the study area in between patches of lowland heath and cover. By contrast, Hartland is dominated by pastures, in particular improved grassland (Table 2.1). Patches of grassland are concentrated in the southern part of this study area (heath occurring to the north) and the distance between grassland patches is much shorter than at Studland and Arne. Cover, mainly offered by deciduous woodland, is scattered across the study area and occupies a lower area than pasture.

Table 2.1: Summary of landscape characteristics of the three study areas

	Studland	Arne	Hartland
Surface area (ha)	792	608	550
Cover area (%)	18.8	38.9	13.7
Pastures area (%)	15.6	28.9	49.8
Improved grassland area (%)	8.8	12.8	39.5
Mean distance to nearest neighbour patch of improved grassland (m)	92.7	94.3	19.3

2.2 METHODS USED TO OBTAIN DATA ON SIKA DEER POPULATION DENSITY

Sika deer population density estimates were obtained at the different study areas by the supporting organizations. The main stake holders at Arne (RSPB), Hartland (NT and Natural England) and Studland (NT) carried out their own deer counts.

A deer count was conducted twice per year (March and October) in all areas managed by The Natural Trust (NT) in Purbeck, including Hartland and Studland. At Hartland, NT also conducted the deer count in the part of land owned by NE. Therefore annual counts are conducted at the time with the lowest number of deer (after culling at the beginning of Spring) and at the time of higher deer numbers (end of Autumn). This count was coordinated by NT staff and conducted by staff and volunteers that received at least one session of training about deer recognition. Study areas were divided into zones to be walked by the surveyors. Surveyors were provided with an aerial photograph and a standard form. Just after sunrise the different surveyors walked the zone (ensuring that all open parts of the zone were viewed directly, and all areas of cover were approached or walked through when possible) and took note on the form and mapped the deer sightings and data about number and species of deer, gender, age group (mature/calf), habitat at location and direction of movement. Surveyors used the direction of movement to avoid double counts and the final data was integrated into a GIS database. Age group might become difficult to be visually assessed by non highly trained observers and therefore only the total number of deer were used in further analysis. The data obtained was analysed by NT staff in order to avoid double counts and it was integrated in a GIS database. During the period March 2007 to March 2009 field data from Hartland was collected by the author of this thesis with the collaboration of Mr. Jerry Lloyd and additional volunteers.

The RSPB carried out its Sika deer count at Arne during the same dates as NT but they repeated the count 7 days after and obtained the average of the two counts. In this case the method was a drive count: a number of volunteers walked gently through the different areas to move the deer out of cover in the direction of trained observers that noted the number of deer, gender, age and direction of movement. The data obtained was analysed on the ground by a trained coordinator (Mr. Johnny O'Brien) to avoid double counts.

When possible, the author of this thesis was present during at least one of the deer counts in March/April and October during the period 2007-2009.

2.3 METHODS USED TO OBTAIN DATA ON SIKA DEER DISTRIBUTION

To address the objectives of this research it was required to know the distribution of Sika deer in the different study areas. This was obtained by deer counts carried out by NT at Hartland and Studland (as described in previous section) and by radio tracking at Arne and Hartland.

2.3.1 Radio tracking

Radio tracking data were obtained by two different means: i) radio tracking data for 21 female Sika deer during the period February 2004 to October 2007 gathered during a previous project carried out by Dr. Anita Diaz, Dr. Sean Walls and Miss Debbie Whitmarsh were made available for re-analysis within the current project; ii) radio tracking data for 10 female Sika deer during the period May 2007 to February 2009 gathered during the development of this research and conducted by the author of this thesis. During the winters of 2004 and 2005, 21 female Sika deer were caught at Arne with nets during drive-beating sessions. At Hartland 10 female Sika deer were caught using the same method between February and March 2007 (Table 2.2). Several attempts were made in different areas of Hartland in order to avoid capturing members of the same group/herd but only attempts conducted at three places were successful (Figure 2.5). Each animal was evaluated in terms of overall body condition, weight, age and sex. The suitable animals (apparently healthy hinds with standard size/weight ratios) were fitted with VHF TW-3 radio collars (Biotrack Ltd.) weighing 170g. including battery and collar.

Table 2.2: Sika deer captured and fitted with radio-transmitters at Hartland

Deer ID No.	Sex/age class	Date of capturing
354	Adult female	18/02/2007
415	Adult female	04/02/2007
425	Adult female	18/02/2007
473	Calf female (9 months)	18/02/2007
504	Adult female	11/02/2007
515	Adult female	21/03/2007
545	Calf female (9 months)	18/02/2007
566	Adult female	11/02/2007
704	Immature female (21 months)	11/02/2007
756	Adult female	18/02/2007

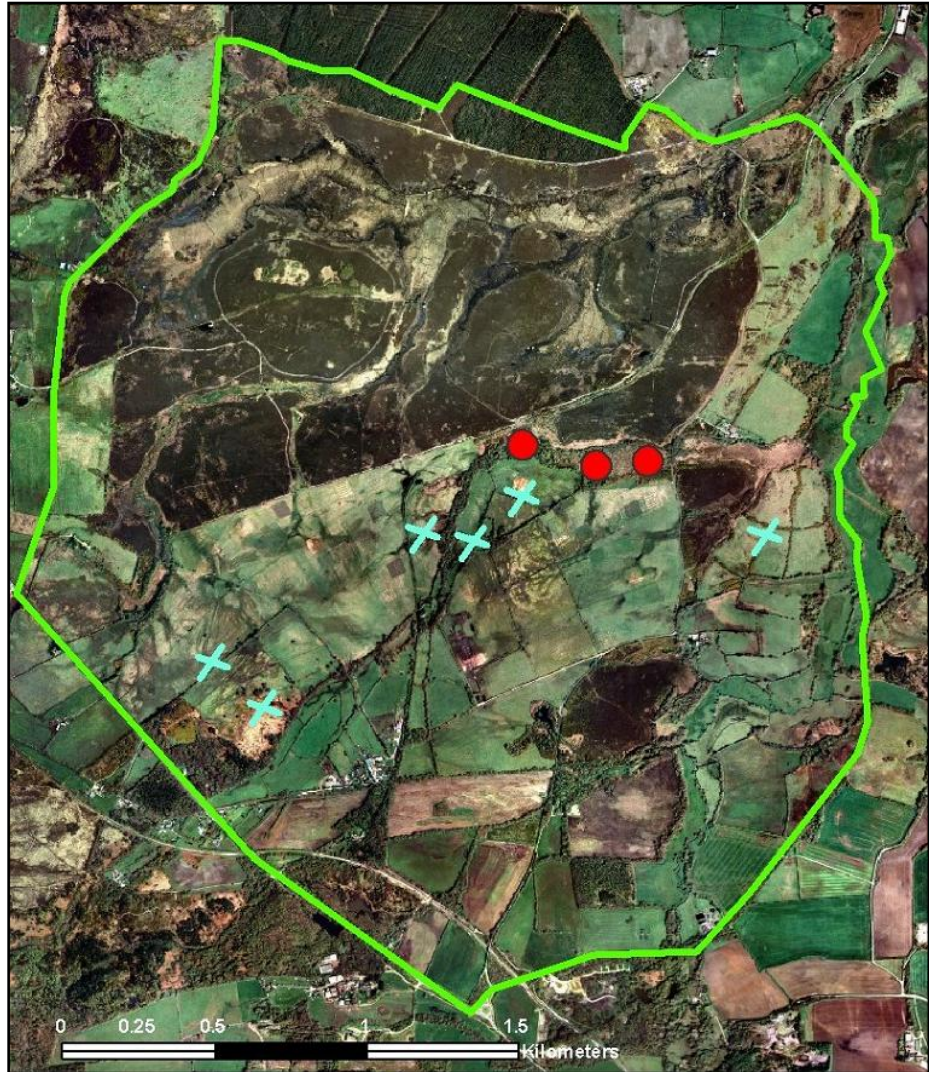


Figure 2.5: Radio tracking catches at Hartland. The crosses indicate the location of failed attempts. The circles indicate the location of successful catches.

Radio locations were obtained by triangulation (Kenward, 2001b) using a Telonics TR-4 receiver (Mesa, USA) and a three element hand-held Yagi antenna. From February 2004 to October 2007 (Arne) and from May 2007 to February 2009 (Hartland) 35-36 locations per deer were obtained during each of the following months: February, May, July and October. An incremental analysis of a pilot study with 50 locations showed that home range size plotted against the number of locations reached and asymptote between 20 and 30 locations in the majority of cases. Therefore a standard 35-36 locations was collected for each deer in each season (winter: February, spring: May, summer: July; autumn: October) during a 2/3 week period. All locations were made within 1.5 hours of taking the first bearing, any location that took more than that period was discarded. A minimum of 2.5 hours were left between locations in order to minimize the bias. No more than 3 locations were obtained within a 12 hour period. The observer attempted to spread the locations in

time as much as possible and balance the number of day and night locations during each season. A subsequent t-test of the differences between consecutive fixes showed that, in general, increasing the number of fixes after the 26th fix did not increase significantly the area by more than 1 hectare between consecutive fixes, which represented 1% increment of the average home range area. Therefore the data were likely to have represented all the places the deer were using during their usual daily activities and so the content of habitats within their home ranges. The accuracy of locations was determined in the field using a test transmitter carried by a researcher placed in various habitats as described by Harris *et al.* (1990), indicating an error buffer of 50 meters radius (average difference between the estimated location and the GPS location). All possible efforts were made to obtain accurate locations, thus animals were located from within a distance of less than 500 meters.

Seasonal and annual home ranges of the tagged female Sika deer at Arne and Hartland were obtained using Ranges8 software (Kenward *et al.*, 2008). Following Borger *et al.* (2006), home ranges were defined using the Kernel method (Worton, 1989) for the 90% isopleths. The kernels, in contrast to Minimum Convex Polygons (MCP), are able to account for multiple centres of activity (Kenward, 2001b) which is a quality of the home ranges that Sika deer have in one of the study areas; multinuclearity has been found yearly and across seasons at Hartland. Also the use of 90% isopleths method has been found to provide more unbiased home range estimates with relatively few data and across sampling regimes than MCP (Borger *et al.*, 2006).

2.4 METHOD TO OBTAIN INFORMATION ON SIKA DEER HABITAT ASSOCIATIONS

To fulfil the first objective of the research and investigate the different ecological factors affecting the habitat selection and distribution of Sika deer it was required to know how Sika deer select habitats.

Habitat selection can occur at four hierarchical levels (Figure 2.6): i) the selection of geographical range; ii) the home range of individuals or social groups; iii) the habitats selected within the home range and iv) the feeding sites within habitats (Johnson, 1980, Aebischer *et al.*, 1993, Said and Servanty, 2005). Therefore, just considering habitat use within the home range may not be sufficient as some degree of selection may have occurred at the landscape scale when the animal chose where to place its home range (Kie *et al.*, 2002). This could have implications for models of habitat selection and distribution on which deer management plans may be based. Therefore the analyses of habitat associations in this study considered the second and third orders of Sika deer habitat selection.

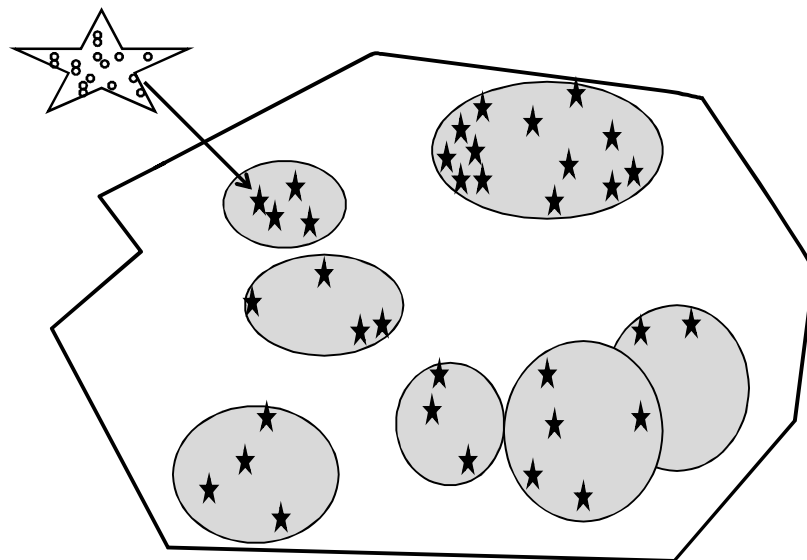


Figure 2.6: Levels of habitat selection: i) selection of geographical range is represented by the external polygon; ii) home range placement of individuals or social groups is represented by the circles; iii) habitats selected within the home range are represented by the stars; and i) feeding sites within habitats represented by the circles within the stars.

2.4.1 Habitat associations obtained from radio tracking data

Compositional analysis (Aebischer *et al.*, 1993) was used to compare the habitat used with the habitat available. Analyses were performed on both individual habitats and grouped habitats as described in section 2.5.1. Compositional analysis and statistics were computed with the Excel macro Compos 6.2 plus (Smith, 2005), which also, due to the potential non-normality of these data, carried out the randomization procedure suggested by Aebischer *et al.* (1993). The advantage of compositional analysis over other indices to measure habitat preference is that compositional analysis is independent of proportions (the negative selection for one habitat is not related to the positive selection of other habitat) and also offers a ranking of multiple habitats by preference. Analyses were also carried out using the Ivlev's selection index (Yeo and Peek, 1992, Doerr *et al.*, 2005) and the Jacob's selection index (Jacobs, 1974), to confirm the consistency of results. As the results did not differ they are not presented in the main thesis document, although are provided in Appendix 3.

The geographical range of all deer at each study site ('MCP 100%') was defined by an MCP using all locations from all animals (MCP 100%) in each study area. This was used to incorporate areas outside individual home ranges as recommended by McClean *et al.* (1998) and is more objective than a pre-defined study area. As well as the kernel home range calculated for each individual deer as described above ('home range'), circles of different radius centred on the kernel mean centre were used to represent i) '250 m radius': the area in which deer had greatest activity (20 ha), ii) '500 m radius': an area similar to the median home range size (79 ha), and iii) '750 m radius': an area larger than the Sika deer home range size in our study areas to incorporate areas outside the home range (177 ha).

The second order of habitat selection, range placement, was assessed by comparing the proportion of habitats in the actual home range, 250 and 500 m radius buffers with the proportion of habitats in the study area (MCP 100%) and 750 m radius buffer. Third order habitat selection, within range, was assessed by comparing the proportion of each habitat

within a 50 m radius of all locations to the habitat proportions within the 90% kernel home range.

2.4.2 Habitat associations obtained from ground counts data

Ground count data were obtained for Hartland and Studland as described in Section 2.2. Counts were averaged over two seasons and three years by dividing each count by the total number of ground counts ($N = 6$).

The method to obtain the habitat associations of Sika deer from ground counts data was based on that developed by Plante *et al.* (2004), although with a few modifications, which are highlighted below, to adapt it to the study area and deer species. As deer observations were point-based and habitat maps were 2 dimensional surfaces, the deer data needed to be converted to a 2 dimensional surface. This conversion was also required to convert the point-count data to the density of deer. A spatial interpolation based on the quartic kernel (see Diggle, 1985 for an example of this kernel function) was applied to the deer data (Plante *et al.*, 2004). In this method, the central point of a quartic kernel curve with a distance-decay function is placed on each of the deer observation and is weighted by the number of deer per observation. A smoothing factor (also referred to as the bandwidth or h statistic) controls how smoothed the kernel density estimate is. As one modification from the method developed by Plante *et al.* (2004), the smoothing factor was based on the average of the annual standard deviation (298 m) of the kernels distribution fitted to the locations of each of the 31 female Sika deer obtained by radio tracking (see Section 2.3.1). This value of the smoothing factor was used to reflect the species local behaviour in terms of movement abilities and the size of the area that deer were using during a season.

Although different values of the smoothing factor affect the specific value of the estimated local density at a given location, correlation analyses conducted during the development of this method showed that the scoring of local density across different locations within the study areas was not affected by the choice of the smoothing factor.

Using a smoothing factor linked to the area occupied by Sika deer over a season was preferred to the option of using a number without any biological meaning. As the direct observations on which the deer data were based were obtained over a period of time spread during a month, other choices of smoothing factor based on data obtained over a much shorter period of time (e.g. the average distance of daily travel or the average distance between successive radio tracking fixes) were not considered appropriate. The statistical standard deviation around mean range size was selected because this measure takes account of the full range of data collected instead of using a mean value that could be highly affected by extreme values.

In biological terms, use of the standard deviation as the smoothing factor implies in effect that there is a 68% likelihood that, during a given season, deer will use an area within a distance of a standard deviation from the actual location of any single observation. The probabilistic nature of the standard deviation also means that in using it as a smoothing factor there is a higher probability that deer will be found closer to the observed location and that the probability will gradually be lower as the distance to the observed location increases up to the value of the standard deviation.

One limitation is that the smoothing factor was based on radio tracking data obtained from female deer as no males were captured in the previous study. However, a certain element of subjectivity in choosing the appropriate value for the smoothing factor is inevitable (Nelson and Boots, 2008).

The value of the smoothing factor affects the spatial distribution of the density of deer, and therefore, potentially the outcome of further analyses; consequently two values were used based on the standard deviation of the kernel distribution fitted to the locations of Sika deer: the standard deviation (298 m, 'SD') and 1.96×298 m (584 m, '2SD', i.e. the distance within which 95% of deer observations occurred). The use of two smoothing factors to account for uncertainty in the smoothing factor was a second extension to the method developed by Plante *et al.* (2004). Habitat features were converted to raster format with a resolution of 10 x 10 m and so, for consistency, Sika deer density was calculated for each cell in the 10 x 10 m grid. The size of the grid was selected as it was considered the highest possible resolution considering the potential error in locating deer and mapping habitats using conventional GPS devices. The analysis was conducted using Hawth's

Analysis Tools for ArcGIS (Beyer, 2004). In order to derive habitat associations, deer density was aggregated to a larger grid size. This was done by calculating the mean density across all 10 x 10 m cells within the larger grid (see below for larger grid sizes used and Figure 2.7 for an example). This process was conducted for both values of the smoothing factor (i.e. SD and 2SD).

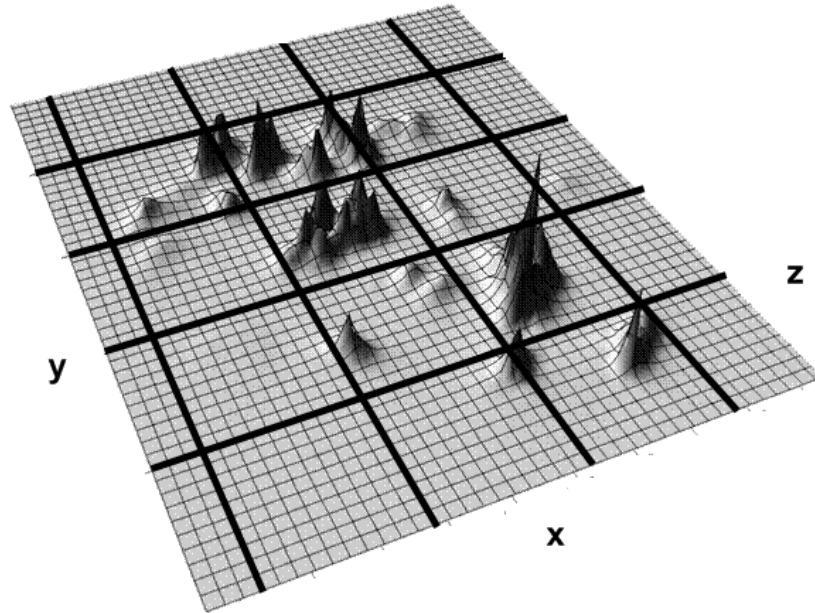


Figure 2.7: Example of a kernel density map. Small cells represent 10 x 10 m cells underlying a larger grid cell of 100 x 100 m. Each observation of deer is located on the x and y axis and is weighted by the number of deer observed and represented on axis z. Figure adapted from de Smith *et al.* (2009).

Analyses at the landscape scale are affected by the size and placement of the starting location of the larger grid (e.g. Jelinski and Wu, 1996, Fortin, 1999, Wu, 2004). As recommended by Plante *et al.* (2004), to overcome the grid size effect, two grid sizes were used: 500 x 500 m (25 ha) and 250 x 250 m (6.25 ha). These grid sizes were used to relate to analyses of habitat associations using radio tracking (see previous section) and to provide adequate sample sizes for analyses considering the limited size of the study areas. To overcome potential effects of the starting location of the larger grid as suggested by Plante *et al.* (2004), three grid starting locations were used for each grid size: Grid I - default starting location; Grid II - starting location 100 m south of Grid I starting location; Grid III - starting location 200 m south of Grid I starting location. To adapt the method to the characteristics of the study areas (smaller size and more irregular boundaries) both the grid sizes and the displacement between grid starting locations differed from those used in

the original method (third modification). Therefore, two values of the smoothing factor, two sizes and three position grids were used for all subsequent analyses at each study area.

The area of each habitat was calculated within each larger grid cell. It was assumed that habitats were positively selected for if their area within grid cells was positively related to the density of deer. No assumptions were made about the relative importance of the different habitats and so all were considered equally in the analyses.

To obtain a measure of habitat area, the habitat class area (HCA) was calculated for each habitat class within the 250 x 250 m and 500 x 500 m grid cells. HCA represents the total area of a grid cell occupied by a given habitat class. HCA was calculated using FRAGSTATS (McGarigal *et al.*, 2002) in the Grid Analyst extension for ArcGis (Ontario Ministry of Natural Resources, Canada). Twelve maps were obtained for each study area, representing each combination of smoothing factor, grid cell size and grid origin. 50 grid cells for the 250 x 250 m grid whose entire area fell within the study area were randomly selected in order to minimize effects of spatial autocorrelation among grid cells as advised by Plante *et al.* (2004). Due to the expected relatively small number of 500 x 500 m grid cells whose entire area fell within each study area, all grid cells of a given grid origin were used in the analysis. Each grid cell was overlaid on the habitat map, and the values of the habitat area measured within each cell. Finally, Spearman rank correlation analysis was conducted to determine the relationships between deer densities and habitat area. Analyses were performed on both individual habitats and grouped habitats.

2.5 METHODS TO OBTAIN ESTIMATES OF LANDSCAPE STRUCTURE AND AREAS OF HUMAN DISTURBANCE

To address the objectives of this research the habitats needed to be mapped and the areas of human disturbance identified.

2.5.1 Habitat mapping

A previous study conducted by Dr. A Diaz, Dr. S Walls and Miss D Whitmarsh mapped Arne using aerial photograph and visits to the area. The maps were digitised using MapInfo (MapInfo Corporation, USA). It was necessary to transform these maps to ArcGis 9.2 (ESRI Inc., USA) using MapInfo Version. 7.0. These maps were also supplemented by visits to the area and the use of aerial photography.

A Phase 1 vegetation survey from 2001 was available from NT. However, after analysing the data from the south part of Hartland managed by NT it was apparent that the information was not accurate enough to use in further analysis, therefore it was necessary to conduct habitat mapping based on aerial photograph, data from NT vegetation survey and direct observations. Two field visits were conducted to classify those patches of habitat that could not be identified using aerial photograph or previous vegetation surveys. The new Hartland map was digitised using ArcGis 9.2. Natural England does not have any digitalised habitat survey of Middlebere Heath (the northern part of Hartland). The only available data were from a habitat survey carried out by R. White in 1985 drawn by hand (© Natural England). It was necessary to digitalise this map and combine its information with aerial photography in order to obtain a digital habitat map of this area. Both maps were integrated in the same GIS database using ArcGis 9.2. The NT map for Studland was accurate enough to be used in further analysis and therefore was transformed from MapInfo format to ArcGIS .

Habitats were classified into 16 main categories: deciduous woodland (DW), deciduous scrubland (DS), mire (M), gorse (G), coniferous woodland (CW), coniferous scrubland

(CS), dry heath (DH), wet heath (WH), improved grassland (IG), acid grassland (AG), saltmarsh (S), reed-beds (R), weed community (WC), crop (C), sand dunes (SND) and anthropic, e.g. roads, buildings or farmyards (U).

As well as using individual habitats, groups of habitats were used, as advised by Aebischer *et al.* (1993), by pooling the habitat types in three “resource groups”. CS, CW, DS, DW, G and R were pooled in the same group ‘cover’ (CO) as they offer ‘standing’ shelter as main resource, although some browsing is also provided by these habitats (i.e ivy, *Hedera helix* is provided by deciduous woodland in the area). AG, C, IG, S, and WC were pooled in the same group ‘grazing’ (GR) as they do not offer shelter but do offer grazing resources. Finally, DH and WH were pooled in the same group ‘heath’ (H) as they offer both ‘lying’ shelter and grazing/browsing resources. Buildings or farmyards (U) were not included in any group as deer were excluded with fencing. Small quantities of buildings or farmyards occurred in the single habitat analyses due to buffers around locations that sometimes encompassed areas that deer could not access.

2.5.2 Landscape structure metrics

In order to characterise the landscape of the study areas and relate it to Sika deer distribution and abundance, landscape structure metrics were obtained using FRAGSTATS (McGarigal *et al.*, 2002) in the Patch Analyst extension for ArcGis (Ontario Ministry of Natural Resources, Canada). The landscape structure metrics used in this thesis are briefly described in Chapter 3. For an extensive list and description of the landscape structure metrics see Elkie *et al.* (1999) and McGarigal *et al.* (2002).

2.5.3 Mapping areas of human disturbance

Areas of disturbance were added to the habitat maps in the same way as vegetation habitats (Figure 2.8). Roads, buildings and walking tracks were considered as the main sources of disturbance that could be identified from a map at the three study areas. Walking tracks were drawn at Arne from information obtained from 85 forms filled by visitors on which

they marked on a map the route they followed (using existing tracks) through the area. At Hartland only two walking tracks were drawn based on observations of visitors.

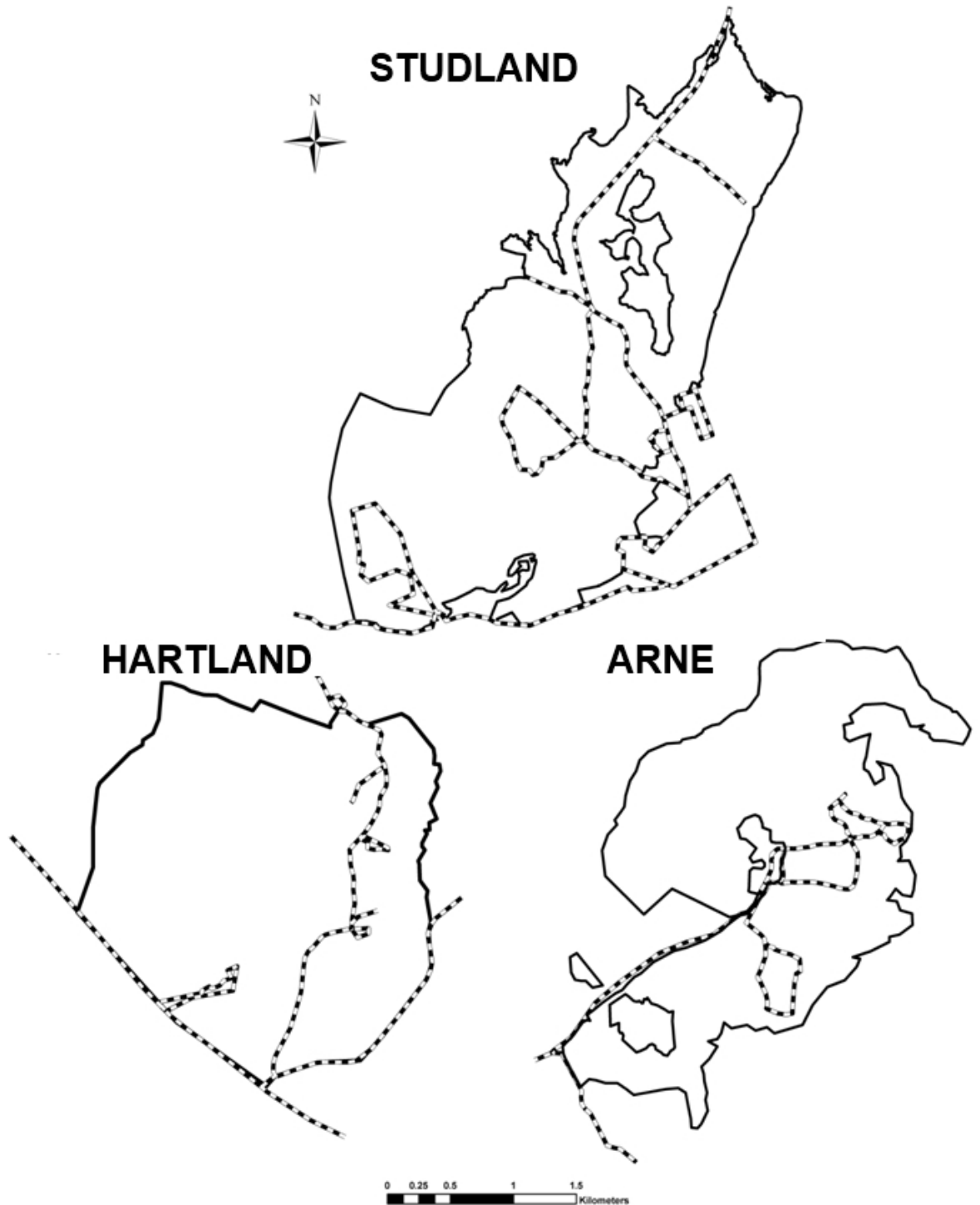


Figure 2.8: Areas of disturbance in the study areas. The dashed line indicates a road, track or the boundaries of built-up areas.

2.6 METHODS TO ANALYZE THE INFLUENCE OF COVER AND SOURCES OF DISTURBANCE UPON THE HABITAT USE AND DISTRIBUTION OF SIKA DEER

2.6.1 Influence of cover

It was hypothesised that when Sika deer were in open areas (heath, pasture) they would select areas close to cover, particularly during the day (when deer would be disturbed by visitors or vehicles). To test this hypothesis, the distances from deer locations to habitats offering cover (CS, CW, DS, DW, G and R) were measured and compared to distances from random locations in open areas to cover using non parametric Kruskal Wallis and Mann Whitney analyses. These statistical tests (and those conducted in following sections of this chapter) were performed using SPSS 15.0 statistical software (SPSS Inc. 2006).

2.6.2 Influence of sources of disturbance

Deer are known to be affected by human disturbance so it was hypothesized that deer locations would be further from disturbance than expected (random locations). However, unlike cover, disturbance varies during the day, for instance farmers are more active during daylight and visitors are excluded during the dark. Therefore, distances were measured (from deer and random locations) to disturbance areas (roads, farm buildings, farm yards, quarries) and then compared (Kruskal Wallis and Mann Whitney) at day and night.

2.6.3 Influence of landscape structure

To investigate the effect of landscape structure on Sika deer distribution, edge density (ED) was selected as a component of the landscape heterogeneity. Edge density, defined as the sum of length of all edge segments divided by total area (Elkie *et al.*, 1999, McGarigal *et al.*, 2002) was measured within all spatial scales (buffers of 250, 500, 750 m radius: home range and MCP 100%). Values of ED were obtained using FRAGSTATS (McGarigal *et al.*,

2002) in the Patch Analyst extension for ArcGis (Ontario Ministry of Natural Resources, Canada). It was hypothesized that Sika deer home ranges would show higher edge density than the available landscape due to the selection for areas close to cover.

Finally, it was tested whether the values for edge density index differed between the used landscape (home range, 250 and 500m radius buffers) and the available landscape (MCP 100% and 750 m radius buffer) using a Wilcoxon Signed Rank Test (W). To test if the content of habitats and groups of habitats selected by Sika deer could affect the relationship between edge density and the distribution of deer, a Spearman rank correlation was conducted between the edge density and the content of habitats within the different spatial scales.

2.7 METHODS TO ESTIMATE THE SPATIAL VARIATION IN THE LOCAL DENSITIES OF SIKA DEER IN AREAS OF LOWLAND HEATH

To address the second objective of this research and explore the potential impacts of Sika deer activity upon plant and animal communities of lowland heath, the density of Sika deer at a local scale (i.e. hundreds of square meters to few hectares) needed to be related to differences in plant and animal communities of lowland heath. The local scale was chosen because several studies have shown that habitat use by wild herbivores, and in particular deer, varies spatially and temporally (e.g. Georgii, 1981, Mann and Putman, 1989b, Yeo and Peek, 1992, Benhaiem *et al.*, 2008). Also, studies on upland heaths have shown that the decline of heather cover under heavy grazing by deer is often patchily distributed and the severity of damage depends on the location of other vegetation and food resources (Clarke *et al.*, 1995b, Hester and Baillie, 1998). Therefore a population density approach which simply considered deer density at a landscape scale might have not accounted for differences in the spatial variation of the local density of deer in the selected study areas and their subsequent effects on plant communities of heath. The need for a clear distinction between estimates of local density at the individual site level and densities calculated across a wider population range has been highlighted by Putman and Watson (2009). Measured at the level of an individual site, ‘local density’ may reflect local aggregation of animals (Putman and Watson, 2009) and may vary significantly between local areas and from season to season. This variation in local aggregations indicates changes in the level of utilization of local areas although the population density for the site may remain the same. Consequently, the term ‘local density’ is used in this chapter to differentiate the concept of deer occupancy at fine spatial scale from the concept of ‘density of deer’ generally used to refer to population density at a higher spatial scale.

2.7.1 Choice of method

Many approaches have been used to obtain indices of deer density at different scales. Different guides and reviews have aimed to provide information about the various methods available and compare the advantages and disadvantages of the different methods for given

situations (e.g. Mayle and Staines, 1998, Mayle *et al.*, 1999), but ultimately the choice of method depends on the objectives set, study area, its scale and research resources.

Due to the nature of this research a number of restrictions had to be applied when selecting a method to obtain the spatial variation in local density of deer: i) the method would have to be carried out by one person; ii) the method would have to be carried out seasonally; iii) the method would have to be suitable to be used in different study areas within the same period; iv) the method would have to be able to estimate the density of deer at a local scale to account for the variation in deer aggregation on different patches of habitat: v) the method would have to be carried out using limited resources.

An exhaustive literature review of the methods to obtain deer densities was carried out to select those that could be applied to obtain the spatial variation in local density of deer within the study areas. Methods for measuring the density of deer (mostly population density) have been broadly divided into direct and indirect methods (Marques *et al.*, 2001, Smart *et al.*, 2004). Direct methods involve counting animals while indirect methods relate the presence of deer signs (e.g. tracks, faeces) to deer numbers. Indirect indices are preferred in concealing habitats (Mayle and Staines, 1998, Mayle *et al.*, 1999, Putman and Watson, 2009) where it is difficult to reliably observe deer. In open areas both direct and indirect methods can be used, although it has been postulated that the most suitable methods (in terms of effectiveness) are those based on direct observations (Marques *et al.*, 2001). Three direct methods (spotlight transects, vantage points and driving/walking transects during daytime) and three indirect methods (standing crop dung method, clearance dung method and way tracks counts) that could potentially fulfil the requirements explained above were pre-selected for use in this study. A comparative list of advantages and disadvantages of the different six methods based on available scientific literature is presented in Table 2.3.

Table 2.3: Comparison based on literature review of advantages and disadvantages of six different methods to obtain an index of deer density (based on a review of Batcheler, 1975, Mitchell *et al.*, 1985, Fafarman and DeYoung, 1986, Whipple *et al.*, 1994, Fritzen *et al.*, 1995, Doney, 1996, Doney, 1998, Mayle and Staines, 1998, Mayle *et al.*, 1999, Ellwood, 2000, Mayle *et al.*, 2000, Barnes, 2001, Buckland *et al.*, 2001, Focardi *et al.*, 2001, Marques *et al.*, 2001, Walsh *et al.*, 2001, Focardi *et al.*, 2002, Koenen *et al.*, 2002, Kusters *et al.*, 2002, Laing *et al.*, 2003, Ruetten *et al.*, 2003, Campbell *et al.*, 2004, Focardi *et al.*, 2005, Thomas *et al.*, 2005, Daniels, 2006). Level of performance based on Mayle *et al.* (1999).

STANDING CROP DUNG METHOD (FSC)	<p>ADVANTAGES</p> <ul style="list-style-type: none"> ▪ If deposition and decay rate are accurate it allows obtaining total number (using distance sampling) and density estimate ▪ Timing could be adjusted to 1 visit per season ▪ Considered by <u>some authors</u> more precise than clearance counts (when decay rate is accurately measured) ▪ Sampling do not depend on weather conditions ▪ Good performance as an estimate and excellent as an index <p>DISADVANTAGES</p> <ul style="list-style-type: none"> ▪ Results depends on accuracy of deposition rate and decay rate ▪ Obtaining decay rate is extremely variable and difficult in patchy habitats ▪ Does not obtain group composition or deer behaviour ▪ High number of replicas needed ▪ High time-consuming ▪ Difficult to allocate plots if patches are small
CLEARANCE DUNG METHOD (FAR)	<p>ADVANTAGES</p> <ul style="list-style-type: none"> ▪ Allows obtaining total number (using distance sampling) and density estimate ▪ Most practical at high deer densities ▪ Timing could be adjusted to 1 visit per season ▪ Considered by <u>some authors</u> as more accurate and reliable than standing crop ▪ Sampling do not depend on weather conditions ▪ Excellent performance as an estimate and as an index <p>DISADVANTAGES</p> <ul style="list-style-type: none"> ▪ Results depend on timing of visits and number of samples obtained ▪ Does not obtain group composition or deer behaviour ▪ High number of replicas needed ▪ High time-consuming : 1.6-1.9 times longer to carry out than FSC ▪ Difficult to allocate plots if patches are small
WAY TRACKS COUNTS	<p>ADVANTAGES</p> <ul style="list-style-type: none"> ▪ Allows obtaining an index of deer presence and abundance ▪ Rapid method ▪ Particularly suitable for use where limited information on deer presence ▪ Fair performance as an index <p>DISADVANTAGES</p> <ul style="list-style-type: none"> ▪ Total deer numbers are not estimated ▪ Does not obtain group composition or deer behaviour ▪ Very poor performance as an estimate*

* After the publication of Mayle *et al.* (1999) this method has been improved by Mayle *et al.* (2000).

Table 2.3 (continuation)

SPOTLIGHT TRANSECTS	<p>ADVANTAGES</p> <ul style="list-style-type: none"> ▪ If distance sampling is used the confidence limits of the deer estimate may be determined ▪ Allows obtaining sex and age-class ratios depending on visibility ▪ Allows obtaining information about behaviour ▪ Fair performance as an index <p>DISADVANTAGES</p> <ul style="list-style-type: none"> ▪ Range and identification depend on visibility, vegetation structure and terrain ▪ Sex/age identification also depends on visibility conditions and equipment ▪ Cannot be undertaken in forested areas nor in portions of transects with forest immediately adjacent to the road if thermal imaging is not applied ▪ Biased if system or rides, roads or tracks is not suitable ▪ Human disturbance can bias results ▪ Biased due to differences in vegetation structure (therefore visibility) between habitats ▪ Difficult to measure the area covered ▪ Possible double counting ▪ Results are specific to count days and liable to influences of seasonal changes in climate and deer behaviour ▪ Poor performance as an estimate
VANTAGE POINTS	<p>ADVANTAGES</p> <ul style="list-style-type: none"> ▪ If distance sampling is used the confidence limits of the deer estimate may be determined ▪ Allows obtaining sex and age-class ratios ▪ Allows obtaining information about behaviour ▪ Same points could be used during the night but being highly limited in visibility ▪ Fair performance as an estimate ▪ Good performance as an index and fair as an estimate <p>DISADVANTAGES</p> <ul style="list-style-type: none"> ▪ Range and identification depend on visibility, vegetation structure and terrain ▪ Some areas cannot be surveyed due to terrain, including therefore a bias because some habitats are more difficult to be surveyed ▪ Human disturbance can bias results ▪ Biased due to differences in vegetation structure (therefore visibility) between habitats ▪ Results are specific to count days and liable to influences of seasonal changes in climate and deer behaviour
DRIVING /WALKING TRANSECTS (daytime)	<p>ADVANTAGES</p> <ul style="list-style-type: none"> ▪ If distance sampling is used the confidence limits of the deer estimate may be determined ▪ Allows obtaining sex and age-class ratios ▪ Allows obtaining information about behaviour <p>DISADVANTAGES</p> <ul style="list-style-type: none"> ▪ Range & identification depend on visibility, vegetation structure and terrain ▪ Cannot be undertaken in forested areas nor in portions of transects with forest immediately adjacent to the road ▪ Biased if system or rides, roads or tracks is not suitable ▪ Human disturbance can bias results ▪ Biased due to differences in vegetation structure (therefore visibility) between habitats ▪ Difficult to measure the area covered ▪ Possible double counting ▪ Results are specific to count days and liable to influences of seasonal changes in climate and deer behaviour ▪ Possible lack of data due to nocturnal behaviour in deer

The six methods selected were also subjected to preliminary trials at Arne and Hartland. Trials were conducted during spring and summer 2007 at day and night time and involved conducting the different methods across different areas at each study area to evaluate their suitability to be used simultaneously at both study areas and during each season. The three direct methods proved to have important limitations due to the terrain conditions, visibility, time restrictions and differences in deer behaviour during day and night that resulted in under or overestimations of deer use on patches of heath. Use of the DISTANCE method (Buckland *et al.*, 2001) was considered in combination with the direct methods (as it has been proved to improve the performance of traditional methods to obtain deer densities) but it was considered unsuitable because of the difficulty of being used at a fine scale. Based on these trials a direct observation method that involved a modification of the established vantage points method was finally adapted and developed.

The method consisted of a survey method, based on a route of vantage points, coupled to a spatial modelling technique to interpolate the spatial variation in the local densities of Sika deer. The method estimated the local density of Sika deer around the 90 sites at Hartland and Arne selected to analyse the ecological effects of Sika deer on plant and animal communities of lowland heath (see Section 2.8 and Chapter 5).

The direct observation technique uses vantage points from which to survey deer, and so it is similar to the established point transects method (e.g. Mack and Quang, 1998, Mayle and Staines, 1998, Koenen *et al.*, 2002, Koenen and Krausman, 2002). However, although in this technique animals are recorded from a number of fixed stations as in the established point transect (see e.g. Buckland *et al.*, 2001, Buckland *et al.*, 2006), the detection distance is not measured, and therefore the statistical analysis differs. Direct observations obtained at different times of the day from vantage points were carried out by a single researcher from November 2007 to September 2008 and classified into four seasons: winter (November-December 2007), spring (March-April), summer (June-July) and autumn (September-October 2008). A powerful spot-light was used to assist night time observations. Routes were designed to be completed in less than 1.5 hours at each study area (Arne and Hartland) in order to reduce double counts and to minimize changes in environmental conditions (e.g. sunrise or sunset) that may affect Sika deer behaviour. Deer were observed and located independently of differences in vegetation and terrain between

dry and wet heath in the study areas. The observer minimized disturbance to the deer while making observations.

Similarly to the method describe in Section 2.4.2, the deer observations obtained were point-based and habitat maps were 2 dimensional surfaces. Therefore the deer data needed to be converted to a 2 dimensional surface in order to interpolate the local deer densities into the gaps between deer locations. The spatial modelling was based on a kernel smoothing with a decay-rate function related to the movement abilities of Sika deer. Previous methods have used similar modelling technique to spatially interpolate densities of terrestrial mammals (e.g. Potvin *et al.*, 2005) or detect hot spots in landscape ecology (Nelson and Boots, 2008). In this case the value of the smoothing factor reflects the movement abilities and the size of the area that Sika deer were using during daily activities. As in the method described in Section 2.4.2 the chosen value was the average of the standard deviation of the kernel distribution of the home ranges of 31 female Sika deer obtained by telemetry (as described in Section 2.3.1). The reasoning behind the choice of the standard deviation of the kernel distribution has been previously explained in Section 2.4.2. The modelling technique, performed using open source software, estimated the level of local density of deer around the specific locations used to investigate the ecological impacts of Sika deer on plant and animal communities of lowland heath that are discussed in Chapter 5.

Appendix 1 contains a more complete description of the direct method used to estimate the spatial variation in the local density of Sika deer in open habitats.

The three indirect methods were also subjected to preliminary trials. Trials involved conducting each of the methods described above at random locations on patches of lowland heath to evaluate their suitability. Trials were conducted during Spring and Summer 2007 at both study areas. The standing crop dung method proved to be unsuitable due to terrain and vegetation differences that could affect decay rates. Calibrating the decay rate for the terrain and vegetation differences across patches of heath (which would also change seasonally) would have been too time consuming for a project of this scale. Also the trials suggested that differences between dry and wet heath and seasons would result in differences in the performance of indirect methods. A positive outcome of the trials was that whilst the clearance dung method would have been highly time consuming,

a variation of this method, based on a total pellet count, was considered as a rapid method to obtain an index of the local density of deer in areas of lowland heath. Also a variation of the way the track count method (Mayle *et al.*, 2000) described below was chosen. This method resulted to be a rapid method that could be simultaneously used in combination with other indirect methods. As a final result of the trials, another two indirect methods (percentage of area trampled and distance to first sign of Sika deer presence) were also added as they could be potentially linked to Sika deer activity/usage. A detailed description of the indirect indices and an investigation into the effects of habitat and temporal variability upon comparisons between direct and indirect methods of measuring deer abundance in open habitats are discussed in Appendix 2.

The results obtained after conducting the direct method and the analyses into the effects of habitat and temporal variability upon the indirect methods were carefully considered. It was decided that the best method to relate the spatial variation in local densities of deer to differences in the communities of plant and animal communities of lowland heath that could fulfil the requirements of this research was the direct method developed in this thesis.

2.8 METHODS TO MEASURE SIKA DEER IMPACTS ON PLANT AND ANIMAL COMMUNITIES OF LOWLAND HEATH

2.8.1 Data collection

Sampling of plant and animal communities on lowland heath

Lowland heath is considered as a main habitat type, however it is usually divided into two habitat types (dry and wet heath) because of the difference in soil drainage and floristic composition (Gimingham, 1992). A preliminary analysis of the species presence and abundance data using the multivariate test ANOSIM (Analysis of Similarities, Clarke & Green 1988) carried out using PRIMER 6.1.6 (PRIMER-E Ltd. 2006) confirmed expected significant differences between the plant communities of dry and wet heath.

A total of 90 sampling points ('sites') were placed at random locations on lowland heath in the two study areas, 60 in Arne and 30 in Hartland, following two restrictions: i) a minimum distance between sites of 25 m; ii) the random sites were divided equally between dry and wet heath as they are the main two habitats on lowland heath in the study areas. The difference in sample size between the two areas reflects the availability of wet heath in each area. A site was classified as located on dry heath when the 5 metres radius area around the centre of the site contained a composition of heath species dominated by *Calluna vulgaris* and/or *Erica cinerea* with a combined percentage higher than 50% of the total vegetation cover. Sites were classified as located on wet heath when they contained *Erica ciliaris* and/or *Erica tetralix* associated or not with *Molinia caerulea* with a combined percentage higher than 50% of the total vegetation cover. During the data collection period, two sites located on wet heath at Arne were accidentally removed due to land management conducted at these sites.

The random locations for the sites within the two study areas were obtained using Hawth's Analysis Tools V.3.26 (Beyer, 2004) integrated in ArcGis 9.2 (ESRI Inc., California USA) which generates random points over a limited surface (in this case the extent of lowland heath on each of the study areas) with a minimum distance between locations.

Surveys of both the communities of plant and surface-active invertebrates were conducted at each site. The vegetation survey was conducted on four plots of 2m x 2m placed at random around each signed post marking the site. The first plot was placed 3.5 metres from the centre of the site, using a random compass bearing; consecutive plots were placed in 45° angle. Plant community surveys were carried out from February to November 2008 and classified into four seasons: winter (February), spring (May), summer (August) and autumn (November 2008).

To determine the species composition of the plant community and the percentage of cover of each species, a vegetation survey was carried out within each plot. Vascular plants were identified to species level. Species of bryophytes were grouped as members of a group of non-vascular plants with similar vegetation structure, while lichens were also grouped as a distinctive group. Above ground vegetation volume ('volume') was assessed visually by recording the percentage of occupancy of slices at 10 cm height intervals. This was converted into total volume by calculating the volume per slice and summing all slices. To assess the possible physical impact of trampling by deer, the percentage of area disturbed by trampling ('area trampled') was recorded. The physical impact of trampling, such as stem breakage or vegetation compaction, was ascribed to trampling by Sika deer only when other signs of Sika deer presence such as tracks or pellets were also found in the proximity of the plot. When it was not possible to confirm the source of the physical damage no data were recorded, resulting in a blank observation, although this was a small percent of field plots (less than 5%). As physical damage of the vegetation by deer can result in an increase of dead vegetation and bare ground, the percentage of dead vegetation ('dead vegetation') and the percentage of bare ground ('bare ground') within the plot was also recorded. Volume, area trampled, dead vegetation and bare ground are grouped and named as 'vegetation structural parameters' in this chapter.

The animal survey was based on the use of pitfall traps to collect surface-active invertebrates. Pitfall trapping, a standard invertebrate sampling method (Southwood and Henderson, 2000), was used because it is an inexpensive technique, labour-efficient, capable of collecting a wide range of arthropods and generating large species-rich samples suitable for statistical analyses (Spence and Niemela, 1994, Weeks and McIntyre, 1997). Pitfall trapping has received criticisms related to the success in determining relative

abundance of species (e.g. Topping and Sunderland, 1992). Thus for example Putman *et al* (1989) note that captures are likely to be biased towards the most active ground invertebrates (e.g. beetles and spiders). However, it has been recognised that this method is adequate to survey invertebrates living close to the ground surface (see e.g. Duelli *et al.*, 1999, Dennis *et al.*, 2004), and is able to provide a realistic estimate of the number of species in the community (e.g. Uetz and Unzicker, 1975, Curtis, 1980). Pitfall trapping was considered as a suitable survey technique because it enables continuous sampling thus obtaining of specimens from a wide array of orders, super families and species with different density and activity patterns. At each site, two invertebrate pitfalls were installed. The first pitfall was located using a random compass bearing and at a random distance from the signed fencing post. The second pitfall was located 5 m away 180° from the first trap and crossing the central point of the site. The traps were plastic cups 75 mm. deep with a diameter of 60 mm. They were inserted in the ground so that the rims were buried flush with the soil surface. Each contained 200-250 ml. of preservative (propylene glycol and water in 1:3 mixture). A drop of liquid soap was added to the glycol to break surface tension so that all animals captured would sink. Arne and Hartland are both wildlife conservation areas and contain important reptile and amphibian species (see above). As pitfall traps often result in high levels of mortality for small mammals and amphibians (Pearce *et al.*, 2005), traps were securely screened with a 1cm² mesh to prevent access by those animals. Traps were set for 100 continuous days from May to September 2008 and were visited every 20 days to collect the invertebrates and refill the traps with preservative. This obtained 5 rounds of samples across the different sites and study areas. Only 70 out of the 90 sites set up were used for the analysis as the other pitfall traps were removed from their locations. Field observations suggest that Sika deer, rabbits and foxes were responsible for such removals. This was especially the case in Arne, where 18 pitfall traps were removed.

Analysis of any possible relationship between the communities of surface-active invertebrates and the level of local density of Sika deer was conducted at three taxonomic levels. The three taxonomic levels considered were i) order level; ii) families within the order Coleoptera (beetles) and iii) detailed classification of the family Carabidae into species. Beetles were selected as they are a group in which its members have been associated with differences in heathland characteristics (e.g. Hopkins and Webb, 1984, Webb and Hopkins, 1984, Gardner, 1991). Species richness and abundance of Carabids

have been also previously linked to grazing pressure (e.g. Garcia *et al.*, 2009). Only non-larvae individuals of the family Carabidae were identified to species level.

2.8.2 Data Analysis

Relationship between vegetation and levels of local density of Sika deer

To relate plant communities of lowland heath to the level of local density of Sika deer, three predictive models were applied: i) a model to relate vegetation structural parameters (i.e. volume, area trampled, bare ground and dead vegetation) to differences in local density of deer; ii) a model to relate the abundances of key plant species on lowland heath to levels of local density of deer; iii) a model to relate the plant species diversity of lowland heath to levels of local density of deer. Finally, it was investigated if differences in the plant community composition of lowland heath were related to the local density of Sika deer.

To relate vegetation structural parameters to differences in the local density of Sika deer, a linear regression model was fitted with each vegetation index as the dependent variable and the level of local density of Sika deer as explanatory variable. Seasonal data were averaged to obtain annual values for vegetation indices and levels of local density of Sika deer. Local density of Sika deer was square-root transformed in order to obtain a more constant variation over the range of values by down-weighting extreme values and also to achieve or approach normality of residuals. This was checked using the graphical structure of residuals for each model. Where preliminary scatter-plot representations of the data suggested the existence of a threshold below which an evident linear relationship between the level of local density of deer and the vegetation index could not be clearly identified, a piecewise linear regression model (Bookstein, 1975) was also fitted following the rules

$$\text{if } x \leq x_{tr} \text{ then } y = y_0 \text{ and if } x > x_{tr} \text{ then } y = y_0 + b(x - x_{tr})$$

where x is the square-rooted value for the local density of Sika deer, x_{tr} is the threshold point, y is the value of vegetation index, y_0 is the level of vegetation index at which the

level of local density of Sika deer has no effects (intercept) and b is the slope of the linear curve.

To relate the abundances of the three most abundant plant species on lowland heath in the study areas (*C. vulgaris*, *E. tetralix* and *M. caerulea*) to the local density of deer, a linear regression model was applied. The abundance of each species was used as the dependent variable and the square-root transformed value of local density of Sika deer was used as the predictor. To investigate whether there was a threshold of the level of local density of deer in the effects of deer on the abundance of individual plant species, a piecewise linear regression model was applied under the circumstances previously described. The diversity of plant communities was estimated using the Shannon diversity index (H) for the plant community on each site and used as dependent variable within the two types of regression models described above. SPSS 15.0 statistical software (SPSS Inc. 2006) was used to conduct the regression models.

Plant community composition on lowland heath was related to the local density of Sika deer in areas of lowland heath by analysing the relationship between the community ordination of the sites and the local density of Sika deer.

Ordination techniques use abundance or presence-absence data of species in order to reveal ecological gradients and relationships between species and their environment (Palmer, 1993, De'ath, 1999). Principal components analysis (PCA), correspondence analysis (CA), including variations such as canonical forms and detrended analysis, and metric and non metric multidimensional scaling (MDS) are the most often used ordination techniques (De'ath, 1999). Ordination techniques can be divided depending on the objective of the ordination and the available data (Ter Brakk and Prentice, 1988):

i) *Gradient analysis* aims to find an ecological gradient(s) in the abundance of species and locate sites according to this gradient (Ter Brakk and Prentice, 1988). Depending on the data used to determine the gradient, techniques can be divided into two groups:

- a) Indirect gradient analysis: when only species data are used. This type of analysis is mainly seen as explorative and hypothesis-generating procedure (Ter Brakk and Prentice, 1988). Principal components analysis (PCA), correspondence analysis (CA) and its detrended version (DCA) are examples of this type of analysis.

b) Direct gradient analysis: species and environmental data are both used to determine the gradient and locate the sites. The most important difference is that systematic species variation is limited to that explained by the environmental data, therefore this analysis can test specific hypothesis related to the link between environmental variables and species abundance (De'ath, 1999). Canonical correspondence analysis (CCA: ter Braak, 1986) and its detrended version (DCCA) are most common examples of this type of analysis.

ii) *Species composition representation*: aims to map sites based on some similarity (or dissimilarity) between species. The location of the sites attempts to reflect the species composition and therefore the distance between sites is proportional to differences in species composition. The main difference with the other techniques is that the axes are not interpretable as a gradient. Multidimensional scaling (MDS) is an example of this type of analysis.

A detrended correspondent analysis (DCA, Hill and Gauch 1980) was firstly conducted to obtain an ordination of sites based on their plant community composition. DCA is an ordination technique that obtains a matrix of site-by-species abundance resulting in a representation of the relative similarity/dissimilarity between each vegetation community at each site and the rest of sites. DCA has the advantage over other ordination techniques such as principal component analysis (PCA) or correspondent analysis (CA) as it removes the “arch effect” frequently produced by these techniques caused because the similarity between sites are determined by the lack of individuals of most species, rather than the presence of members of the same species (Wartenberg *et al.*, 1987). The output of DCA was an ordination map in two dimensions of the sites by the composition of their plant communities and the eigenvalues (percentage of variation explained) for each of the axis. Once the ordination of sites was obtained, site scores for the two first axis obtained by DCA (which indicate similarity of species composition among sites) were compared to the Sika deer scoring using a Spearman rank correlation to relate differences in the vegetation community composition among sites on lowland heath to the associated level of local density of Sika deer. If there was a relationship between the composition of plant communities and the level of local density of Sika deer, those sites with plant communities that are considered closer (in terms of the composition of their plant community) would be found at a similar local density of deer. The VEGAN package for R (Oksanen *et al.*, 2007)

was used to conduct multivariate community analysis and SPSS 15.0 statistical software (SPSS Inc. 2006) was used to conduct correlation analyses.

Relationship between surface-active invertebrates and levels of local density of Sika deer

To relate differences in the diversity and composition of communities of surface-active invertebrates of lowland heath to levels of local density of Sika deer in areas of lowland heath two analyses were applied: i) a model to relate the diversity of surface-active invertebrates to the level of local density of deer was obtained; ii) it was investigated if differences in the composition of the communities of surface-active invertebrates were related to levels of local density of deer. Seasonal data were averaged to obtain annual values for invertebrates measurements.

The Shannon diversity index (H) at each site was calculated to obtain the diversity of surface-active invertebrates at the three levels previously defined (order, family and species). Then, the diversity of invertebrates was related to the level of local density of deer by using the Shannon diversity index as the dependent variable within the two types of regression models described above.

The ordination of the sites by the composition of their communities of surface-active invertebrates was related to the level of local density of Sika deer as described above for the plant community. The order Diplura was removed from the ordination analysis of communities of surface-active invertebrates on dry heath as it was only found in one of the samples. Also those families and species of beetles only found in one sample were removed from the ordination analysis.

Relationship between surface-active invertebrates and vegetation: indirect effects of Sika deer activity

To relate the diversity and composition of surface-active invertebrates to Sika deer activity through its effects on vegetation structural parameters and diversity of plant species, two predictive models were applied: i) a model to relate two vegetation indices related to heath

fragmentation (i.e. vegetation volume and bare ground) as predictors to differences in the diversity of surface-active invertebrates; ii) a model to relate the plant species diversity of lowland heath (predictor) to diversity of surface-active invertebrates. Finally, it was investigated if differences in the community composition of surface-active invertebrates were related to differences in the plant community composition using a Spearman rank correlation analysis.

CHAPTER 3: EFFECTS OF HABITAT AVAILABILITY, LANDSCAPE STRUCTURE AND DISTURBANCE ON SIKA DEER DISTRIBUTION AND HOME RANGE USE

ABSTRACT

In a humanized biosphere, habitat availability, landscape structure and human disturbance (as a form of predation risk) are likely to interact and produce combined responses in the distribution and habitat use of wildlife. This research explicitly considered the combined effects of habitat availability, landscape structure and disturbance on the distribution and habitat use of Sika deer (*Cervus nippon*). Female Sika deer were radio-tracked to obtain individual locations and the habitat associations. The content and landscape structure of the home ranges was related to the availability of habitats and landscape structure of the surrounding landscape while individual locations were related to availability of cover, sources of disturbance and available habitats within the home ranges. Results showed that Sika deer appeared to select habitats to optimise food requirements with avoidance of human disturbance and with contrasting habitat associations between the study areas. The availability of cover played a crucial role in the placement of Sika deer home ranges in both study areas and also in the distribution within the home ranges. The apparent differences in habitat associations by Sika deer between the two study areas and seasons can potentially be explained by a balance between high quality food resources and cover, the landscape structure in terms of the spatial arrangement of cover, food and risk and differences in sources of disturbance. The integration of these factors in the distribution and habitat use of deer populations within management strategies is discussed in this chapter.

INTRODUCTION

Predicting the distribution of species is important, if not essential, for conservation and wildlife management (Buckland and Elston, 1993, Rushton *et al.*, 2004). Both the availability of habitats and the landscape structure, defined by the distribution and configuration of habitat patches (Dunning *et al.*, 1992), have been linked to the distribution and abundance of species (e.g. Andren, 1994, Fahrig, 2003). Also, animal distributions may be affected by human presence if they are perceived as a predation risk (see Frid and Dill, 2002 for a review of disturbance effects on the behavior of individuals). In a humanized biosphere (e.g. Vitousek *et al.*, 1997), these three factors (habitat availability, landscape structure and disturbance) are likely to interact and produce combined responses in the distribution and habitat use of wild mammals such as deer.

Landscape structure has been linked to the size and spatial distribution of home range deer species such as Roe deer and Mule deer (*Odocoileus hemionus*) (Kie *et al.*, 2002, Said and Servanty, 2005, Lamberti *et al.*, 2006, Aurélie *et al.*, 2008). In particular edge density, as a component of landscape heterogeneity, has been linked to deer home range size (Kie *et al.*, 2002, Said and Servanty, 2005) and its importance has been linked to a good interspersion of cover and forage (Said and Servanty, 2005). Extensive work has also shown that the availability of food and/or cover affects deer distribution and habitat use (e.g. Kearney and Gilbert, 1976, Suring and Vohs, 1979, Virgós and Tellería, 1998, Mysterud *et al.*, 1999a, Godvik *et al.*, 2009). Several effects of human disturbance on deer behavior have been described, such as flushing or alert responses (Miller *et al.*, 2001, Li *et al.*, 2007, Stankowich, 2008), feeding site selection (Benhaiem *et al.*, 2008) or changes in rutting behaviour (Clair and Forrest, 2009). However, much less effort has been directed towards understanding how human disturbance might affect how deer select their home range placement and also their habitat selection within ranges.

Sika deer are native to East Asia and have been introduced worldwide (for a complete review of distribution see McCullough *et al.*, 2009). Large populations of Sika deer occur in parts of the south of England (Swanson and Putman, 2009). Field observations (see Section 2.7) indicate that Sika deer make an extensive use of lowland heaths. Lowland heath is a priority for nature conservation due to its status as a rare and threatened habitat, of which UK has about 20% of the international total (UK Steering Group 1995, p248).

There is a need to quantify the extent to which Sika deer might affect plant and animal communities in mosaics of lowland heath, woodland and grassland. Within this context it is required to firstly analyse the habitat associations of Sika deer in lowland heath to better understand how Sika deer select the placement of their home ranges and their distribution within their ranges. The most extensive investigation into the habitat use of Sika deer in UK was carried out by Mann and Putman (Mann, 1982, Mann and Putman, 1989b). However, these studies depended on directly observing deer which is affected by landscape, vegetation and daylight. A solution to this is radio tracking, which allows individual deer to be found at all times of day/night, even if in thick vegetation. Previous studies have investigated Sika deer habitat preferences (e.g. Mann and Putman, 1989b, Borkowski and Furubayashi, 1998a, Borkowski, 2000, Sakuragi *et al.*, 2002, Sakuragi *et al.*, 2003b, Ito and Takatsuki, 2009), the relationship between landscape structure and Sika deer ecology (e.g. Miyashita *et al.*, 2007, Miyashita *et al.*, 2008), and to a limited extent the effects of disturbance on Sika deer behaviour (e.g. fleeing behaviour, Borkowski, 2001) and on diurnal/nocturnal pattern of activity (Mann and Putman, 1989b). However, the present study is the first with the aim of explicitly considering the combined effects of habitat availability, landscape structure and disturbance on the distribution and habitat use of Sika deer. Radio-tagged deer at two study areas (Arne and Hartland) were tracked to (1) investigate the habitat associations of Sika deer; (2) relate the availability of cover and sources of disturbance to their habitat selection and distribution; (3) relate the landscape structure of the available landscape to their distribution.

RESULTS

The available study area (100% MCP of all deer locations) was 696.75 ha at Arne and 539.38 ha at Hartland. The median of the fixed kernel 90% annual home ranges was 89.98 ha, (range 35.51 -159.85 ha). There were no significant differences in the size of annual home range size between study areas (Mann-Whitney U test: $U = 61$, $P = 0.05$). However, significant differences in the size of home ranges between seasons and between areas were found (Table 3.1). Home ranges were significantly bigger at Hartland than at Arne during spring and winter and smaller in summer and autumn. The size of the seasonal home ranges also varied between the seasons at Arne (KW = 13.78, $P < 0.01$) and Hartland (KW = 23.31, $P < 0.001$).

Table 3.1: Comparison of annual and seasonal home range size between Arne and Hartland. Values indicate the median and the range (min-max): Asterisks indicate level of significance * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$ after a Mann Whitney U test.

	Annual (ha)	Spring (ha)	Summer (ha)	Autumn (ha)	Winter (ha)
Arne	87.37 (35.51-159.85)	63.62 (21.07-119.92)	66.64 (42.05-139.92)	74.83 (21.35-137.27)	75.65 (35.69-128.59)
Hartland	107.76 (58.52-137.49)	62.59 (31.38-122.56)	27.30 (12.77-81.57)	37.38 (10.36-68.49)	98.97 (69.45-211.99)
Difference. between study areas	$U = 61$	$U = 99$	$U = 25^{***}$	$U = 13^{***}$	$U = 54^*$

Habitat associations: placement of home ranges

Annual ranges

Table 3.2 shows habitat selection at Arne and Hartland by comparing the habitat within the used landscape (home range, 500m radius and 250m radius buffer) to the habitat available in the surrounding landscape (750m radius buffer and study area –MCP 100%). Deciduous woodland in both study areas and across all spatial scales was within the top two habitats selected by Sika. However, whilst deciduous woodland was the most selected habitat at Arne, at Hartland improved grassland was significantly selected over deciduous woodland across four out of six possible scales. At Arne, gorse was the next most important individual habitat within the group of cover habitats after deciduous woodland, while at

Hartland there is more variation and depending on the spatial scale, reed-beds or deciduous scrubland follow deciduous woodland in the ordination of selection of habitats.

Table 3.2: Habitat selection of range placement by Sika deer as determined by compositional analysis. On each line habitat classes to the left of the symbol > are selected over those to the right. >>> indicates significant (at 95%) difference between two consecutive habitat classes. Differences from random use are indicated by λ and randomized *P* values (1000 interactions). AG, acid grassland; CS coniferous scrubland; CW, coniferous woodland; DH, dry heath; DS, deciduous scrubland; DW, deciduous woodland, G, gorse; IG, improved grassland; R, reed-beds; S, saltmarsh; U, urban-anthropoc; WC, weed community; WH, wet heath.

Study Area	Available landscape	Used landscape	Wilk's λ	<i>Pr</i>	Ranked habitat types
Arne	Study area (MCP100)	Home Range	0.02	<0.01	DW>DH>G>CS>WH>IG>S>U>DS>WC>CW>R
		500 m radius	<0.01	<0.01	DW>G>DH>WH>CS>IG>S>U>CW>DS>WC>>>R
		250 m radius	0.03	<0.01	DW>G>DH>DS>WC>WH>U>CS>IG>R>CW>S
	Buffer 750 m	Home Range	0.06	<0.01	DW>G>DH>CS>WH=IG>S>AG=DS=R>U>CW
		500 m radius	0.09	<0.01	DW>G>DH>WH>IG>S>CS>CW>AG>U>DS>>>R
		250 m radius	<0.01	0.02	G>DW>DH>AG=DS>WH>IG>U>R=CW>CS>S
Home range	Locations	0.07	0.02	IG>DH>DS>S=WH=G>>>DW>CS>CW>AG	
Hartland	Study area (MCP100)	Home Range	<0.01	0.38	IG>DW>DS>R>G>DH>WH
		500 m radius	<0.01	<0.01	IG>DW>>>G>DS>R>>>WH>DH
		250 m radius	<0.01	0.02	IG>DW>DS>R>G>WH>DH
	Buffer 750 m	Home Range	<0.01	<0.01	IG>DW>R>G>DS>>>DH>WH
		500 m radius	<0.01	0.62	DW>R>IG>>>G=DS=WH>DH
		250 m radius	<0.01	0.05	IG>DW>DS>R>DH>G>WH
Home range	Locations	0.03	<0.01	R>DS>G>DW>IG>DH	

When habitats were pooled into the three resource groups (CO, GR and H) cover was significantly selected over the other two groups in four out of six spatial scales at Arne ($P < 0.05$), whilst at Hartland grazing was significantly selected over cover across all spatial scales ($P < 0.05$, Table 3.3).

Table 3.3: Comparison between Arne and Hartland of habitat selection of grouped habitats by Sika deer as determined by compositional analysis. On each line habitat classes to the left of the symbol > are selected over those to the right. >>> indicates significant (at 95%) difference between two consecutive habitat classes. Differences from random use are indicated by λ and randomized P values (1000 interactions). Cover (CO) was obtained by pooling CS, CW, DS, DW, G and R; Grazing (GR) was obtained by pooling AG, C, IG, S, and WC; Heath (H) was obtained by pooling DH and WH.

Available habitat scale		Arne			Hartland		
		Wilk's λ	Pr	Ranking	Wilk's λ	Pr	Ranking
Study area (MCP100)	Home Range	0.62	0.01	H>CO>>>GR	0.33	0.01	GR>>>CO>>>H
	500 m radius	0.42	<0.01	H>CO>>>GR	0.37	0.03	GR>>>CO>>>H
	250 m radius	0.40	<0.01	CO>H>GR	0.11	<0.01	GR>>>CO>>>H
Buffer 750 m	Home Range	0.61	<0.01	CO>H>>>GR	0.55	0.13	GR>CO>H
	500 m radius	0.31	<0.01	CO>H>GR	0.46	0.03	GR>>>CO>>>H
	250 m radius	0.48	<0.01	CO>H>GR	0.18	0.02	GR>CO>>>H
Home range	Locations	0.69	0.03	H>GR>>>CO	0.14	<0.01	CO>>>GR>H

Seasonal ranges

For single habitats at Arne, deciduous woodland, dry heath and gorse were selected over other habitats across all spatial scales and seasons (Table 3.4). However, at Hartland there were differences between winter and the rest of the year. Although results at two spatial scales were not significant ($P = 0.11$ and $P = 0.08$), the analyses indicate a tendency of selection for gorse or reed-beds at Hartland over the rest of single habitats across all spatial scales during winter. Deciduous woodland and improved grassland were selected over remaining single habitats at Hartland during the rest of the year ($P \leq 0.05$ in 12 combinations season-scale and $P > 0.05$ in the remaining six combinations season-scale).

At Arne, cover and heath were selected over grazing across all seasons and scales when placing the range ($P < 0.05$ in spring, autumn and winter; $P < 0.01$ in summer). At Hartland, cover was selected over grazing and heath in winter ($P < 0.05$) while during the rest of the year grazing was selected over cover ($P < 0.05$).

Table 3.4: Seasonal habitat selection by Sika deer at Arne and Hartland as determined by compositional analysis. On each line habitat classes to the left of the symbol > are selected over those to the right. >>> indicates significant (at 95%) difference between two consecutive habitat classes. Differences from random use are indicated by λ and randomized *P* values (1000 interactions). AG, acid grassland; CS coniferous scrubland; CW, coniferous woodland; DH, dry heath; DS, deciduous scrubland; DW, deciduous woodland, G, gorse; IG, improved grassland; R, reed-beds; S, saltmarsh; U, urban-anthropogenic; WC, weed community; WH, wet heath.

a) Spring (May)

	Available landscape	Used landscape	Wilk's λ	<i>Pr</i>	Ranked habitat types
Arne	Study area (MCP100)	Home Range	0.04	<0.01	DW>>>G>DH>WH>CS>>>IG>AG>S>DS>U>CW>R
		500 m radius	<0.01	<0.01	G>DW>DH>AG>WH>CS>U>IG>S>CW>DS>WC>R
		250 m radius	0.08	<0.01	G>DW>DH>WH>DS>WC>U>R>CS>IG>S>CW
	Buffer 750 m	Home Range	0.10	0.01	DW>>>G>DH>WH>CS>IG>S=R>DS>AG>U>CW
		500 m radius	0.07	0.03	G>DH>DW>WH>IG>AG=CW>S>CS=R>DS=U
		250 m radius	0.07	0.08	G>DW>DH>DS>WH>AG>>>U=IG>R>CS=CW>S
Hartland	Study area (MCP100)	Home Range	<0.01	<0.01	IG>DW>>>DS>U>R>G>WH>DH
		500 m radius	<0.01	0.06	DW>IG>>>U>DS>>>G>>>R>DH
		250 m radius	<0.01	<0.01	IG>DW>>>U>DS>>>G>>>D
	Buffer 750 m	Home Range	0.05	0.05	IG>DW>>>U>DS>DG>G>>>C
		500 m radius	<0.01	<0.05	DW>IG>>>U>G>DS>>>C>DH
		250 m radius	<0.01	0.05	IG>DW>U>DS>>>G>>>DH>C

b) Summer (July)

	Available landscape	Used landscape	Wilk's λ	<i>Pr</i>	Ranked habitat types
Arne	Study area (MCP100)	Home Range	0.02	<0.01	DW>G>DH>CS>WH>IG>S>DS>WC>U>CW>R
		500 m radius	0.01	<0.01	DW>G>DH>CS>WH>IGs>S>DS>CW>PM>U>R
		250 m radius	0.01	<0.01	DW>CS>G>DH>WH>IG>S>U>DS>CW>>>WC>R
	Buffer 750 m	Home Range	0.05	<0.01	DW>G>DH>CS>WH>IG>S>DS>AG>U>CW
		500 m radius	0.07	<0.01	DW>G>DH>WH>CS>S=IG>CW>DS=AG>U
		250 m radius	0.07	<0.01	DW>G>DH>DH>AG>U>WH>CW>S>CS>IG
Hartland	Study area (MCP100)	Home Range	<0.01	0.01	IG>>>DS>DW>>>U>G>R>DH
		500m radius	<0.01	0.02	IG>DW>>>U>G>DS>R>C>DH
		250 m radius	<0.01	0.02	IG>DW>DS>R>U>G>WH>DH
	Buffer 750 m	Home Range	<0.01	<0.01	DS>IG>DW>U>G>>>DH>C
		500 m radius	<0.01	<0.01	DW>IG>>>DS>G>>>DH>C
		250 m radius	<0.01	0.34	R=DW=IG>DS>U>DH>G

Table 3.4 (Continued)

c) Autumn (October)

	Available landscape	Used landscape	Wilk's λ	Pr	Ranked habitat types
Arne	Study area (MCP100)	Home Range	0.023	<0.01	DW>DH>G>CS>IG>WH>WC>S>DS>U>>>R>CW
		500 m radius	<0.01	<0.01	G>DW>DH>CS>WH>IG>DS>S>WC>U>CW>>>R
		250 m radius	0.04	<0.01	DW>G>DH>DS>WC>WH>CS>U>IG>R>S>CW
	Buffer 750 m	Home Range	0.15	<0.01	DW>G>DH>IG>CS>WH>AG>S>DS>U>CW
		500 m radius	0.09	<0.01	G>DW>DH>CS>IG>WH>AG>DS>S>U>CW
		250 m radius	0.10	<0.01	DW>G>DH>DS>AG>IG=WH=U>CW>CS>S
Hartland	Study area (MCP100)	Home Range	<0.01	<0.01	IG>R>DW>>>DS>G>U>DH>WH
		500 m radius	<0.01	0.022	IG>DW>G>U>DS>DH>R>>>WH
		250 m radius	<0.01	0.09	IG>DW>R>DS>U>G>WH>DH
	Buffer 750 m	Home Range	<0.01	0.05	IG>DW>R>DS>U>DH>G>WH
		500 m radius	<0.01	<0.01	DW>IG>G>DS>DH>R
		250 m radius	0.02	0.02	IG>DW>DS>U=G=R>DH

d) Winter (February)

	Available landscape	Used landscape	Wilk's λ	Pr	Ranked habitat types
Arne	Study area (MCP100)	Home Range	0.0216	<0.01	DW>DH>G>CS>WH>IG>S>DS>U>WC>>>CW>R
		500 m radius	0.0009	<0.01	DW>DH>G>CS>WH>IG>WC>U>S>DS>CW>R
		250 m radius	0.0520	<0.01	G>DW>DH>WH>DS>WC>U>IG>CS>CW>R>S
	Buffer 750 m	Home Range	0.0685	<0.01	DW>DH>G>WH>CS>WC=IG>S>>>AG>DS>CW=U
		500 m radius	0.0479	<0.01	G>DH>DW>CS=WH>S>AG=WC=IG>CW>U>DS
		250 m radius	0.0147	<0.01	G>>>DW>DH>WH>AG=CW=IG>DS>U>CS>S>WC
Hartland	Study area (MCP100)	Home Range	<0.01	<0.01	G>IG>DW>R>DS>DH>WH
		500 m radius	<0.01	<0.01	G>IG>U>DW>R>DS>WH>>>DH
		250 m radius	<0.01	0.01	G>R>IG>>>DS>DW>DH>U>WH
	Buffer 750 m	Home Range	0.06	0.11	G=DW>R>IG=DA>>>DH>WH
		500 m radius	<0.01	0.01	R>U>DW>IG>G>DS>DH>WH
		250 m radius	<0.01	0.08	R>>>G>DS>>>IG>DW>DH>>>WH

Habitat associations: use within ranges

Annual ranges

Within home range selection showed contrasting results; at Arne, improved grassland was the most positively selected habitat, whilst at Hartland cover habitats (reed-beds, deciduous scrubland, gorse and deciduous woodland) were significantly selected over improved pasture (Table 3.2, locations vs. home range). When habitats were pooled into three groups, the two study areas still contrasted (Table 3.3), with selection for grazing over cover at Arne and a selection of cover over grazing at Hartland.

Seasonal ranges

At Arne compositional analysis only showed a significant ranking of habitat selection within home ranges in Autumn and Spring with wet heath, dry heath and deciduous scrubland as the three habitats most selected in Spring and improved grassland, dry heath and saltmarshes as the three habitats most selected during Autumn (Table 3.5). At Hartland, reed-beds was the most selected habitat ($P < 0.01$) during Autumn and Winter, while in Spring dry heath was the most selected habitat and in Summer there was no significant habitat ranking ($P > 0.05$).

Table 3.5: Habitat selection by Sika deer within home ranges at Arne and Hartland as determined by compositional analysis. On each line habitat classes to the left of the symbol > are selected over those to the right. >>> indicates significant (at 95%) difference between two consecutive habitat classes. Differences from random use are indicated by λ and randomized P values (1000 interactions). AG, acid grassland; CS coniferous scrubland; CW, coniferous woodland; DH, dry heath; DS, deciduous scrubland; DW, deciduous woodland, G, gorse; IG, improved grassland; R, reed-beds; S, saltmarsh; U, urban-anthropoc; WC, weed community; WH, wet heath.

		Wilk's λ	Pr	Ranked habitat types
Arne	Spring	0.07	<0.01	WH>>>DH=DS=CW=IG>G>CS>S=DW>AG
	Summer	0.04	0.06	DH>S=DW>IG>CW=WH>G>CS>DS>WC>R
	Autumn	<0.01	<0.01	IG>DG>S>G=CS>DW=DS>>>WH>CW>AG>WC
	Winter	0.11	0.07	DH>G>CS>CW>S=DS>IG=DW>WH>AG>WC
Hartland	Spring	<0.01	0.04	DH>R>AG>DS>DW>IG>G>C
	Summer	<0.01	0.86	IG>DS>DW>C>DH>U>G
	Autumn	<0.01	<0.01	R>>>DS>DW>DH=IG=G>AG>U
	Winter	<0.01	<0.01	R>>>G>DS>>>DW>DH>IG>AG>WH

No significant selections for resource groups was found during spring and winter at Arne, but during summer and autumn grazing habitats were selected over cover habitats ($P < 0.05$). Within the seasons when significant selection was found, contrasting results in relation to heath selection during autumn ($H > GR > CO$, $P < 0.05$) and summer ($GR > H > CO$, $P < 0.01$) were found. At Hartland cover was selected over grazing habitats ($P < 0.01$) except during summer, when there was no significant selection ($P > 0.05$). In spring heath was the most positively selected group of habitats ($H > CO > GR$, $P < 0.01$) whilst in autumn contrasting results with both cover and grazing being selected over heath were found ($CO > GR > H$, $P < 0.01$). During winter heath was selected over grazing but not over cover ($CO > H > GR$, $P < 0.01$).

Influence of cover and sources of disturbance: distance of Sika deer to cover

Annual ranges

Figure 3.1a shows how locations obtained from pastures during the day were significantly closer to shelter than expected by random for Arne (Median observed = 56 (5-387) m, expected = 87 (5-485) m, $U = 60850$ $P < 0.01$) and Hartland (Median observed = 60 (5-251) m, expected = 68 (5-316) m, $U = 111824$ $P < 0.01$). However, when on heath (Figure 3.1b) during the day, distances to cover were no different from random locations at Arne ($U = 408824$ $P > 0.05$) but at Hartland day locations were closer to cover than expected by random (Median observed = 44 (5-298) m, expected = 84 (5-364) m, $U = 1358$ $P < 0.01$). Night locations showed no significant differences from random, with the exception of grazing locations at Arne, that were still significantly closer to cover than expected by random (Median observed = 65 (5-385) m, expected = 87 (5-485) m, $U = 99109$ $P < 0.01$).

Day locations were also significantly closer to cover than night locations in both Arne (Median day = 56 (0-387) m, night = 65 (5-386) m, $U = 88693$, $P < 0.01$) and Hartland (Median day = 60 (0-251) m, night = 69 (0-292) m, $U = 85294$ $P < 0.01$), but again the same was not true for heath locations in either area ($P > 0.05$). The 75% quartiles seen in Figure 3.1 show that Sika deer rarely ventured beyond 100-110 m from cover, even during the night, and there were no significant differences between study areas. Whilst distance to cover from pasture did not differ between study sites ($P > 0.05$) locations on heaths were significantly closer to cover at Hartland than at Arne ($U = 22532$, $P < 0.01$).

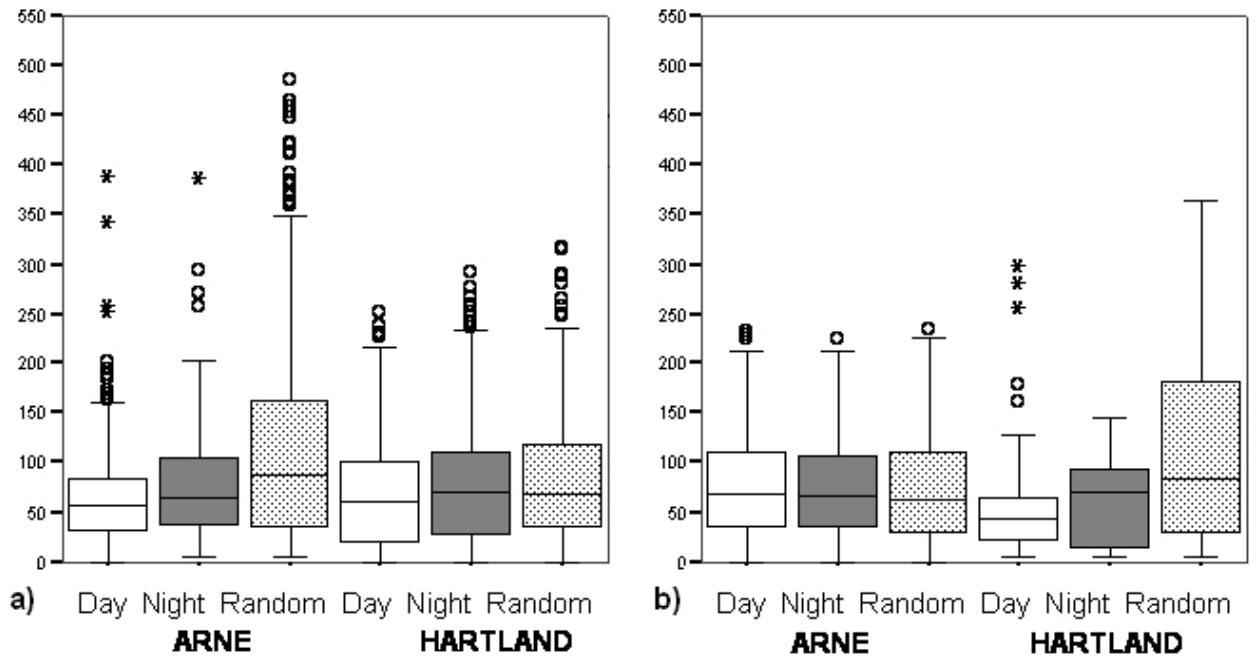


Figure 3.1: Distances to cover during day and night in both study areas from (a) pastures and (b) heath. White: day locations; grey: night locations; dotted: random locations. Boxes delimit the 25 to 75 percent quartile and median distances to cover. Circles indicate outliers and asterisks indicate extremes.

Seasonal ranges

Unlike Arne, Hartland showed significant seasonal differences in distance to cover from pastures for both night ($X^2 = 29.803$ $P < 0.01$) and day locations ($X^2 = 12.972$ $P < 0.01$). The seasonal ranking of distances to cover from pastures during the night at Hartland was (furthest to closest): autumn > winter > spring > summer and during the day: winter > summer > spring > autumn.

Influence of cover and sources of disturbance: distance of Sika deer to disturbance areas

Figure 3.2a shows that deer on pasture were significantly closer to areas of disturbance during the night, when there was little or no disturbance, than during the day for both Arne (Median day = 263 (0-789) m, night = 126 (0-786) m, $U = 66108$, $P < 0.01$) and Hartland (Median day = 256.65 (0-666) m, night = 195 (0-758) m, $U = 85294$ $P < 0.01$). However,

there were no significant differences between day and night locations on heath (Figure 3.2b) in the distance to disturbance at Arne or Hartland ($P > 0.05$). During the day only 25% of Sika deer locations on pastures were closer to disturbance areas than 126 m at Arne and 150 m at Hartland. During the night this distance was halved to 69 m at Arne and less markedly reduced to 123 m at Hartland.

Surprisingly, day locations on pasture were significantly closer to areas of disturbance than expected by random at Arne (Median observed = 263 (0-789) m, expected = 386 (0-852) m, $U = 59255$, $P < 0.01$) although at Hartland they were significantly further than expected by random (Median observed = 257 (10-666) m, expected = 195 (0-851) m, $U = 59255$, $P < 0.01$). On heath, day locations were significantly closer to areas of disturbance than expected by random in both areas (Median observed = 194 (0-1102) m, expected = 382 (0-1169) m, $U = 300584$, $P < 0.001$ for Arne, Median observed = 170 (79-785) m, expected = 556 (75-1279) m, $U = 1203$, $P < 0.01$ for Hartland).

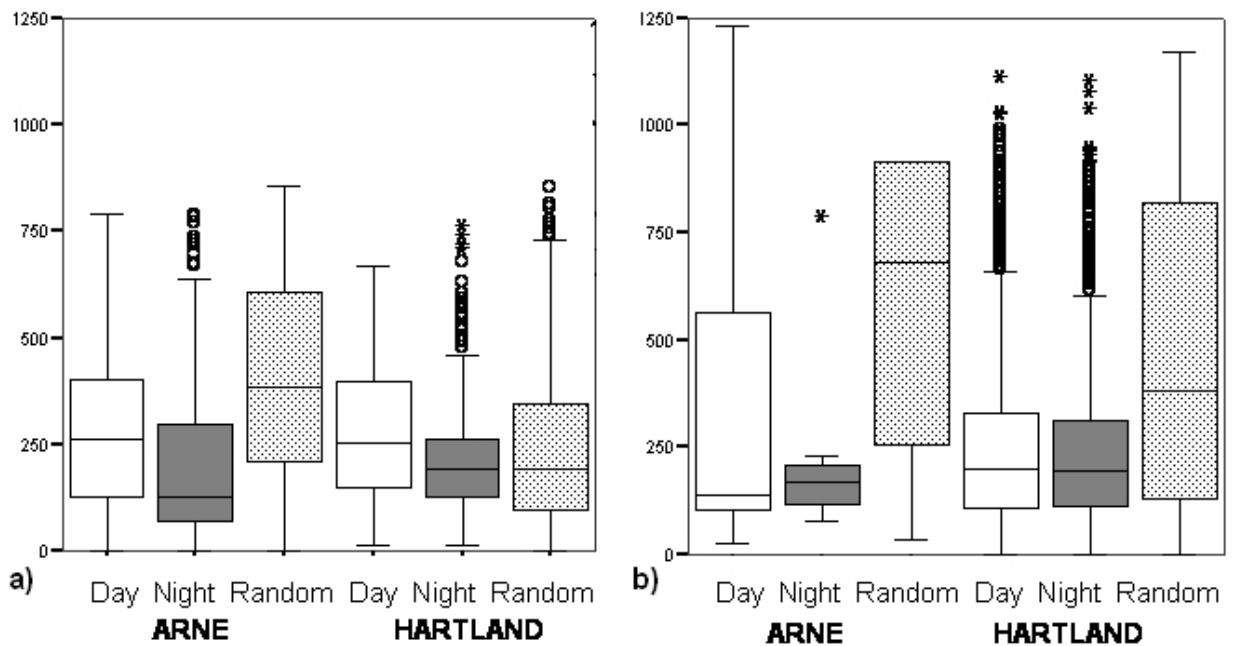


Figure 3.2: Distances to areas of disturbance during day and night in both study areas from pastures (a) and heath (b). White: day locations; grey: night locations; dotted: random locations. Boxes delimit the 25 to 75 percent quartile and median distances to areas of disturbance. Circles indicate outliers and asterisks indicate extremes.

During the night, locations were significantly closer to areas of disturbance than expected by random on pastures at Arne (Median observed = 126 (0-786) m, expected = 386 (0-852)

m, $U = 52424$, $P < 0.01$) but were not significant at Hartland ($U = 99273$, $P > 0.05$). On heaths, night locations were significantly closer to areas of disturbance than expected by random in both areas (Median observed = 200 (0-1111) m, expected = 378 (0-1168) m, $U = 117494$, $P < 0.01$ for Arne, Median observed = 138 (25-1231) m, expected = 721 (32-1160) m, $U = 56$, $P < 0.01$ for Hartland).

Influence of landscape structure on Sika deer distribution

There were significant differences in edge density between what was within the used landscape (home range, 500 m and 250 m radius buffer) and what was in the surrounding area (MCP 100% and 750 m radius buffer). The used landscape showed higher edge diversity than the available landscape across all spatial scales ($P < 0.001$). When both study sites were analyzed independently Arne showed the same pattern across all spatial scales. However, at Hartland edge density between the 500 m radius buffer and MCP100% ($W = -1.72$, $P = 0.09$) was not quite significant at the 5% level. Other spatial scales at Hartland showed a significantly higher edge density within the used landscape ($P < 0.05$ in two cases, $P < 0.01$ in three cases).

Significant relationships were found between edge density and the percentage of improved grassland, deciduous woodland and the groups of habitats offering grazing and cover resources at the different spatial scales (Table 3.6). At Arne, lower edge density at the home range and 500 m radius was related to higher content in improved grassland, while higher edge density at the same spatial scales was related to lower content in deciduous woodland. Higher edge density at the home range and 500 m radius was related to higher content in deciduous woodland. At Arne, no relationship was found between edge density and the content of heath. At Hartland, only lower edge density within buffers 250 m radius was not significantly related to higher content of improved grassland and grazing resources. The content of deciduous woodland was only related to edge density at the home range level, with higher edge densities in those areas with higher content in deciduous woodland. The same positive relationship with edge density was only found at Hartland with the content of cover at the home ranges, while edge density had a significant positive relationship with the content heath within the home range and buffers of 500 m radius.

Table 3.6: Relationship between edge density and the content of habitats at different spatial scales. ED = edge density; IG = % of improved grassland; DW = % of deciduous woodland Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$.

	Spatial scale	Spearman r ED vs. IG	Spearman r ED vs. % GR	Spearman r ED vs. % DW	Spearman r ED vs. % CO	Spearman r ED vs. % Heath
Arne	Home Range	- 0.53*	- 0.10	0.47*	0.14	0.24
	750 m radius	- 0.04	0.14	0.32	- 0.47*	0.16
	500 m radius	- 0.53*	- 0.36	0.47*	- 0.03	0.26
	250 m radius	0.33	- 0.33	0.26	0.42	-0.40
Hartland	Home Range	- 0.73*	- 0.73*	0.73*	0.63	0.76*
	750 m radius	- 0.80**	- 0.80**	0.20	0.02	0.41
	500 m radius	- 0.82**	- 0.82**	0.63	0.93**	0.77*
	250 m radius	0.17	0.57	- 0.13	- 0.02	-0.29

DISCUSSION

The apparent differences in habitat associations by Sika deer between the two study areas and seasons can potentially be explained by a balance between high quality food resources and cover, the landscape structure in terms of the spatial arrangement of cover, food and risk and differences in sources of disturbance. This research has used radio tracking to obtain the locations of animals throughout the day and night, therefore locations of deer were obtained even when they were hidden in cover. Also two study areas with contrasting landscape structure, availability of habitats and intensity and form of disturbance have been used and so the present study has explicitly considered the combined effects of habitat availability, landscape structure and disturbance on the distribution and habitat use of Sika deer at both home range and landscape scale.

The analysis of the habitat associations has shown that Sika deer at Arne chose to place their home ranges in areas of more cover rather than pastures, while Hartland deer showed a positive selection for pastures over cover habitats. Contrasting results were also found at the home range level. Sika deer selected grazing over cover habitats at Arne and showed the opposite situation at Hartland. Differing results in Sika deer habitat use between study areas related to the availability of forage and shelter have been also recorded in other parts of the UK (Mann and Putman, 1989b). Moreover, results of this research have found that heath use is affected by both the availability of pastures (as preferred foods) and the landscape structure, in terms of the distribution of heath patches in relation to cover and pastures. At Hartland, through all spatial levels, heath (i.e. dry and wet heath combined) was the group of habitats least selected. In this case cover and pasture were adjacent and therefore no switches involving movements across heath were required. Also, Hartland had a high percentage of good quality food resources (i.e. improved grassland), therefore deer might not have needed heath for feeding unless the good quality resources are depleted. Results from direct observations seem to agree with this explanation, as they showed a higher usage of heaths during the winter (See Chapter 5 and Appendix 1), when grass biomass is reduced. In contrast, heath at Arne is ranked middle between cover (most selected) and pastures (least selected) in 4 out of 6 scales. At Arne, patches of dry and wet heath are located in between areas of pastures and cover, and in some cases heath surrounds patches of grass and saltmarshes, forcing deer to travel across patches of heath

in order to reach pastures or cover. The distance to patches of grass and the fragmentation of the available grass have been found to affect the use of heath patches by deer and sheep (e.g. Clarke *et al.*, 1995a, Palmer *et al.*, 2003). Also, high quality pastures are rare and the density of deer is higher at Arne than at Hartland, therefore there may be stronger competition for high quality food resources (i.e. improved grassland) and therefore deer are forced to use alternative resources such as heath to cope with a quicker depletion of food resources, hence the higher use of heaths. Diet analyses conducted at Arne (Diaz pers. com.), have demonstrated the considerable importance of *C. vulgaris* in the diet of Sika deer (18% of the rumen content of Sika deer hinds, 13% of rumen content of stags). A future study involving diet analyses at Hartland would establish the seasonal importance of heather as an alternative source of food resources at this area.

Cover is important to deer for reducing deer heat loss (Grace and Easterbee, 1979, Schmitz, 1991) and reducing the risk of predation; both these factors are likely to improve the survival of deer (Tufto *et al.*, 1996). Deciduous woodland was the only habitat uniformly selected across all scales and study areas when comparing the habitat content within the available and used landscape. Deciduous woodland offers both cover and seasonal browsing resources that might attract Sika deer more than other cover habitats, such as coniferous woodland. At Arne, the most abundant 'cover' habitat is coniferous woodland (10.20% of the total vegetation) but surprisingly it is least selected. However, coniferous wood has very sparse ground vegetation due to poor light conditions, which could explain why coniferous woodland is one of the least selected habitats in the area. The importance of thick cover for Sika deer at Arne is again highlighted by the apparent selection for gorse or deciduous scrubland when placing their home ranges.

Human disturbance has been shown to affect animal behaviour as a form of predation risk (e.g. Miller *et al.*, 2001, Papouchis *et al.*, 2001, Frid and Dill, 2002, Fernández-Juricic and Schroeder, 2003, Stankowich, 2008). In the case of deer species human disturbance has been related to effects on behaviour such as adaptations of daily activity, alert response and/or vigilance (Georgii, 1981, Borkowski and Furubayashi, 1998a, Li *et al.*, 2007, Benhaiem *et al.*, 2008). Disturbance by humans has been also recorded to have effects on Sika deer activity patterns (Mann and Putman, 1989b), habitat use (Borkowski and Furubayashi, 1998a, Sakuragi *et al.*, 2003a) and possibly group size (Borkowski and Furubayashi, 1998b). However, previous studies have not accounted for differences

between study areas in the intensity and form of human disturbance (visitors, vehicles, culling). Results of this research have shown that variation in disturbance intensity and the availability of cover can potentially explain differences in where Sika deer are found between sites.

Compared to Hartland, deer stayed closer to cover at Arne suggesting a perceived greater risk by deer, which corresponds with much higher visitor numbers. Also, at Arne the routes used by visitors during the day are located next to and between patches of improved grassland (high quality pasture). This may explain why Arne's deer use grass more at night, when there is little or no disturbance, while during daylight deer at Arne switch to other pastures of lower quality further from disturbance. At Hartland high quality pastures are less fragmented and further away from sources of disturbance, therefore not many shifts between patches of pasture are needed as long as some relatively close cover is secured. If Sika deer perceive visitors as a risk, selecting areas with more surrounding cover and with some cover between pasture areas allows Sika deer at Arne to switch "safely" between feeding sites during the day and night. Due to spatial distribution of patches of pasture and cover at Hartland, deer do not need to shift between pastures so frequently so pastures are selected over cover habitats when deer place their home ranges. Despite some seasonal fluctuations, visitor numbers at Arne remain high so there are no seasonal changes in their choice of home range placement, clearly selecting deciduous woodland, gorse and dry heath over the rest of habitats. However, at Hartland the level of disturbance increases during winter with culling, as shown with Roe deer (Benhaiem *et al.*, 2008), and that might be the reason why during the hunting season Sika deer show a tendency to positively select denser cover habitats (that offer better protection from hunting) over pastures, which is a selection not observed at Arne during the hunting season.

Sika deer appeared to have a maximum bolting distance of 100-110 m from cover that was maintained by deer during day and night. Although the value of this bolting distance from cover has to be taken cautiously due to the inherent location error of radio tracking techniques, it clearly indicates that Sika deer might perceive that exceeding the distance from cover increases the predation risk. Similar result was obtained by Takatsuki (1989): the number of faecal pellets deposited by Sika deer decreased suddenly after 150 m out of the forest. Also, results of the present research suggested that differences in the intensity of disturbance during the day had an impact on the selection of Sika deer locations on pasture

in both study areas. During the day, when Sika deer left the safety of cover in order to use the pastures, they selected locations closer to shelter than expected by random, which could be linked to a perceived risk of predation as a result of human activity (i.e. visitors, dog walkers, vehicles). During the night, when the level of disturbance was lower (on roads) or absent (visitors) the distance to cover from pastures showed no differences from random at Hartland, although Arne deer locations were still closer to cover than expected by random. This perceived higher risk, compared to Hartland, might be related to a higher number of walkers, which are perceived as a greater risk than vehicles (main disturbance at Hartland) as it has been shown on Mule deer (Freddy *et al.*, 1986), bighorn sheep *Ovis canadensis* (Papouchis *et al.*, 2001) and in general on ungulates (Stankowich, 2008).

Deer on pasture were found to be closer to areas of disturbance during the night than during the day in both areas. However, there were differences in the distribution of deer locations in relation to the distance to areas of disturbance between study areas. Such differences between study areas could be explained by differences in the spatial distribution of areas of disturbance and pastures. At Arne high quality pastures are concentrated next to and between walking routes used by visitors while at Hartland high quality pastures are located at different distances to areas of disturbance. Therefore Arne deer are forced to use areas closer to areas of disturbance than expected by random during day and night in order to obtain high quality food resources.

The landscape structure, in terms of the distribution of habitats, affected the distribution and habitat use of Sika deer. The distribution appeared affected by patch characteristics (i.e. the quantity of ecological edges) within their home ranges. Several studies have suggested that edges are high quality habitats for deer; home ranges are smaller (Kie *et al.*, 2002, Said and Servanty, 2005), utilization rates are higher than expected by random (Tufto *et al.*, 1996, Lamberti *et al.*, 2006) and reproductive rates can be enhanced (Miyashita *et al.*, 2008). Here the apparent selection for higher edge density could indicate a buffer area of cover surrounding pastures. However, further investigation showed that there were significant relationships between edge density and different habitats and groups of habitats selected by Sika deer. In particular, at Hartland the edge density was negatively related to the percentage of improved grassland and other grazing habitats. Analyses of Sika deer habitat associations at Hartland have shown that inner areas (i.e. core areas and home ranges) contained more improved grassland than the surrounding landscape. If edge

density was only linked to the content of those habitats, a lower edge density would be expected here compared to the surrounding landscape. Results contradict this explanation as a selection for higher edge densities were found at Hartland. By contrast, at Arne the relationship between edge density and the content of the most preferred habitat (deciduous woodland) was limited to only two spatial scales. At those spatial scales (i.e. home range and 500m radius) higher content in deciduous woodland was related to higher edge density. The habitat selection analysis has shown that inner areas had higher content of deciduous woodland than the surrounding landscape. Therefore the relationship between edge density and content of deciduous woodland might have had an effect on the results at those specific spatial scales.

As a conclusion Sika deer place their home ranges with a trade-off between preferred resources and a perceived risk linked to human disturbance, which highlights the importance of a balance between grazing and cover resources. Also, the landscape structure in terms of the distribution of habitats affects the distribution and the habitat use of deer. This has management implications in areas of natural interest containing deer populations. Management of deer populations should integrate not only the direct control of deer numbers but also the possible modification of landscape features (i.e. availability of cover) that could modify the intensity in which deer utilize patches of protected habitats. Management strategies are recommended to incorporate the idea that the visitors might affect the behavior of animals and use it to benefit wildlife where possible (Pépin *et al.*, 1996, Taylor and Knight, 2003). Changes in deer behaviour related to habitat selection and distribution might increase deer impacts on protected habitats; for instance it is likely that an increase in disturbance and therefore a higher selection for cover could increase the impact on commercial or natural forests. However, properly managed, disturbance could also help to decrease deer impacts; for instance, an appropriate management directed to increase disturbance or the distance from cover to agricultural fields could decrease commercial losses, as an alternative to culling.

CHAPTER 4: SEARCHING FOR BETWEEN-AREA CONSISTENCY IN THE HABITAT ASSOCIATIONS OF SIKA DEER

SUMMARY

Large populations of Sika deer (*Cervus nippon*) overlap in distribution with mosaics of habitats containing lowland heath, a key conservation habitat in Western Europe. Knowledge of the habitat associations and potential impacts of Sika deer can advise conservation management, particularly if habitat associations derived in one area can be used to predict or understand deer behaviour and impacts in another. The previous chapter showed that habitat associations derived from radio tracking were not consistent between two areas (Arne and Hartland) that differed in the availability and spatial distribution of key resources (i.e. food and cover). However, the chapter did not compare the habitat associations of deer in areas with similar landscape characteristics. The aim of this chapter was to test the hypotheses that the habitat associations of Sika deer will be similar in areas with similar landscape structure in terms of availability and spatial distribution of pasture and cover, but that habitat associations will be different between areas that differ in these characteristics. In order to do this, the habitat associations of Sika deer were determined in a third study area (Studland), which has a similar landscape structure to Arne, and different landscape structure to Hartland. Deer distribution data derived from ground counts were available for both Studland and Hartland, and so habitat associations could be derived from ground counts for Studland, and from both radio tracking and ground counts for Hartland. As both radio tracking and ground counts occurred at Hartland, the habitat associations derived from these methods were compared for this area. Both methods yielded similar habitat associations, implying that any differences in habitat associations between Arne (radio tracking) and Studland (ground counts) would be due to differences in the areas rather than differences in the methods used to derive habitat associations. The habitat associations of Sika deer were similar in Arne and Studland and different in Hartland and Studland, in support of the hypothesis of this chapter. This study identifies the importance of the availability and spatial distribution of key resources at the landscape scale on the habitat associations of Sika deer, and hence the importance of incorporating these landscape characteristics into habitat association models used to predict the distribution and impacts of the deer.

INTRODUCTION

Concerns over the ecological impacts of deer on ecosystems have grown over the last century (e.g. Putman and Moore, 1998, Fuller and Gill, 2001, Cote *et al.*, 2004, Gordon *et al.*, 2004). In response to an increasing awareness of deer damage on agriculture, forestry and conservation areas, abundant work has been dedicated to determine the ecological impacts of deer on the plant and animal communities of different ecosystems (reviewed for example by Putman and Moore, 1998, Fuller and Gill, 2001, Cote *et al.*, 2004). An important step in predicting the large-scale impacts of deer is to understand the influence of habitat and other environmental factors on their distribution and abundance, as impacts will tend to be higher in areas favoured by the deer.

Large populations of a non-native deer species, Sika deer (*Cervus nippon*) occur in parts of the south of England (Swanson and Putman, 2009), and overlap in distribution with mosaics of lowland heath, woodland and grassland. Previous research (Chapter 3) based on radio tracking data has investigated the ecological interaction of Sika deer with lowland heath mosaics to better understand the factors that affect Sika deer habitat selection and distribution, while Chapter 5 investigates the processes through which Sika deer might be affecting plant and animal communities of lowland heath. Knowledge of the habitat associations and potential impacts of Sika deer is of potential value to heathland managers, particularly if habitat associations derived in one area can be used to predict or understand deer behaviour and impacts in another. If habitat associations are consistent between different areas, they can be used to predict the impacts of deer over a wider scale than just the areas in which deer have been studied in detail. The research presented in Chapter 3 showed that habitat associations differed between two areas (Arne and Hartland) of contrasting landscape structure (i.e. habitat availability, spatial distribution of habitats). However, the chapter did not compare the habitat associations of Sika deer in areas with similar landscape structure. The aim of this chapter is to test the hypotheses that the habitat associations of Sika deer are similar in areas with similar landscape structure in terms of habitat availability and spatial distribution of habitats, but that habitat associations differ between areas that differ in these characteristics. In order to do this, the habitat associations of Sika deer were determined in a third study area (Studland), which has a similar landscape structure to Arne, and different structure to Hartland.

Studying Sika deer habitat associations required suitable data on the spatial distribution of both deer and habitat / environmental variables. In the previous chapter deer distribution data were obtained from radio tracking at Arne and Hartland. Ideally, in the present chapter, habitat associations would have been derived using the same methods in all study areas (i.e. from deer distribution data derived from radio tracking), but this was not possible, as no suitable radio tracking data were available from Studland (or any other areas within the study region). However, deer distribution data derived from ground counts (i.e. from direct observations by an observer walking through an area) were available for both Studland and Hartland, and so habitat associations could be derived from ground counts for Studland, and from both radio tracking and ground counts for Hartland. As both radio tracking and ground counts occurred at Hartland, the habitat associations derived from these methods were compared for this area.

While radio tracking is widely used to study the physiology, movements, resource selection and demographics of wild animals (e.g. Kenward, 2001b, Millspaugh and Marzluff, 2001), ground counts are usually conducted to obtain the population size of deer in a given area (see examples in Mayle *et al.*, 1999, Daniels, 2006), and are less often used to determine their habitat associations. One reason for this is the lack of precision with which deer can be located during ground counts. Counts will often disturb the deer, sometimes prior to observation, and so the recorded deer locations will not necessarily be within the same habitat as occupied by the deer prior to disturbance. This leads to difficulty in analysing habitat associations based on the individual locations recorded during surveys. An alternative strategy to using the specific location of deer counts is to calculate spatial variation in the density of deer by interpolating densities between the individual count locations, and to relate the density of deer to landscape characteristics, such as habitat content. Plante *et al.* (2004) calculated the spatial variation in the density of deer from count data from aircraft, but their technique is equally applicable to count data from ground counts. The method derived by Plante *et al.* (2004) was used to derive habitat associations from ground count data at Hartland and Studland. This method was used as it was designed to determine deer habitat associations at different spatial scales, which is consistent with the analyses conducted in Chapter 3 and therefore allow a comparison of results. In addition, the method of Plante *et al.* (2004) was designed to derive habitat associations from field data similar to those obtained from ground counts (i.e. location and

number of individuals recorded during a fixed period of time). Previous methods have used similar modelling technique to spatially interpolate densities of terrestrial mammals (e.g. Potvin *et al.*, 2005) or detect hot spots in landscape ecology (Nelson and Boots, 2008). However, to the best of the author's knowledge no comparable method to that developed by Plante *et al.* (2004) derived from a spatial interpolation of direct observations has linked areas of high density of large herbivores to their habitat associations at a landscape scale.

The specific objectives of this chapter were: (1) to compare the habitat associations derived from ground counts with those obtained from radio tracking in the same area (Hartland); (2) to compare the habitat associations of Sika deer between areas with similar landscapes characteristics in terms of the availability and spatial distribution of habitats (Arne and Studland) and also between areas with different landscape characteristics (Hartland and Studland).

RESULTS

Comparison of habitat associations derived from ground counts and radio tracking

Between March 2006 and October 2008, 124 observations of Sika deer groups (1 – 80 individuals) were obtained at Hartland, with a total of 1,231 deer observed over the three years of ground counts (Figure 4.1). As deer were not identified individually, the possibility that some deer were counted more than once during a survey cannot be ruled out. At Studland, 312 observations of Sika deer groups (1 – 31 individuals) were obtained, with a total 1,119 deer. These result in an average density of Sika deer for the period 2006-2008 of 37.3 deer/km² at Hartland and 23.5 deer/km² at Studland.

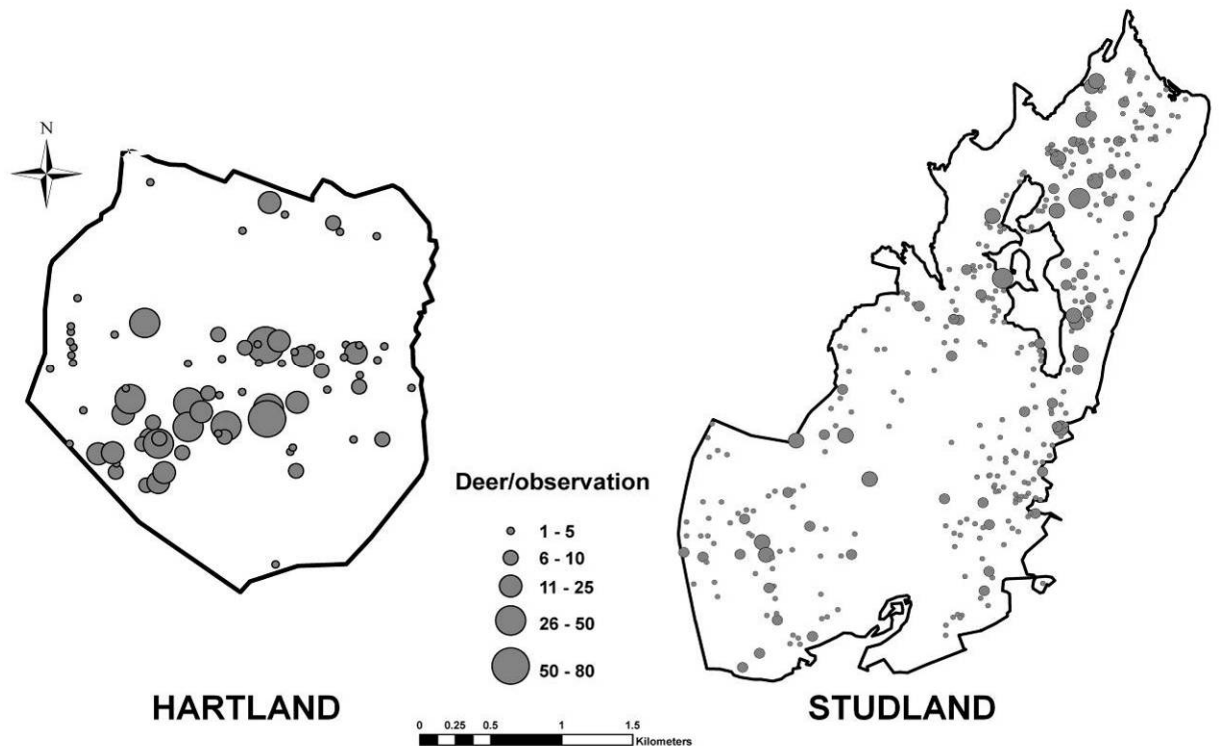


Figure 4.1: Sika deer observations at Hartland and Studland between March 2006 and October 2008.

After conducting the spatial interpolation of Sika deer densities for the period 2006-2008 based on two values of the smoothing factor (SD and 2SD), two maps were obtained (Figures 4.2 and 4.3). As the value of the smoothing factor increased, the value of the maximum density of deer per hectare decreased, resulting in a more smoothed output. The

difference in the maximum density of deer between areas (identified from the figure scales) reflects a higher level of deer aggregation in Hartland compared to Studland.

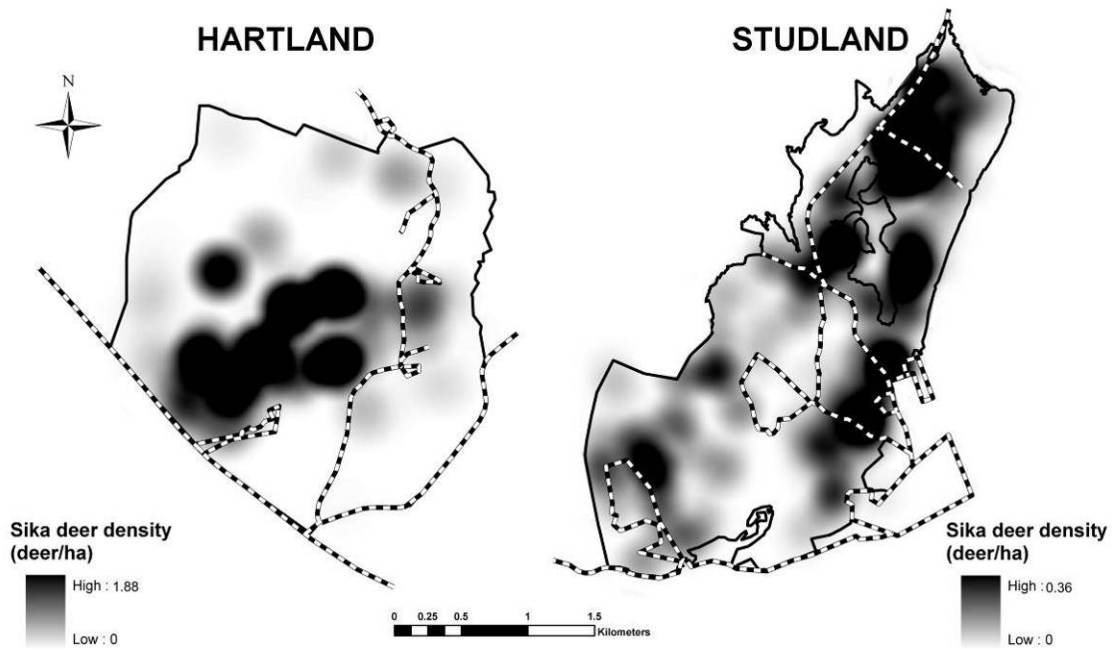


Figure 4.2: Interpolation of densities of Sika deer at Hartland and Studland for the period 2006-2008. The dashed lines indicate a road, track or the boundaries of built-up areas. Value of the smoothing factor = standard deviation of the kernel distributions fitted to the locations of Sika deer.

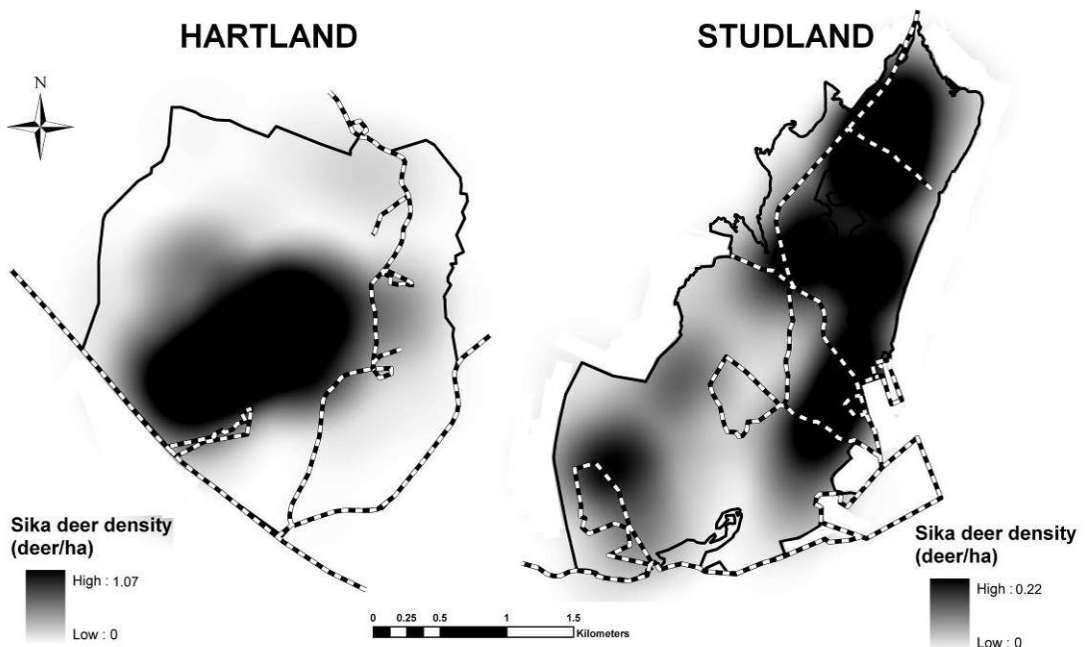


Figure 4.3: Interpolation of densities of Sika deer at Hartland and Studland for the period 2006-2008. The dashed lines indicate a road, track or the boundaries of built-up areas. Value of the smoothing factor = $1.96 \times$ standard deviation of the kernel distributions fitted to the locations of Sika deer.

At Hartland, the smoothing factor, grid cell size and grid origin all influenced the results of the correlation analysis (Table 4.1). When significant results for the same variable were found for both grid size cells, the relationship was generally stronger (i.e. higher r) for the 500 m grid cells. Despite some differences in results depending on the smoothing factor, grid cell size and grid origin, the overall results showed that Sika deer in Hartland had a positive selection for grazing resources (in particular improved grassland) and avoided wet heath (Table 4.1).

Table 4.1: Summary of habitat content (HCA) that are significantly correlated with the density of Sika deer at Hartland for a given smoothing factor, grid cell size and grid position. SD = standard deviation of deer home ranges, 2SD = 1.96 x SD, IG = improved grassland, WH = wet heath, M = mire, AG = acid grassland, CW = coniferous woodland, GR = grazing, H = heath. Asterisks indicate probability level: * $P < 0.05$, ** $P < 0.01$.

Smoothing factor	Grid cell size	Grid position	N	HARTLAND variables
SD	250 x 250 m	I	50	IG* (0.33), WH** (-0.37), GR* (0.28)
		II	50	IG** (0.37), WH** (-0.38), M** (-0.41), GR* (0.31)
		III	50	WH* (-0.35)
	500 x 500 m	I	16	WH* (-0.55), GR* (0.51)
		II	18	IG* (0.49), GR* (-.48)
		III	20	CW* (-0.49)
2SD	250 x 250 m	I	50	IG* (0.33), WH** (-0.37), GR* (0.30)
		II	50	IG* (0.33), WH* (-0.31), AG* (-0.33), M**(-0.43)
		III	50	WH* (-0.30), AG* (0.30), M* (-0.29)
	500 x 500 m	I	16	IG* (0.55), WH** (-0.62), M* (-0.50), GR* (0.57), H* (-0.50)
		II	18	AG* (0.49)
		III	20	CW* (-0.52)

Table 4.2 shows habitat selection as obtained from radio tracking at Hartland by comparing the habitat within the used landscape (home range, 500 m radius and 250 m radius buffer) to the habitat available in the surrounding landscape (750 m radius buffer and study area). Improved grassland was the most selected habitat across four out of six possible scales at Hartland, which agrees with results derived from the ground counts. The least selected habitats at Hartland were dry and wet heath. When habitats were pooled into the three resource groups (CO, GR and H), grazing was the most selected group across all spatial scales at Hartland, ($P < 0.05$) with only one exception in which no significant selection was found. Results obtained from both methods were able to identify similarly the habitats most and least preferred by Sika deer.

Table 4.2: Habitat selection by Sika deer at Hartland as determined by compositional analysis from radio tracking data. On each line habitat classes to the left of the symbol > are selected over those to the right. >>> indicates significant (at 95%) difference between two consecutive habitat classes. Differences from random use are indicated by λ and randomized *P* values (1000 interactions). AG, acid grassland; CS coniferous scrubland; DH, dry heath; DS, deciduous scrubland; DW, deciduous woodland, G, gorse; IG, improved grassland; R, reed-beds; WH, wet heath. Cover (CO) was obtained by pooling CS, CW, DS, DW, G and R; CO, habitats offering cover resources; GR, habitats offering grazing resources, H, heath habitats.

Available landscape	Used landscape	Wilk's λ	Pr	Ranked habitat types
MCP100	Home Range	<0.0001	0.376	IG>DW>DS>R>G>DH>WH
		0.3346	0.013	GR>>>CO>>>H
	500 m radius	0.0013	0.009	IG>DW>>>G>DS>R>>>WH>DH
		0.3714	0.027	GR>>>CO>>>H
	250 m radius	<0.0001	0.018	IG>DW>DS>R>G>WH>DH
		0.1139	0.005	GR>>>CO>>>H
Buffer 750m	Home Range	0.0001	0.004	IG>DW>R>G>DS>>>DH>WH
		0.5542	0.127	GR>CO>H
	500 m radius	<0.0001	0.621	DW>R>IG>>>G=DS=WH>DH
		0.4559	0.027	GR>>>CO>>>H
	250 m radius	0.0001	0.051	IG>DW>DS>R>DH>G>WH
		0.1850	0.023	GR>CO>>>H

Comparison of the habitat associations of Sika deer across areas with similar and different landscape structure

The analysis of ground counts from Studland shows that Sika deer selected areas with higher cover (and in particular deciduous woodland) and avoided areas of wet heath (Table 4.3). These results are similar to those obtained by radio tracking at Arne, as both deciduous woodland and the group of habitats offering cover were also the most preferred habitats across the majority of spatial scales (Table 4.4). However, habitat association analyses based on radio tracking data at Arne showed that the less selected habitats were reedbeds, saltmarshes or coniferous woodland.

Table 4.3: Indices of habitat content (HCA) that are significantly correlated with the density of Sika deer at Studland for a given smoothing factor, grid cell size and grid position. SD = standard deviation of deer home ranges, 2SD = 1.96 x SD, WH = wet heath, DW = deciduous woodland, M = mire, AG = acid grassland, CO = cover, H = heathland. Asterisks indicate probability level: * P < 0.05, ** P < 0.01, *** P < 0.001.

Smoothing factor	Grid cell size	Grid position	N	Habitat content vs. density of Sika deer
SD	250 x 250 m	I	50	WH** (-0.44), DW*** (0.50), M* (0.34), CO* (0.36), H** (-0.38)
		II	50	WH* (-0.40), DW*** (0.55), CO*** (0.49), H** (-0.36)
		III	50	DW*** (0.51), AG** (-0.42), CO** (0.44)
	500 x 500 m	I	15	CO* (0.57)
		II	13	CO* (0.58)
		III	13	CO** (0.75)
2SD	250 x 250 m	I	50	WH** (-0.43), DW*** (0.58), AG* (-0.32), CO** (0.42), H* (-0.34)
		II	50	WH* (-0.35), DW*** (0.67), CO*** (0.51), H* (-0.34)
		III	50	WH* (-0.33), DW*** (0.58), AG* (-0.33), CO*** (0.53), H* (-0.34)
	500 x 500 m	I	15	CO* (0.58)
		II	13	AG* (-0.63)
		III	13	WH** (-0.43), DW*** (0.58), AG* (-0.32), CO* (0.64)

Table 4.4: Habitat selection by Sika deer at Arne as determined by compositional analysis from radio tracking data. On each line habitat classes to the left of the symbol > are selected over those to the right. >>> indicates significant (at 95%) difference between two consecutive habitat classes. Differences from random use are indicated by λ and randomized *P* values (1000 interactions). AG, acid grassland; CS coniferous scrubland; CW, coniferous woodland; DH, dry heath; DS, deciduous scrubland; DW, deciduous woodland, G, gorse; IG, improved grassland; S, saltmarsh; U, urban/anthropic; WC, weed community; WH, wet heath. CO, habitats offering cover resources; GR, habitats offering grazing resources, H, heath habitats.

Available landscape	Used landscape	Wilk's λ	<i>P</i> r	Ranked habitat types
(MCP100)	Home Range	0.0173	0.001	DW>DH>G>CS>WH>IG>S>U>DS>WC>CW>R
		0.6246	0.012	H>CO>>>GR
	500 m radius	0.0016	0.001	DW>G>DH>WH>CS>IG>S>U>CW>DS>WC>>>R
		0.4204	0.001	H>CO>>>GR
	250 m radius	0.0266	0.001	DW>G>DH>DS>WC>WH>U>CS>IG>R>CW>S
		0.3956	0.001	CO>H>GR
Buffer 750 m	Home Range	0.0642	0.008	DW>G>DH>CS>WH=IG>S>AG=DS=R>U>CW
		0.6075	0.007	CO>H>>>GR
	500 m radius	0.0872	0.002	DW>G>DH>WH>IG>S>CS>CW>AG>U>DS>>>R
		0.3128	0.001	CO>H>GR
	250 m radius	0.0001	0.012	G>DW>DH>AG=DS>WH>IG>U>R=CW>CS>S
		0.4776	0.001	CO>H>GR

By contrast, for both values of the smoothing factor and grid cell size, and the three grid positions, results indicate that there are differences in the habitat selection of Sika deer between Hartland (Table 4.1) and Studland (Table 4.3). The main difference between Hartland and Studland was that at Hartland, Sika deer showed a positive selection for grazing resources (in particular improved grassland), while at Studland, Sika deer positively selected cover (in particular deciduous woodland). The same opposite habitat selection can be observed between Arne and Hartland as it has been shown in the previous chapter and results presented in Table 4.1 and 4.4).

DISCUSSION

Comparison of habitat associations derived from ground counts and radio tracking

At Hartland, both ground counts and radio tracking indicated that Sika deer selected areas with a higher content of grazing resources, in particular improved grassland. Both methods also identified wet heath as a habitat that was not preferred by Sika deer, although the radio tracking method also identified dry heath as a non-preferred habitat. Therefore, the results suggest that radio tracking and ground counts provide similar habitat associations for Sika deer. Both methods were able to identify the habitats most and least preferred by Sika deer. These tests were required because the subsequent comparison of habitat associations between Arne (radio tracking data) and Studland (ground count data) would not have been possible if, within a site, different habitat associations were derived from the different methods.

There were a number of reasons to suspect that the methods would not have yielded similar habitat associations. Radio tracking and ground counts will vary in the accuracy with which they estimate habitat use, the time scale over which habitat use is estimated and any bias in the estimation of habitat use. There were two main field differences between ground counts and radio tracking. The first difference was that ground counts represented a “snap shot” of the location of deer at a particular point in time, while radio tracking obtained locations at different times of the day and during different seasons. The second difference was that the detectability of animals by ground counts depended on the visibility due to the weather and habitat characteristics such as the density of cover. These differences may have introduced bias into the ground counts, as observing animals is dependant upon habitat, time, season, the animal’s behaviour and observer skills (Kernohan *et al.*, 2001, Franco *et al.*, 2007). By contrast, radio tracking offers the potential of sampling without bias (Kenward, 2001a), which is the reason for its common use in the study of deer ecology. However, in most cases, the goal of analyses of habitat associations based on tracked animals is to make statistical inferences to a population of animals that the radio tracked sample is assumed to represent (Erickson *et al.*, 2001). Therefore, in reality, population-level habitat associations derived from radio tracking may not be free of bias if the tracked individuals do not comprise a representative sample of the population as a whole (i.e. they are a random sample).

Apart from potential differences in the field data between radio tracking and ground counts that would have yielded different habitat associations, a potential problem with the method of deriving habitat associations from ground counts was, as expected from previous studies (e.g. Jelinski and Wu, 1996, Fortin, 1999, Plante *et al.*, 2004, Wu, 2004), that some variation in derived habitat associations were found for different smoothing factors and the size and placement of the larger grid. However, by using two different values of the grid size and smoothing factor and three different values for the starting grid location, it was possible to identify associations that occurred consistently and disregard those that occurred for just one or two combinations of smoothing factor, grid size or starting location. Another potential problem was the choice of the smoothing factor as it was based on data from female Sika deer. In some cases the size of deer home ranges do not differ among sexes (e.g. Inglis *et al.*, 1979, Tierson *et al.*, 1985) but in other cases larger home ranges have been described for male deer in comparison to females (e.g. Catt and Staines, 1987, Borkowski and Pudelko, 2007, Kamler *et al.*, 2008, Vila *et al.*, 2008). It is possible that the movement abilities attributed to Sika deer in the present work underestimate the movement of male deer. However, despite these anticipated differences and potential disadvantages of the method derived from ground counts, similar habitat associations were derived from radio tracking and ground count data. Therefore, any differences in habitat association between the tree study areas are likely to result from differences between the sites rather than differences in data collection and analysis methods.

Results of the comparison of habitat associations derived from radio tracking and ground count data, which enable the comparison of habitat associations between Arne and Studland, might also yield information that has implications for management. The potential use of ground counts to study the habitat associations of deer would be of interest to those managers with limited conservation budgets. Radio tracking has proved to be useful in the study of the relationship between habitat availability, landscape structure, disturbance and animal distribution (e.g. Mladenoff *et al.*, 1995, Ferreras, 2001 or Chapter 3 of this thesis, among many others). However, radio tracking is labour intensive and might be expensive (Franco *et al.*, 2007). Unlike radio tracking, having local people visually tracking wildlife is not dependent upon expensive equipment and might have a conservation value related to increased public awareness (Attum *et al.*, 2008).

Comparison of the habitat associations of Sika deer across areas with similar and different landscape structure

A key assumption of many conservation management practises that is rarely tested, is that organisms exhibit the same patterns of selection across different region/s of interest (Whittingham *et al.*, 2007). The potential consistency of habitat relationships across regions is an important conservation question (McAlpine *et al.*, 2008). Still, the potential transferability of predictive species distribution models has not received enough attention (McAlpine *et al.*, 2008). The present study has compared habitat associations across different areas as they can be used to predict the impacts of deer over a wider scale only if (at least) habitat associations are consistent in similar landscapes.

Arne and Studland are characterized by a landscape where pastures are limited, fragmented and interspersed between patches of cover and heath. By contrast, the landscape of Hartland is characterized by abundant and adjacent pastures that are mostly isolated from heath by patches of cover. The similarity in landscape structure (i.e. availability and distribution of key resources) and deer habitat selection at Arne and Studland supports the hypothesis that Sika deer habitat selection will be similar in areas of similar landscape structure.

There are few studies that have explored transferability in the habitat and resources associations among different areas or regions with contrasting results. Vanreusel *et al.* (2007) found high levels of transferability in distribution models based on habitat resources for two butterflies between adjacent areas within the same ecoregion. However, the Vanreusel *et al.* (2007) study was conducted, like the present study, in areas that shared similar climate, general topography and vegetation types. By contrast, McAlpine *et al.* (2008) found regional differences in habitat associations of koalas in Australia. Whittingham *et al.* (2007) concluded that farmland-bird habitat associations were generally not transferable across regions. Likewise, Bamford *et al.* (2009) after evaluating the transferability of a model to predict vulture nest occurrence based on variables such as food availability, human disturbance and nesting trees, concluded that models of species distribution are not transferable between regions. Those differences in the transferability of distribution models based on habitat resources suggest that the assumption of similar

habitat associations between different areas, even with similar landscapes, needs to be tested prior to predictive models being developed. The present study is only an initial step towards developing a predictive model for the distribution and abundance of Sika deer, and has only addressed the consistency in habitat associations across different areas within a relatively small region. However, the results of the present research suggest that models to predict Sika deer distribution based on habitat associations at the landscape scale are only valid between areas with similar landscape structure.

The reason for the consistency between areas with similar landscape structure (suggested by the results presented in Chapter 3, that are supported by the present study) is that in the landscapes in which good quality food resources are limited and fragmented, Sika deer require cover to access pastures safely and therefore place their home ranges in areas with a higher content of cover than the surrounding landscape. Cover is important to ungulates for reducing the risk of predation (Mysterud and Ostbye, 1999). If human visitors are perceived as a source of predation risk, as indicated by previous research on different animal species (e.g. Miller *et al.*, 2001, Papouchis *et al.*, 2001, Frid and Dill, 2002, Fernández-Juricic and Schroeder, 2003, Stankowich, 2008), selecting areas with more surrounding cover, and with some cover between pasture areas, allows Sika deer to switch between feeding areas that might become “safer” during the day or night while avoiding perceived risk in the form of human disturbance. The opposite situation (and consequently the behaviour of Sika deer) was found in landscapes with different landscape structure, where high quality pastures were abundant, forming large patches with adjacent cover. In this contrasting landscape, pastures seemed to become more important than cover for Sika deer as a higher content of pastures was found within their home ranges than in the surrounding landscape.

The knowledge acquired in the present research suggesting consistency in the habitat associations of Sika deer between areas with similar landscape structure could be used in the development of an empirical model to predict the distribution and abundance of Sika deer. However, in agreement with Bamford *et al.* (2009) models to inform management decisions in regions (even in areas) other than those used for model development should be considered with caution. Further work should aim to better predict how local and regional landscape characteristics affect the spatial distribution of Sika deer and use that information to guide the co-management of Sika deer and conservation areas.

CHAPTER 5: SIKA DEER IMPACTS ON PLANT AND ANIMAL COMMUNITIES OF LOWLAND HEATH

ABSTRACT

Few studies have focused on the impacts of wild grazers on lowland heath communities. This research aimed to investigate the response of plant and animal communities of dry and wet lowland heath to the different levels in the local density of an invasive ungulate, Sika deer (*Cervus nippon*), and to identify the level of local density of Sika deer at which lowland heath might show evidence of decline in quality. A loss of quality is defined as any of the following: a decrease in the abundance of key species, an increase in the establishment of opportunistic species or a detrimental change in the vegetation structure and community composition as a result of grazing and physical damage by trampling. Plant communities of dry heath seemed to be more sensitive than those of wet heath in their response, showing a threshold level in the local density of deer which there is a significant decline in the quality of lowland heaths. No consistent pattern was found in the response of the diversity (richness and evenness) of surface-active invertebrates across taxonomic levels and/or heath types to higher local density of deer, higher plant diversity or to differences in the vegetation structure. However, the community composition of surface-active invertebrates differed significantly with the level of local density of Sika deer; this was detected as a direct relationship on wet heath and indirectly through an effect on vegetation community composition (but not structure) on dry heath. In conclusion, this research has found a different response between dry and wet heath in the response of plant and animal communities to local densities of Sika deer and has also identified the existence of a threshold in the local density of Sika deer above which dry lowland heath showed signs of decline.

INTRODUCTION

The effects on plants of trampling and grazing by herbivores, frequently considered together (Hobbs and Huenneke, 1992), have been related to changes in species diversity (Hobbs and Huenneke, 1992, Fleischner, 1994, Olf and Ritchie, 1998), density, biomass and vegetation stratification (Fleischner, 1994). Large herbivores also have direct and indirect effects on the animal communities of the areas they occupy (e.g. Putman, 1986, Feber *et al.*, 2001, Flowerdew and Ellwood, 2001, Rooney and Waller, 2003, Dennis *et al.*, 2008). Some direct effects on invertebrates are linked to their presence (e.g. some species are dependant on animal dung, Lake *et al.*, 2001), whilst indirect effects can be related to modifications of the availability of suitable microhabitats for invertebrates, as has been shown after the introduction of non native herbivores in new areas (e.g. Allombert *et al.*, 2005b, Martin *et al.*, 2010). These effects on the communities of invertebrates are reflected up the food chain as invertebrates are an important food resource for other animals such as reptiles and bird species (e.g. Fuller and Gough, 1999, Allombert *et al.*, 2005a, Dennis *et al.*, 2008)

Lowland and upland heaths (moorlands) are ecosystems subjected to grazing and browsing by wild and domestic herbivores across Western Europe (Gimingham, 1972). At the beginning of the 21st century heathland had been reduced to less than 10% of its former European extent (Rose *et al.*, 2000). Nowadays lowland and upland heaths are international priority conservation areas (i.e. Habitats Directive 92/43/EEC). There are fundamental differences in the ecology of upland and lowland heaths in terms of the composition of plant and animal species (Gimingham *et al.*, 1979). Extensive work has been dedicated to exploring the effects of large herbivores (mostly Red deer *Cervus elaphus* and domestic ungulates) on upland heath plant communities (e.g. Welch, 1984a, Welch, 1984b, Welch, 1985, Clarke *et al.*, 1995b, Hester and Baillie, 1998) and associated animal communities (Bell *et al.*, 2001, Hartley *et al.*, 2003, Jauregui *et al.*, 2008). In contrast, little research has focused on the impacts of grazing on lowland heath vegetation. Existing research has focused on domestic herbivores and has investigated the response of lowland heaths to particular density of herbivores in order to predict the stocking rates at which the heath starts to decline (reviewed in Lake *et al.*, 2001).

Studies on upland heaths have shown that the decline of heather cover under heavy grazing by deer is often patchily distributed and the severity of damage depends on the location of other vegetation and food resources (Clarke *et al.*, 1995b, Hester and Baillie, 1998). Therefore an approach based on measuring deer population density might not account for differences in the spatial variation of local densities of deer and the subsequent effects on plant communities of lowland heath. Moreover, there is a lack of knowledge of how the level of local density of deer might affect the plant communities of lowland heath and whether there is a threshold level of local density of deer above which there is a significant decline in the quality of lowland heaths. Also, lowland heaths are not only important because of their rare plant communities, they also support breeding populations of invertebrates, rare reptiles, amphibians and birds that have long been a UK Biodiversity Action Plan priority (DOE, 1995). An evaluation into the effects of deer on the communities of plant and animals of lowland heath would be of great interest for managers and conservationists of lowland heath areas where deer are overabundant. Within a broader context, the need for improved monitoring and experimental analysis of grazing effects by herbivores on lowland heath has been highlighted by Newton *et al.* (2009).

Large populations of Sika deer occur in parts of the south of England (Swanson and Putman, 2009) and they overlap in distribution with habitat mosaics including lowland heath, grassland and woodland. This link between Sika deer distribution and lowland heath suggest that Sika deer, through grazing and trampling might be affecting vegetation structure, plant community composition and abundance of plant species. Also Sika deer might be affecting directly or indirectly (through the modification of vegetation structure, fragmentation and/or diversity of plant species) the composition and abundance of animal communities in lowland heath habitats. This research aimed to investigate the response of plant and animal communities of lowland heath to different levels of local density of Sika deer and identify the level of the local density of Sika deer at which lowland heath might show signs of decline in terms of quality. A loss of quality is defined as any of the following: a decrease in the abundance of key species, an increase in the establishment of opportunistic species or a detrimental change in the modification of the vegetation structure and community composition as a result of grazing and physical damage by trampling.

This research had two specific objectives. The first objective was to examine the relationship between the level of the local density of Sika deer and the plant communities of lowland heath (in terms of vegetation structural parameters, abundance and diversity of plant species and plant community composition). The second objective was to examine the direct and indirect relationship between the extent of the usage of heath by Sika deer and the communities of surface-active invertebrates associated to lowland heath (in terms of diversity and community composition). Surface-active invertebrates were selected as the animal group to be investigated because they have been identified as a potential food resource for some of the rare species of lowland heath (e.g. Joly and Giacoma, 1992, Gvozdkik and Boukal, 1998, Siirro *et al.*, 2001, Buchanan *et al.*, 2006). Also, due to their large number and high species turnover along environmental gradients, invertebrates are likely to be useful bio-indicators of grazing impacts (Garcia *et al.*, 2009).

RESULTS

Estimation of the local density of Sika deer on lowland heath

Field observations of deer covered the majority of the heath patches and surrounding open habitats in both study areas. The estimated error in locating deer was 31.85 ± 4.11 m S.E. for both study areas combined (29.20 ± 5.79 m S.E. for Arne, 34.50 ± 4.25 m S.E. for Hartland).

Totals of 12,048 deer (in 684 groups) and 4,363 deer (in 236 groups) were observed at Arne and Hartland respectively during the survey period (Figure 5.1), therefore some deer were counted more than once. Annual results showed a much higher number of deer observed at Arne ($N = 12,048$) than at Hartland ($N = 4,359$) of which 2,015 and 425 deer were observed on heath patches at Arne and Hartland respectively.

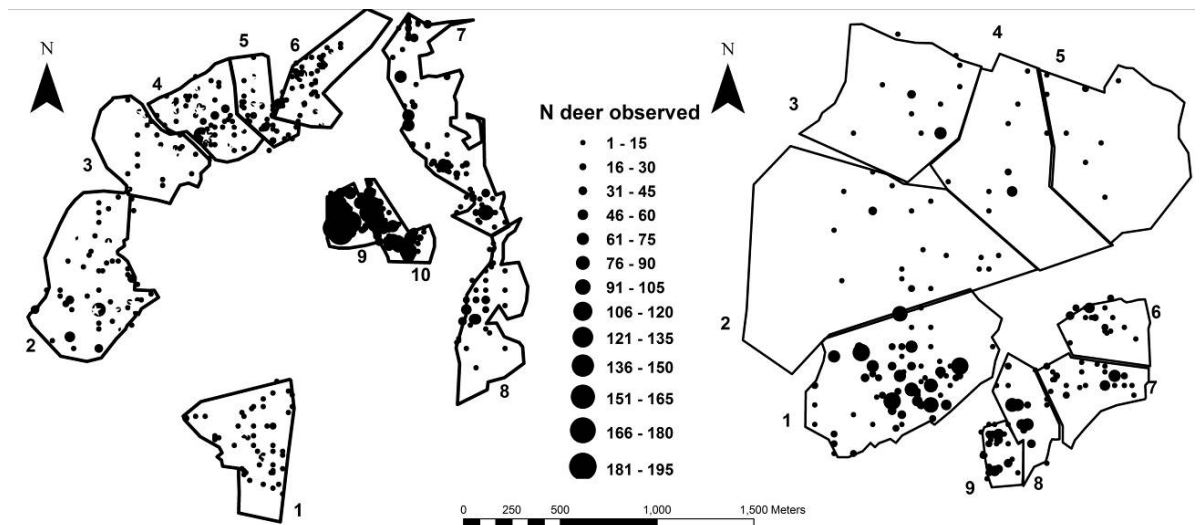


Figure 5.1: Observations of Sika deer at Arne and Hartland. Polygons represent the areas surveyed in both study areas. Polygons 1 to 6 at Arne (left) and 2 to 5 at Hartland (right) represent areas of lowland heath; Polygons 7 to 10 at Arne and 1, 6 to 9 represent open habitats (i.e. saltmarshes and improved grassland).

Home range analysis (see Section 2.3.1) obtained an average annual value of the standard deviation (σ) of the kernels distribution fitted to the locations of each of the female Sika deer home range of 289.50 m at Arne and 306.86 m at Hartland. A spatial interpolation of

the spatial variation in local density of Sika deer based on the deer observations was obtained (Figure 5.2) for each of the study areas as described in Section 2.7.

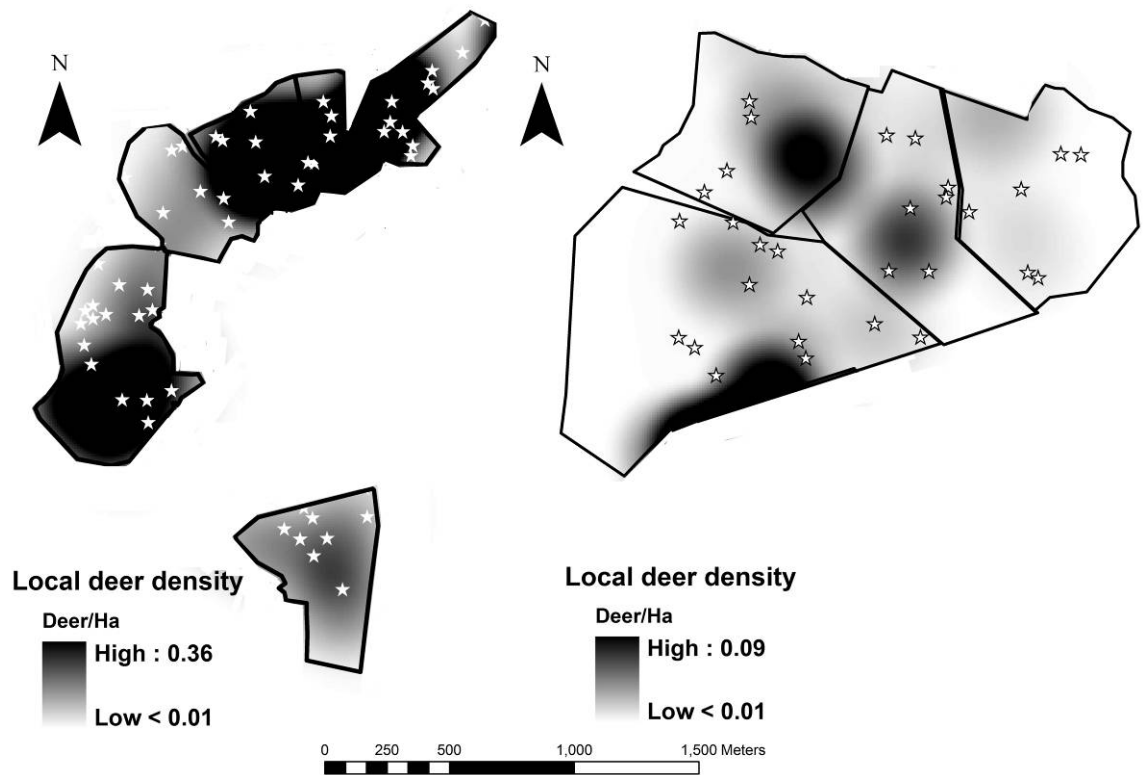


Figure 5.2: Spatial interpolation of the local density of Sika deer at Arne (left) and Hartland (right). Polygons represent areas of lowland heath. Darker shading indicates higher level of habitat usage. Stars represent the impact plots where vegetation and animal communities were surveyed.

Relationship between vegetation and local density of Sika deer

Significant relationships were found between the vegetation structural parameters and the local density of Sika deer on dry heath (Figure 5.3, Table 5.1). Plots located in areas with higher local density of by deer also contained more area trampled (Figure 5.3a), more bare ground (Figure 5.3b) and dead vegetation (Figure 5.3c) but contained less vegetation volume (Figure 5.3d).

When the local density of deer was plotted against the four vegetation structural parameters, the output suggested a threshold in the local density of Sika deer under which a relationship with these four vegetation indices was not evident from the graph. Therefore a

piecewise linear regression model was applied (Figure 5.3, solid line). Results from this second analysis showed a stronger relationship (i.e. higher R^2) between the four variables and the local density of deer on dry heath. The thresholds for the level of heath usage by Sika deer were between 0.04 and 0.08 deer/ha. This indicates that the four vegetation parameters were only significantly related to the level of heath usage by deer when the level of heath usage by Sika deer was above the threshold. On wet heath, only a weak marginally significant ($R^2 = 0.09$, $P < 0.05$) negative linear relationships was found between the percentage of dead vegetation and the local density of Sika deer (Table 5.1).

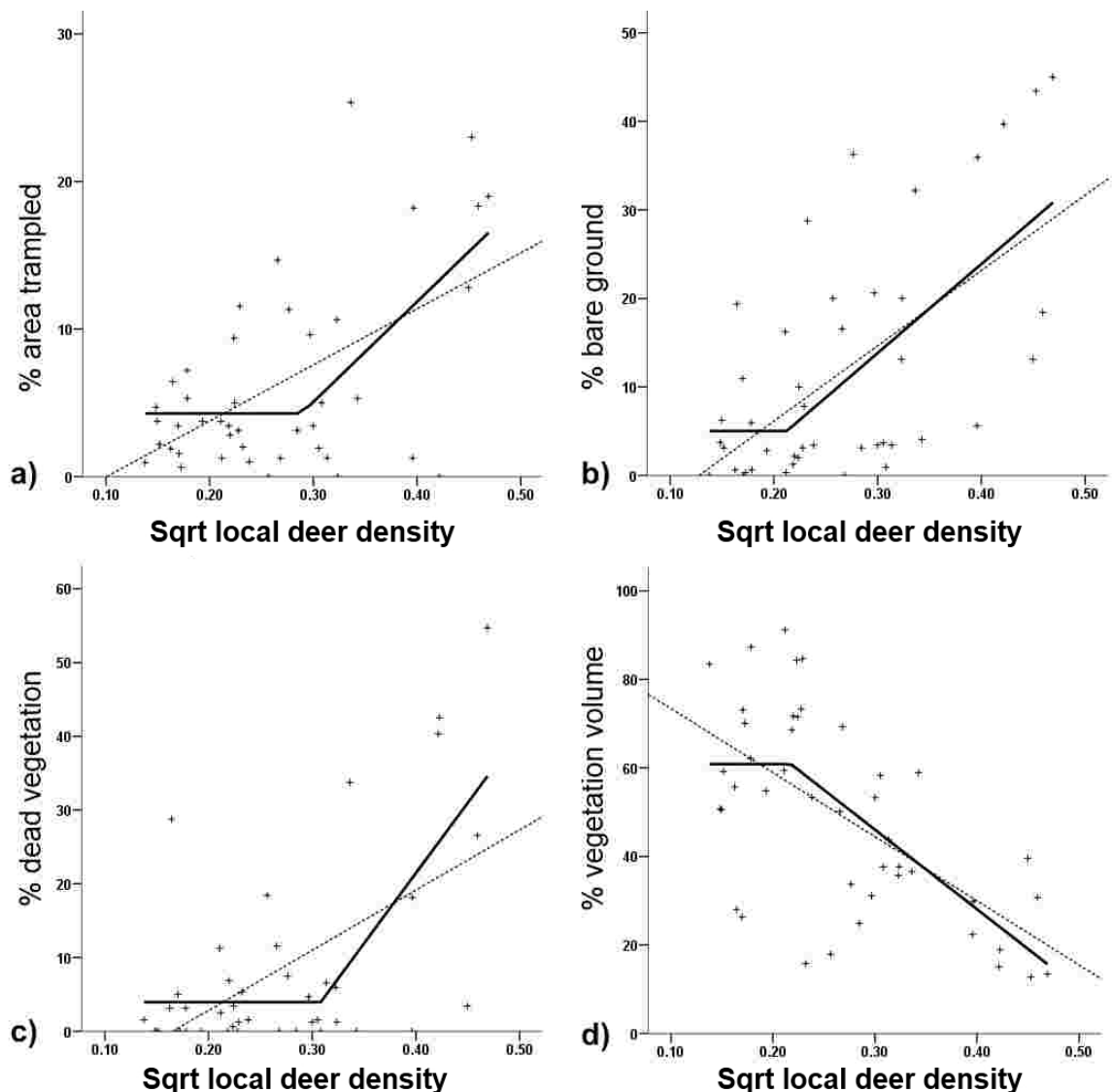


Figure 5.3: Effect of the local density of Sika deer (deer/ha) on the vegetation structural parameters of dry heath. a) area trampled, b) bare ground, c) dead vegetation d) volume. The dotted line indicates the linear regression line and the solid line indicates the piecewise non linear regression line.

Table 5.1: Relationship between four vegetation structural parameters (area trampled, bare ground, volume and dead vegetation) and the level of local density of Sika deer on dry and wet heath. Piecewise non linear regression model was applied when scatter-plot representations of the data suggested the existence of a deer threshold of the local density of deer below which there was not a non-evident effect of habitat usage by deer. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

	Vegetation index	Linear regression R^2	Piecewise regression R^2	Threshold
Dry Heath	Area trampled	0.30 ***	0.33 ***	0.08 deer/ha
	Bare ground	0.37 ***	0.38 ***	0.04 deer/ha
	Volume	0.38***	0.42 ***	0.05 deer/ha
	Dead vegetation	0.33 **	0.45 ***	0.09 deer/ha
Wet Heath	Area trampled	0.04		
	Bare ground	<0.01		
	Volume	0.09		
	Dead vegetation	0.09*		

Results from the vegetation survey showed a clear dominance of *C. vulgaris* and *E. cinerea* in the communities of lowland dry heath in both study areas (Table 5.2). On wet heath *E. tetralix*, *M. caerulea* and *C. vulgaris* were the most abundant species in Arne, whilst in Hartland *M. caerulea* was the most abundant species followed by *E. ciliaris*, which was the most abundant ericoid in the area. In both areas *E. cinerea* and *Rynchospora alba* were locally abundant on dry and wet heath respectively.

Table 5.2: Abundance of different plant species on dry and wet lowland heath. Values correspond to the estimated percentage of each species at the sites. + indicates a value lower than 0.1.

	ARNE		HARTLAND	
	Dry Heath	Wet Heath	Dry Heath	Wet Heath
	Median (min/max)	Median (min/max)	Median (min/max)	Median (min/max)
Bryophytes	3.3 (0/52.8)	1.8 (0/38.1)	0 (0/1.9)	0.9 (0/23.7)
<i>C. epithymum</i>	0 (0/+)	0 (0/2.5)	0 (0/0)	0 (0/0)
<i>C. vulgaris</i>	61.9 (12.8/96.9)	12.7 (0/47.5)	77.5 (60.6/91.2)	10.6 (0/43.4)
<i>E. ciliaris</i>	0 (0/1.9)	0 (0/26.2)	0 (0/7.2)	18.7 (3.7/42.5)
<i>E. cinerea</i>	3.6 (0/31.9)	0 (0/19.1)	8.6 (0/21.2)	0 (0/11.2)
<i>E. tetralix</i>	0 (0/45.9)	32.6 (0/65.9)	+ (0/15.3)	13.8 (1.1/36.9)
<i>I. aquifolium</i>	0 (0/+)	0 (0/0)	0 (0/0)	0 (0/0)
Lichens	+ (0/11.6)	+ (0/15.0)	0 (0/2.6)	+ (0/5.6)
<i>M. caerulea</i>	0 (0/55.9)	18.9 (0/81.0)	1.9 (0/7.5)	32.5 (7.2/67.5)
<i>M. gale</i>	0 (0/0.01)	0 (0/15.0)	0 (0/0.6)	0 (0/3.7)
<i>P. aquilinum</i>	0.5 (0/10.3)	0 (0/42.2)	0 (0/2.6)	0 (0/0)
<i>P. sylvestris</i>	+ (0/4.5)	0 (0/2.2)	0 (0/0)	0 (0/+)
<i>R. alba</i>	0 (0/0)	0 (0/11.6)	0 (0/0)	0.3 (0/20.6)
<i>R. fruticosa</i>	0 (0/+)	0 (0/+)	0 (0/0)	0 (0/0.3)
<i>U. europaeus</i>	0 (0/40.6)	0 (0/8.1)	+ (0/5.9)	0 (0/1.3)
<i>U. gallii</i>	0 (0/0)	0 (0/6.2)	0 (0/0)	0 (0/0.3)
<i>U. minor</i>	0 (0/1.6)	0 (0/8.7)	3.6 (0/9.1)	0 (0/2.2)

When abundances from the three most abundant species on heath (*C. vulgaris*, *E. tetralix* and *M. caerulea*) were related to the local density of Sika deer, the abundance of *C. vulgaris* on dry heath and *M. caerulea* on wet heath showed negative significant relationships with the level of local density of Sika deer ($R^2 = -0.37$, $P < 0.001$ for *C. vulgaris*, $R^2 = -0.40$, $P < 0.001$ for *M. caerulea*, Figure 5.4). The abundance of *E. tetralix* was positively related to the local density of Sika deer on wet heath although it was a weak relationship ($R^2 = 0.10$, $P = 0.04$). Piecewise linear regression models improved the negative relationship between *C. vulgaris* and local density of deer ($R^2 = 0.404$, $P < 0.001$), obtaining a threshold of 0.05 deer/ha under which no level of local density was significantly related to abundance of *C. vulgaris*.

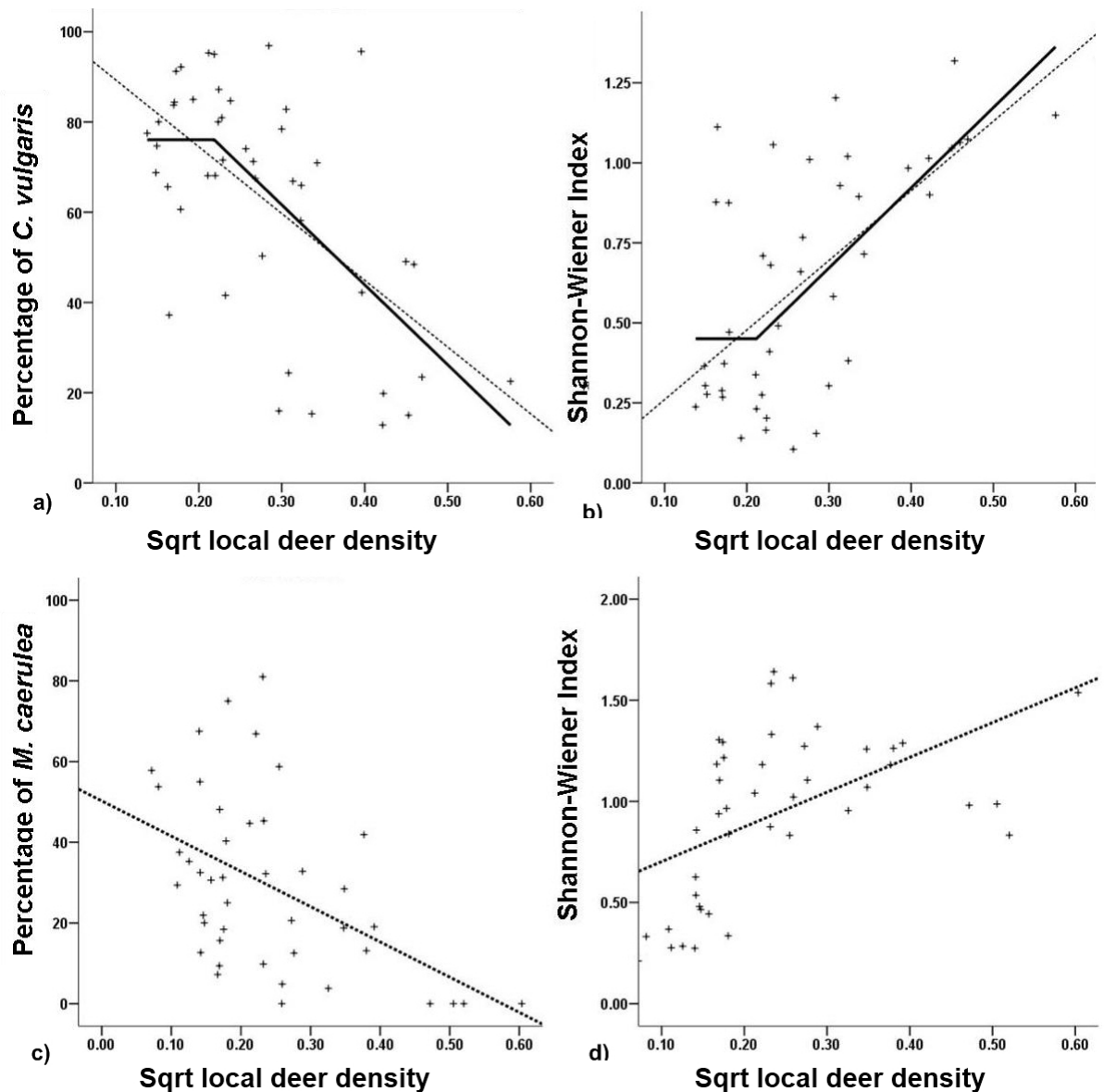


Figure 5.4: Effect of the local density of deer (deer/ha) on the percentage of *C. vulgaris* and the diversity of plant community of dry heath (top) and on the percentage of *M. caerulea* and the diversity of plant community of wet heath (bottom). The dotted line indicates the linear regression line and the solid line indicates the piecewise non linear regression line.

Higher plant diversity was related to higher local density of Sika deer on dry heath ($R^2 = 0.40$, $P < 0.001$, Figure 5.4b) and wet heath ($R^2 = 0.27$, $P < 0.001$, Figure 5.4d). On dry heath, piecewise regression identified a threshold of 0.045 deer/ha (although somewhat less obvious from the plotted data) under which plant diversity was not significantly related to the local density of deer on dry heath ($R^2 = 0.42$, $P < 0.001$).

The multivariate community analysis conducted by DCA on dry heath was able to explain 43% (first axis) and 30% (second axis) of the variation in the ordination of sites by the composition of their plant communities (Figure 5.5). The ordination of sites showed a low number of outliers (two/three) while the rest of sites were uniformly distributed around the centre of the axis. The resultant ordination showed two contrasting groups of species at each extreme of the first axis of the DCA representation with a group of species linked to wet heaths (*E. ciliaris*, *E. tetralix* and *M. caerulea*) at one extreme (left) while *Pinus sylvestris*, *Pteridium aquilinum* and bryophytes was at the other extreme of the axis (right). The second axis also showed two contrasting groups with both species of *Ulex* (*Ulex minor* and *Ulex europaeus*) at one extreme (top) and lichens and bryophytes at the other extreme of the axis (bottom). There was a significant relationship between the sites ordination on dry heath and the local density of Sika deer. The first axis of DCA was positively correlated to the local density of Sika deer ($r = 0.47$, $P = 0.002$), whilst the second axis was negatively correlated ($r = -0.48$, $P = 0.001$). This ordination indicates that sites with plant communities that had higher abundance of bryophytes, lichens, *P. sylvestris* and *P. aquilinum* are found in areas of higher level of habitat usage by Sika deer while sites with higher abundance of *U. minor*, *U. europaeus*, *E. ciliaris*, *E. tetralix* and *M. caerulea* are related to lower levels of habitat usage by Sika deer.

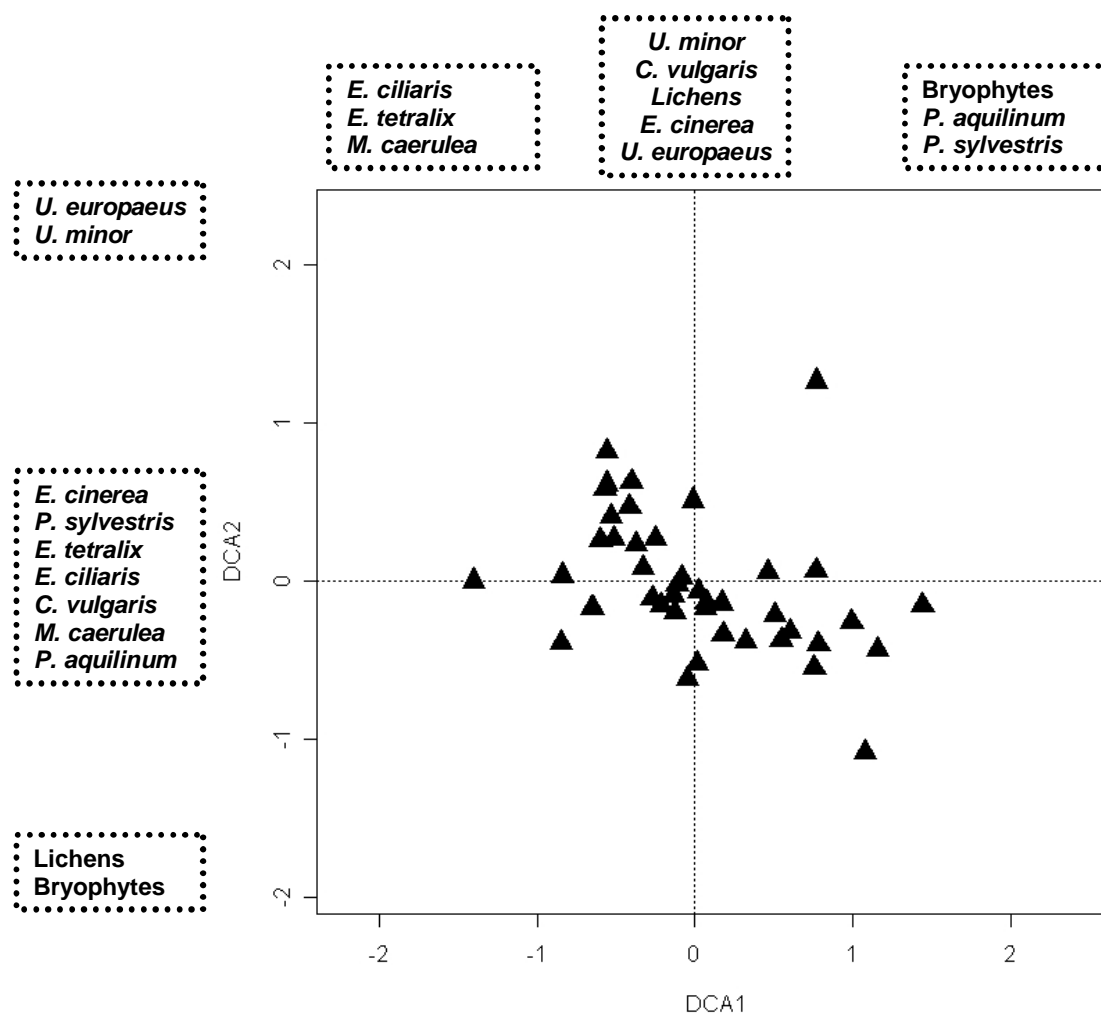


Figure 5.5: Ordinations of sites on dry heath by the composition of their plant community using detrended correspondence analysis. Triangles refer to individual sites. Species are allocated by the position on their ordination along each axis depending on their abundance.

DCA conducted on wet heath only explained 35% (first axis) and 31% (second axis) of the variation in the ordination of sites by the composition of their plant communities (Figure 5.6). Sites were located around the centre of the ordination representation and showed only two/three outliers. On wet heath the extremes of the first axis of DCA were represented by sites with abundant bryophytes, *Myrica gale* and *P. aquilinum* at the left extreme and sites with abundant *E. cinerea* and *U. minor* at the right extreme. The second axis had sites with higher abundance of *P. aquilinum* at the top extreme and sites with higher abundance of bryophytes and *Rhynchospora alba* at the bottom extreme. No significant relationship was found on wet heath between the sites ordination and the local density of Sika deer ($r = 0.10$ for first axis, $r = 0.03$ for second axis).

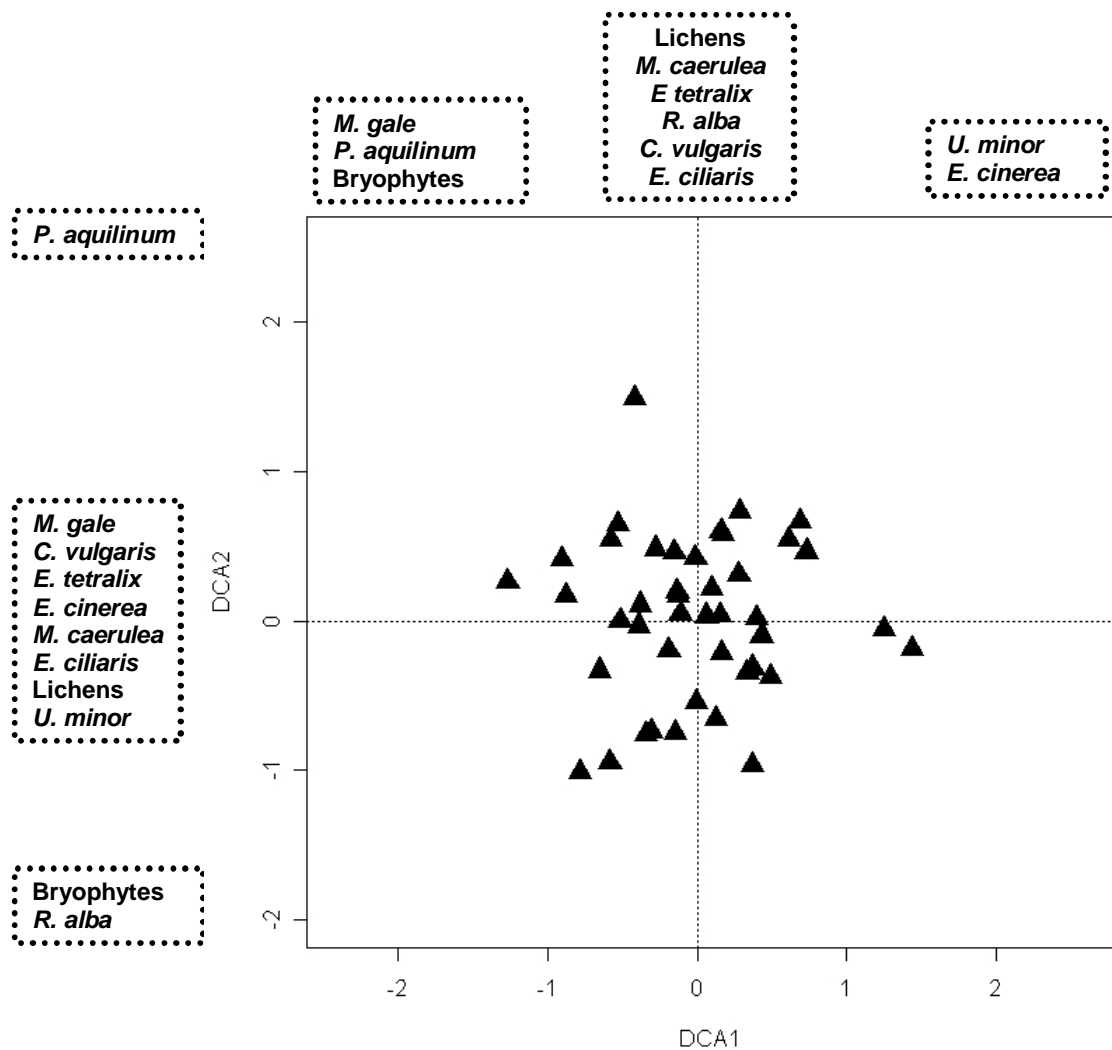


Figure 5.6: Ordinations of sites on wet heath by the composition of their plant community using detrended correspondence analysis. Triangles refer to individual sites. Species are allocated by the position on their ordination along each axis depending on their abundance.

**Relationship between surface-active invertebrates and local density of Sika deer:
direct effects**

First level of analysis: orders

Results from the survey of surface-active invertebrates resulted in the identification of 42,269 specimens from 18 orders (Table 5.3). Chilopoda, Dermaptera, Diplura, Orthoptera, Pseudoscorpionidea and Odonata were found in very low numbers. Araneae, Collembola, Diptera and Hymenoptera were consistently abundant across study areas and heath types.

Table 5.3: Abundance of different orders of surface-active invertebrates of dry and wet lowland heath. Values correspond to the number of individuals collected.

	ARNE		HARTLAND	
	Dry Heath	Wet Heath	Dry Heath	Wet Heath
ORDER	Median	Median	Median	Median
	(min/max)	(min/max)	(min/max)	(min/max)
Acari	48.0 (3/194)	21.0 (6/119)	24.8 (4/70)	11.1 (5/63)
Araneae	66.9 (36/197)	87.8 (36/324)	58.3 (33/100)	102.0 (53/147)
Chilopoda	0.0(0/2)	0.0 (0/1)	0.8 (0/8)	0.0 (0/8)
Coleoptera	16.5 (3/33)	11.6 (4/47)	48.9 (2/128)	21.8 (7/113)
Collembola	61.3 (25/184)	33.4 (6/96)	38.0 (16/99)	27.0 (8/54)
Dermoptera	0.0 (0/1)	0.0 (0/1)	0.0 (0/1)	0.0 (0/0)
Diplopoda	0.8 (0/3)	0.0 (0/1)	1.0 (0/13)	0.0 (0/2)
Diplura	0.0 (0/3)	0.0 (0/0)	0.0 (0/3)	0.0 (0/3)
Diptera	53.6 (27/669)	44.0 (24/245)	49.5 (27/132)	33.8 (11/141)
Hemiptera	9.4 (2/19)	9.2 (2/16)	8.3 (2/14)	7.5 (1/16)
Hymenoptera	56.6 (21/1275)	94.9 (17/1485)	40.5 (14/122)	55.7 (20/297)
Isopoda	20.6 (1 /870)	8.4 (1/199)	12.0 (0/123)	8.3 (0/63)
Lepidoptera	1.5 (0/4)	0.4 (0/8)	3.0 (0/6)	0.8 (0/5)
Odonata	0.0 (0/0)	0.0 (0/11)	0.0 (0/0)	0.0 (0/0)
Opiliones	12.1 (2/25)	6.8 (1/20)	21.4 (7/72)	3.4 (0/12)
Orthoptera	0.0 (0/2)	0.8 (0/8)	0.0(0/1)	0.9 (0/7)
Pseudoscorpionida	0.0 (0/1)	0.0 (0/0)	0.0 (0/1)	0.0 (0/3)
Thysanura	5.1 (0/12)	2.3 (0/9)	0.8 (0/9)	2.3 (0/8)

No significant relationship was found between the diversity (measured by Shannon-Weiner index) of the community of surface-active invertebrates and the local density of Sika deer in areas of lowland heath either for communities of dry heath ($R^2 = 0.03$, $P = 0.27$), or for the communities of wet heath ($R^2 = 0.02$, $P = 0.38$).

The two first axes of the DCA for the ordination of dry heath sites by the composition of their communities of surface-active invertebrates were able to explain only 18 and 13% percent of variability (eigenvalues of 0.18 and 0.13 for the first and second axis respectively, Figure 5.7). The ordination of sites showed the majority of them concentrated around the centre of the ordination axis, which shows that their communities of

invertebrates were very similar. The resultant ordination also showed six orders located on the extremes of the first ordination axis (Orthoptera, Hymenoptera, Isopoda, Diplopoda, Chilopoda and Pseudoscorpionidea) while the rest of orders occupied central positions. The second axis of the DCA had Isopoda, Diplopoda and Chilopoda at the top extreme while Hymenoptera and Pseudoscorpionidea were located on the bottom extreme. No significant relationship was found between the ordinations of sites on dry heath by the composition of their communities of surface-active invertebrates and the local density of Sika deer. Neither of the axes of the community ordination was significantly correlated to the local density of Sika deer (first axis $r = -0.27$, $P = 0.11$; second axis $r = -0.26$, $P = 0.11$).

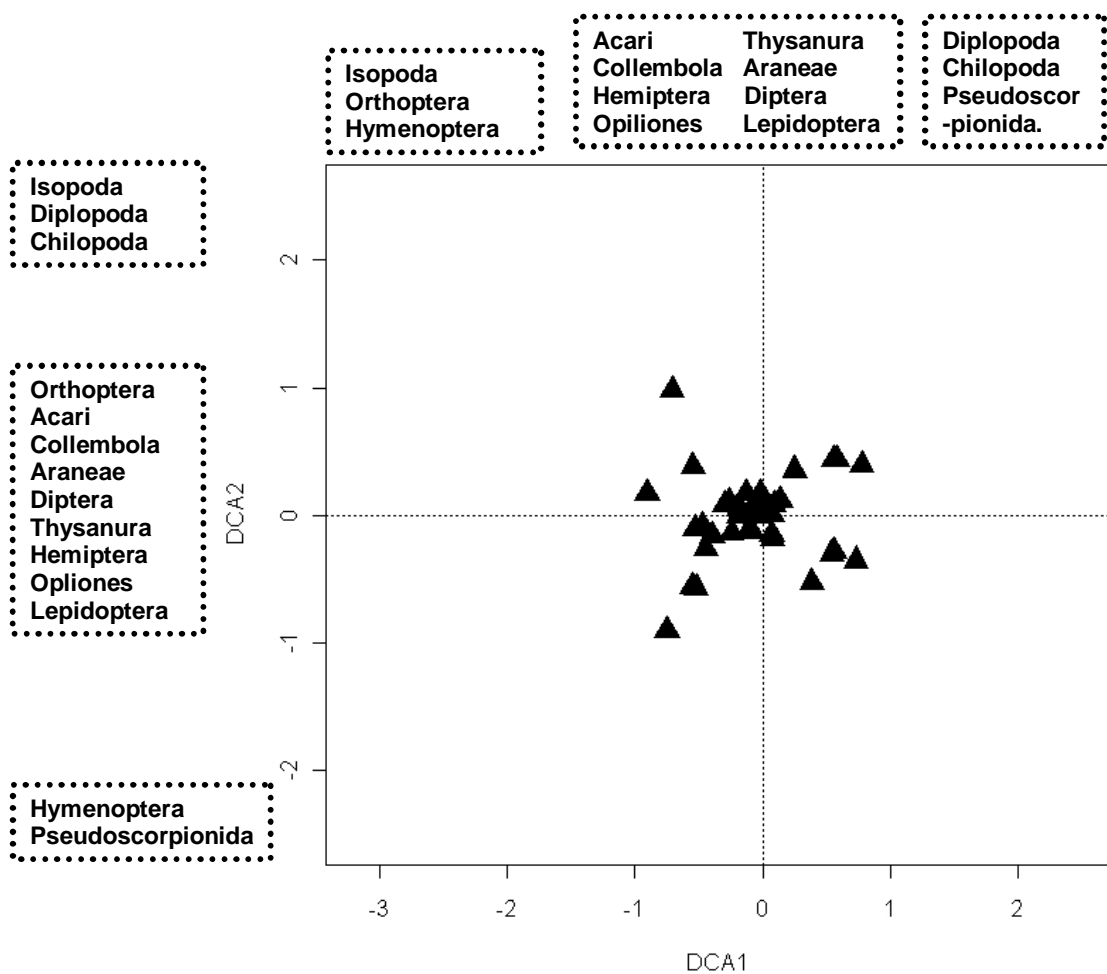


Figure 5.7: Ordinations of sites on dry heath by the composition of their communities of surface-active invertebrates using detrended correspondence analysis. Triangles refer to individual sites. Species are allocated by the position on their ordination along each axis depending on their abundance.

DCA on wet heath was able to explain only 18% (first axis) and 10% (second axis) of the variability in the ordination of the sites by their community of surface-active invertebrates (Figure 5.8). Sites distribution along the two axes was more even than on dry heath, showing that sites on wet heath had more different composition of surface-active invertebrates. On wet heath the distribution of orders on the two axes was also more uniform than on dry heath, with Isopoda, Orthoptera, Diplopoda and Pseudoscorpionidea located at the extremes of the first axis of DCA. The second axis of the community ordination of surface-active invertebrates had Hymenoptera and Lepidoptera at one of the extremes (top) while Orthoptera, Opiliones and Araneae were at the opposite extreme (bottom). A significant negative relationship was found between the first axis of the ordination of sites on wet heath by the composition of their communities of surface-active invertebrates and local density of Sika deer ($r = -0.38$, $P = 0.03$). Sites with communities of invertebrates with higher abundance of Isopoda and Orthoptera were found in areas with higher local density of Sika deer, while sites with more abundant Pseudoscorpionidae and Diplopoda were related to lower local density of Sika deer. However, the second axis of the DCA for the ordination of sites by their surface-active invertebrate communities was not significantly correlated to the local density of Sika deer ($r = -0.09$, $P = 0.61$).

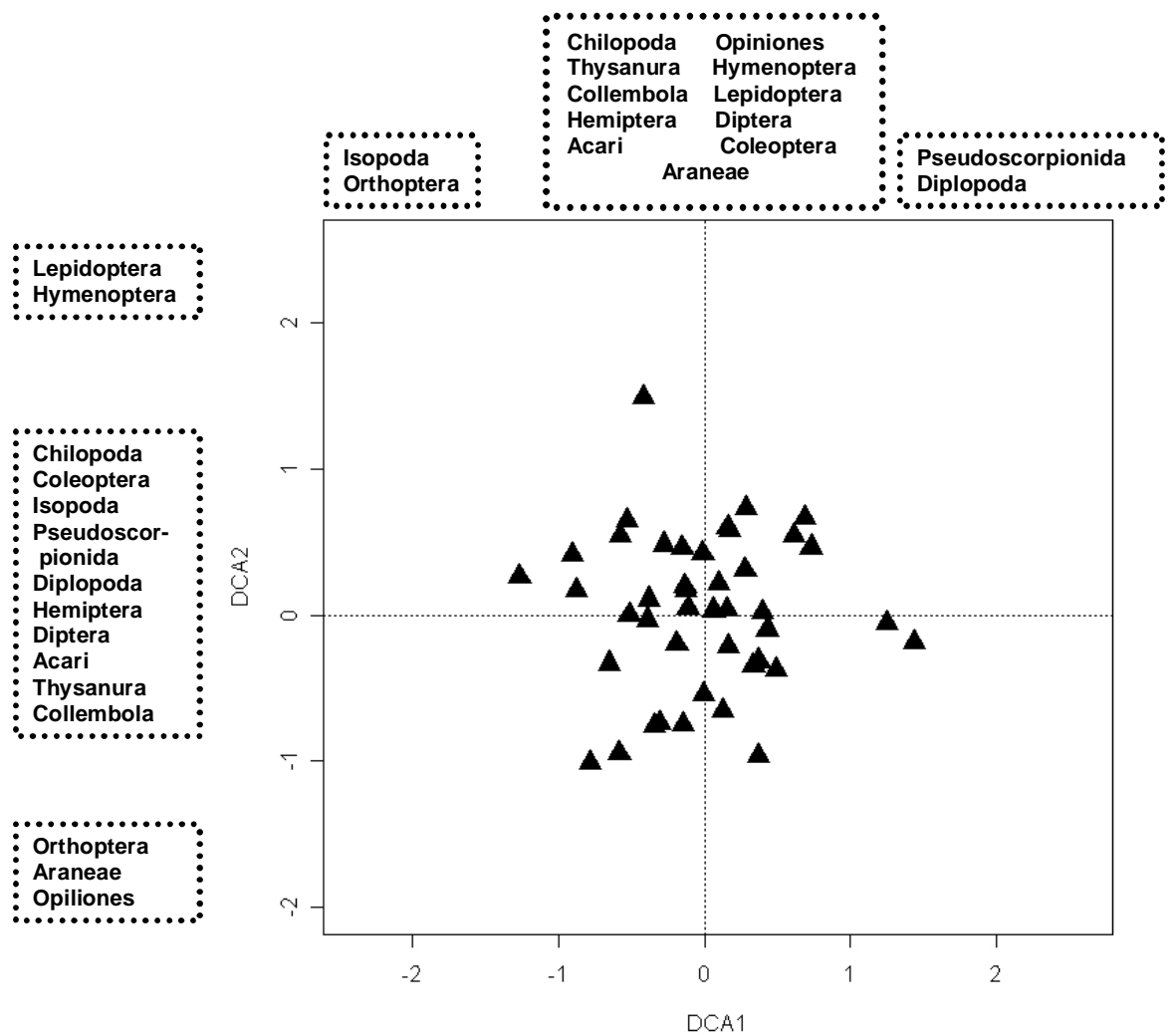


Figure 5.8: Ordinations of sites on wet heath by the composition of their communities of surface-active invertebrates using detrended correspondence analysis. Triangles refer to individual sites. Species are allocated by the position on their ordination along each axis depending on their abundance.

Second level of analysis: families of beetles

Results from the survey of families of beetles resulted in the identification of 2,635 specimens from 17 families (Table 5.4). Carabidae and Staphylinidae were the most common families across heath types and study areas, while Dytiscidae and Catopidae were rarely found.

The Shannon diversity index of the families of the beetle community had a positive weak relationship with the local density of Sika deer on dry heath ($R^2 = 0.28$, $P < 0.01$). No

relationship was found on wet heath between the diversity of the beetle community and the local density of Sika deer ($R^2 = 0.07$, $P = 0.15$)

Table 5.4: Abundance of different families of beetles of dry and wet lowland heath. Values correspond to the number of individuals collected.

FAMILY	ARNE		HARTLAND	
	Dry Heath Median (min/max)	Wet Heath Median (min/max)	Dry Heath Median (min/max)	Wet Heath Median (min/max)
Byrrhidae	0 (0/2)	0 (0/1)	0 (0/0)	0 (0/0)
Leptodiridae	0 (0/2)	0 (0/0)	0 (0/0)	0 (0/0)
Curculionidae	1.7 (0/6)	0.8 (0/4)	1.5 (0/2)	0.7 (0/3)
Elateridae	0 (0/2)	0 (0/6)	0 (0/3)	0 (0/1)
Cantharidae	0 (0/0)	0 (0/2)	0 (0/0)	0 (0/0)
Carabidae	2.6 (0/6)	4.0 (1/16)	5.1 (1/27)	9 (2/62)
Staphylinidae	4.5 (0/23)	7.1 (0/28)	36 (0/87)	7.7 (1/48)
Silphidae	0 (0/3)	0 (0/8)	0 (0/12)	0 (0/1)
Cryptophagidae	0.9 (0/27)	0 (0/6)	6 (0/52)	0.7 (0/10)
Coccinellidae	0 (0/0)	0 (0/0)	0 (0/1)	0 (0/1)
Chrysomelidae	0 (0/2)	0 (0/1)	0 (0/0)	0 (0/1)
Scarabaeidae	0.9 (0/6)	0 (0/4)	0 (0/2)	0 (0/1)
Dytiscidae	0 (0/0)	0 (0/1)	0 (0/0)	0 (0/0)
Catopidae	0 (0/0)	0 (0/0)	0 (0/1)	0 (0/0)
Hydrophilidae	0 (0/0)	0 (0/1)	0 (0/0)	0 (0/1)
Tenebrionidae	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/2)
Histeridae	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/2)

The ordination of sites on dry heath by the composition of their families of beetles using DCA was able to explain 48% (first axis) and 32% (second axis) of the variation in the relative position along the two axes (Figure 5.9). On dry heath, the resultant ordination showed a quite even distribution of families along the two axes of the DCA, with few outliers, although Catopidae and Byrrhidae were at each extreme of the first axis and Chrysomelida and Elateridae at each of the extremes of the second axis. This suggests that those four families were only locally abundant. No significant relationship was found between the ordination of sites by their composition of families of beetles on dry heath and the local density of Sika deer (first axis: $r = -0.06$, $P = 0.73$; second axis: $r = -0.29$, $P = 0.08$).

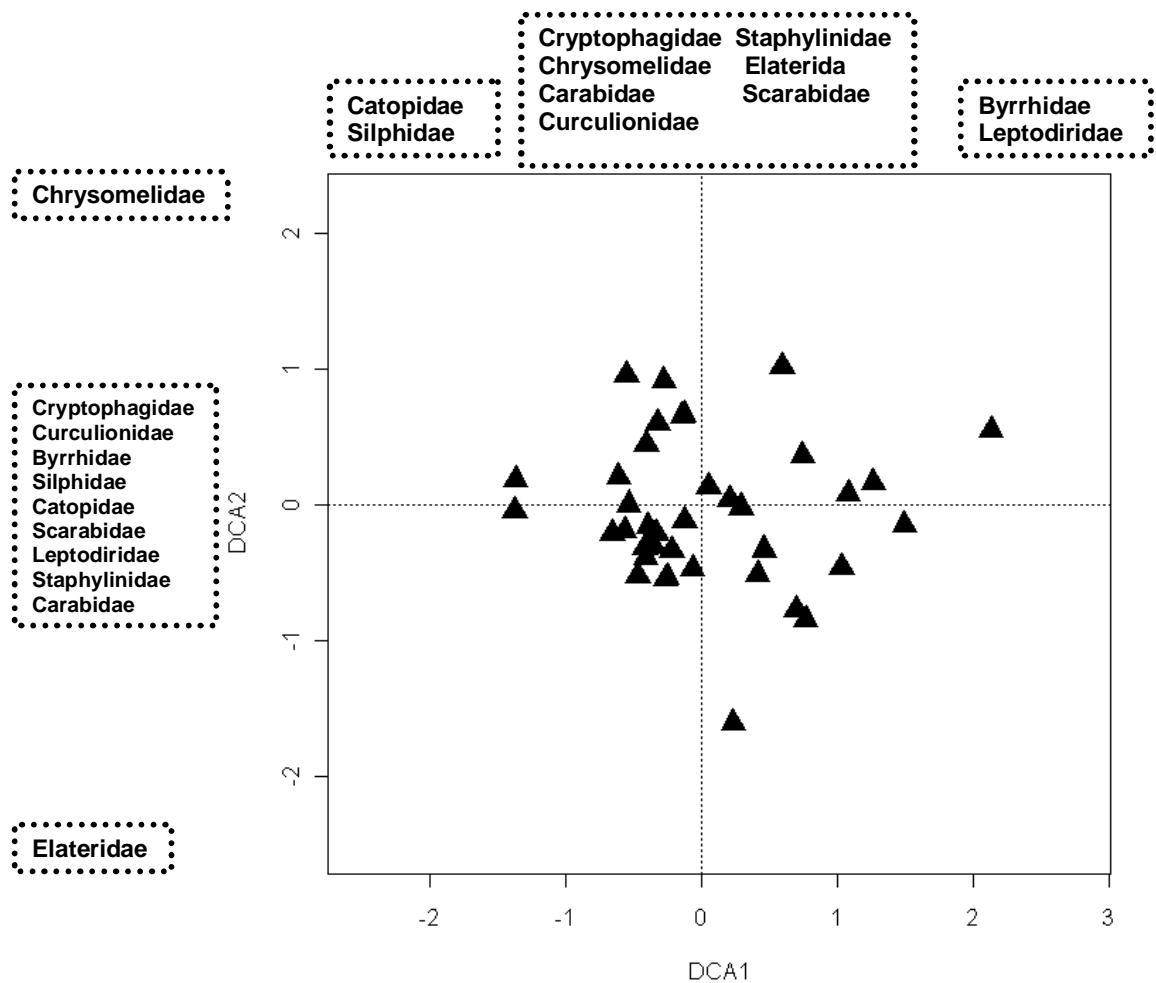


Figure 5.9: Ordinations of sites on dry heath by the composition of their communities of families of beetles using detrended correspondence analysis. Triangles refer to individual sites. Species are allocated by the position on their ordination along each axis depending on their abundance.

On wet heath the ordination of sites by their composition of families of beetles was able to explain 46% (first axis) and 40% (second axis) of variance (Figure 5.10). The distribution of the sites along both axes showed a cluster of sites around the centre with similar composition of families of beetles, although Tenebrionidae, Hydrophilidae and Histeridae were located at the left extreme and Dystiscidae at the right extreme of the first axis of the ordination. Four families, Tenebrionidae and Cryptophagidae at the top and Silphidae and Hydrophilidae at the bottom, were represented as outliers at each of the extremes of the second axis of the sites ordination. The first axis of the ordination of sites by their composition of families of beetles was not correlated to the local density of Sika deer on wet heath ($r < -0.01$, $P = 0.99$). However, the second axis of the DCA was significantly correlated to the local density of Sika deer ($r = -0.39$, $P = 0.02$), which means that sites

with communities of beetles with higher abundance of the families Hydrophilidae and Silphidae were found in areas more used by deer while sites with higher abundances of Tenebrionidae and Cryptophagidae were related to lower local density of deer.

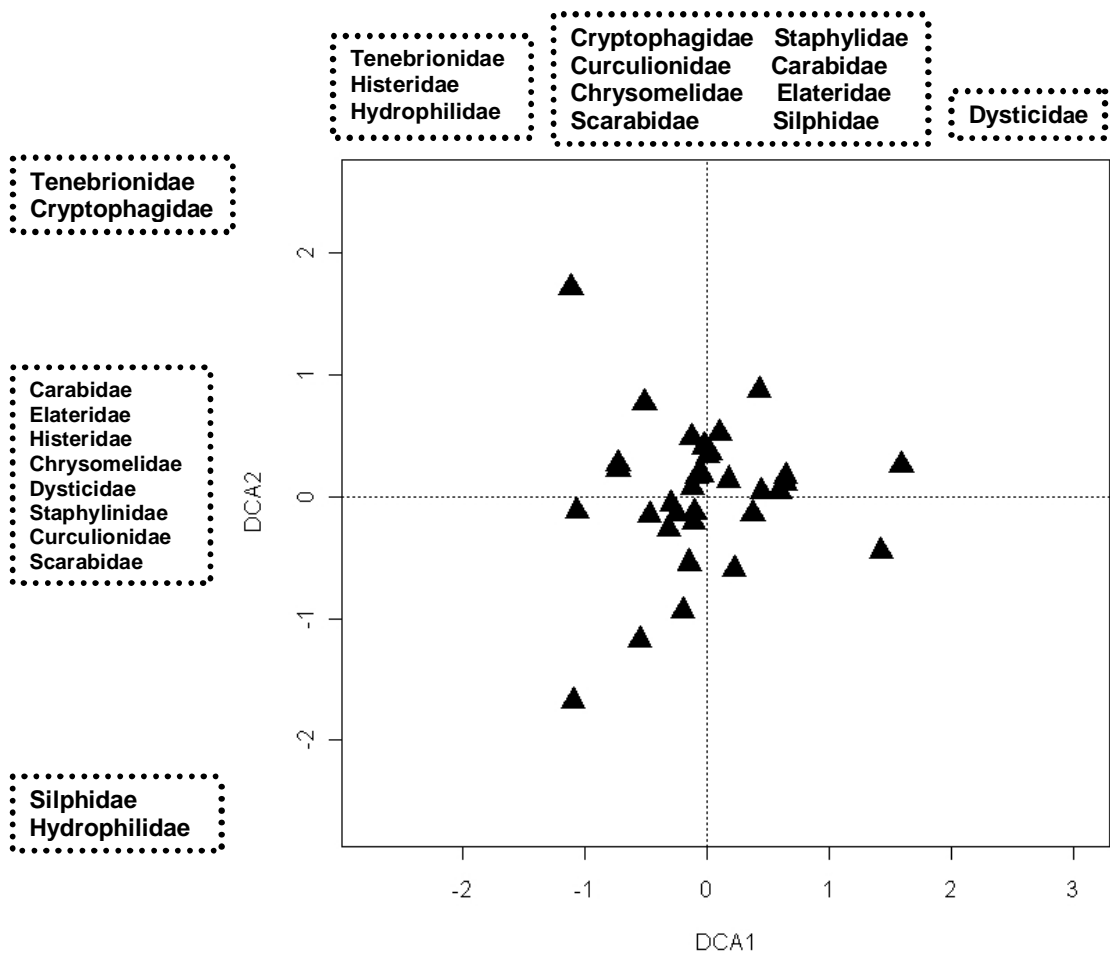


Figure 5.10: Ordinations of sites on wet heath by the composition of their communities of families of beetles using detrended correspondence analysis. Triangles refer to individual sites. Species are allocated by the position on their ordination along each axis depending on their abundance.

Third level of analysis: species of Carabidae

Results from the survey of species of Carabidae resulted in the identification of 250 specimens from 19 species (Table 5.5). Only five species (*Abax parallelepipedus*, *Amara aenea*, *Carabus arvensis*, *Carabus problematicus* and *Poecilus cupreus*) were found across both study areas and both heath types. *C. arvensis* was found locally abundant at Arne, while *P. cupreus* was also found locally abundant on wet heath in both study areas.

Table 5.5: Abundance of different species of Carabidae of dry and wet heath. Values correspond to the number of individuals collected.

SPECIES	ARNE		HARTLAND	
	Dry Heath	Wet Heath	Dry Heath	Wet Heath
	Median (min/max)	Median (min/max)	Median (min/max)	Median (min/max)
<i>Abax parallelepipedus</i>	+ (0/1)	+ (0/2)	+ (0/5)	+ (0/1)
<i>Agonum ericeti</i>	0	+ (0/2)	0	+ (0/8)
<i>Amara aenea</i>	+ (0/1)	+ (0/5)	+ (0/1)	+ (0/2)
<i>Calathus fucipes</i>	0	0	+ (0/2)	0
<i>Carabus arvensis</i>	+ (0/16)	1 (0/10)	+ (0/1)	+ (0/4)
<i>Carabus nemoralis</i>	+ (0/1)	0	+ (0/1)	0
<i>Carabus nitens</i>	0	+ (0/1)	0	0
<i>Carabus problematicus</i>	+ (0/2)	+ (0/2)	+ (0/2)	+ (0/1)
<i>Carabus violaceus</i>	+ (0/2)	0	+ (0/2)	0
<i>Harpalus rubripes</i>	0	0	+ (0/1)	+ (0/1)
<i>Harpalus rufipes</i>	+ (0/1)	+ (0/1)	+ (0/1)	0
<i>Leistus fulvibarbis</i>	0	0	0	+ (0/1)
<i>Nebria brevicollis</i>	+ (0/1)	+ (0/1)	0	+ (0/3)
<i>Notiophilus biguttatus</i>	0	0	+ (0/1)	0
<i>Poecilus cupreus</i>	+ (0/1)	+ (0/7)	+ (0/2)	+ (0/7)
<i>Pterostichus madidus</i>	+ (0/2)	0	+ (0/1)	0
<i>Pterostichus melamarius</i>	0	0	+ (0/1)	0
<i>Prerostichus minor</i>	0	+ (0/1)	0	+ (0/2)
<i>Pterostichus versicolor</i>	0	+ (0/1)	0	+ (0/2)

No significant relationship was found between the diversity (measured by Shannon-Weiner index) of the community of species of Carabidae and the local density of Sika deer, either for communities of dry heath ($R^2 < 0.01$, $P = 0.78$) or for the communities of wet heath ($R^2 = 0.02$, $P = 0.45$).

Due to the small sample size of specimens of Carabids on dry heath (N=78) it was not possible to conduct an ordination analyses of sites by their composition of the community of Carabidae. On wet heath the ordination of sites by their composition of their Carabids community was able to explain 72% (first axis) and 55% (second axis) of variance (Figure 5.11). The distribution of sites along both axes, that allowed differencing each one of the sites, suggested differences in the composition of their communities of Carabidae. Two

species of Carabidae (*C. problematicus* and *Prerostichus minor*) occurred at each extreme of the first axis whilst *Harpalus rufipes* and *Agonum ericeti* occurred at each extreme of the second axis of the ordination of sites by their communities of Carabidae.

A significant but weak negative relationship was found between the first axis of the ordination of sites by their composition of the Carabidae community and the local density of deer in wet heath ($r = -0.43, P = 0.01$). Sites with the presence of *C. problematicus* and *A. parallelepipedus* were found in areas of higher local density of deer, while sites with presence of *Nebria brevicollis* and *P. minor* were found in areas of lower local density of deer. However, the weakness of this relationship might indicate that, in fact, this result might be a statistical artefact. No relationship was found between the second axis of the sites ordination by their communities of Carabidae and the local density of deer.

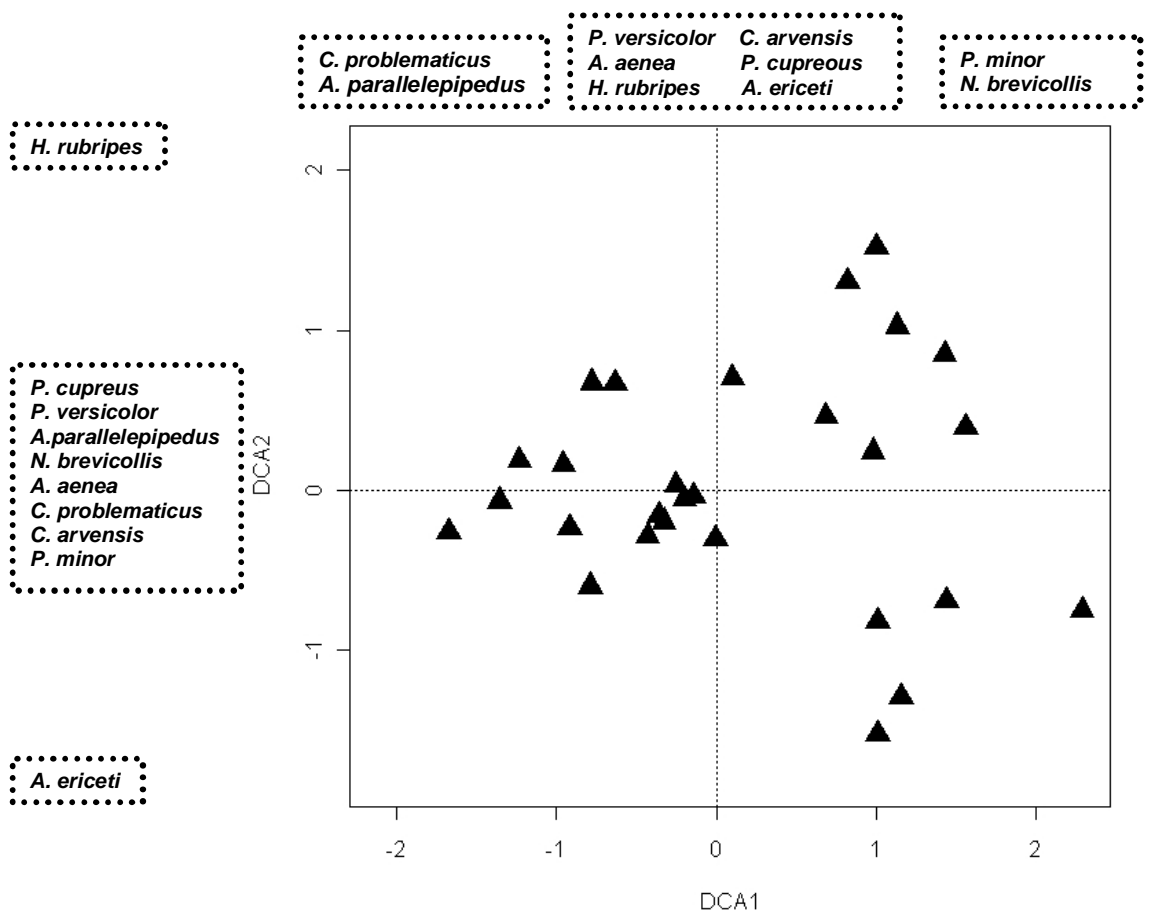


Figure 5.11: Ordinations of sites on wet heath by the composition of their communities of species of Carabids using detrended correspondence analysis. Triangles refer to individual sites. Species are allocated by the position on their ordination along each axis depending on their abundance.

Relationship between surface-active invertebrates and vegetation: indirect effects of Sika deer activity

First level of analysis: orders

The diversity of the communities of surface-active invertebrates showed no significant relationship with total vegetation volume, percentage of bare ground and the diversity of plant communities in any of the heath types (Table 5.6). However, the composition of the community of surface-active invertebrates at each site on dry heath was significantly related to the composition of their plant community. The first axis of the DCA for the sites ordinated by their communities of invertebrates was significantly correlated to both the first axis of the DCA by their plant community ($r = -0.46$, $P < 0.01$) and the second axis of the DCA ($r = 0.73$, $P < 0.001$) for the sites ordinated by their plant community. These relationships, the first one negative and the second positive, indicated that sites with higher abundance of Pseudoscorpionidea and Diplopoda were found in areas with higher abundance of *U. minor*, *U. europaeus*, *E. ciliaris*, *E. tetralix* and *M. caerulea*, while sites with more abundant Orthoptera and Hymenoptera were found in areas with more abundance of bryophytes. Lichens, *P. sylvestris* and *P. aquilinum*.

Table 5.6: Relationship between the diversity of orders of surface-active invertebrates and vegetation volume, bare ground and diversity of plant communities of lowland heath.

Dry heath			Wet heath		
Volume	Bare Ground	Plant diversity	Volume	Bare Ground	Plant diversity
$R^2 = -0.006$	$R^2 = 0.008$	$R^2 = -0.002$	$R^2 = -0.003$	$R^2 = -0.008$	$R^2 = -0.031$

No significant relationship was found on wet heath between the ordination of sites by their communities of surface-active invertebrates and the ordination of sites by the composition of their plant communities for any of the possible combinations between the DCA axes.

Second level of analysis: families of beetles

The diversity of families of beetles showed no significant relationship to the total vegetation volume and percentage of bare ground in any of the heath types (Table 5.7).

However, a significant positive relationship was found on dry heath between the diversity of the families of the beetles community and the diversity of plant communities. This indicates that sites with higher diversity of plant species also had higher diversity of families of beetles.

Table 5.7: Relationship between the diversity of families of beetles and total vegetation volume, bare ground and diversity of plant communities of lowland heath. (***) indicate the only significant relationship ($P < 0.001$).

Dry heath			Wet heath		
Volume	Bare Ground	Plant diversity	Volume	Bare Ground	Plant diversity
$R^2 = 0.10$	$R^2 = 0.10$	$R^2 = 0.30***$	$R^2 < 0.01$	$R^2 < 0.01$	$R^2 = 0.01$

The composition of the community of families of beetles at each site on dry heath was significantly related to the composition of their plant community. The first axis of the DCA for the ordination of sites by the composition of their communities of superfamilies of beetles was significantly correlated to both the first axis ($r = 0.35$, $P = 0.04$) and the second axis ($r = -0.48$, $P = 0.001$) of the DCA for the samples ordinated by their plant community. These relationships, which the first one was positive and the second negative, indicated that sites with more abundant Byrrhidae and Leptodiridae were found in areas with more abundance of bryophytes. Lichens, *P. sylvestris* and *P. aquilinum*, while sites with more abundant Catopidae and Silphidae were found in areas with higher abundance of *U. minor*, *U. europaeus*, *E. ciliaris*, *E. tetralix* and *M. caerulea*.

No significant relationship was found between the ordination of sites by their communities of families of beetles and the ordination of sites by their plant communities on wet heath for any of the possible combinations between the DCA axis.

Third level of analysis: species of Carabidae

The diversity of species of Carabids showed no significant relationship to the total vegetation volume and percentage of bare ground in any of the heath types (Table 5.8). However a significant weak positive relationship was found on wet heath between the diversity of the species of Carabids and the diversity of plant communities. This indicates that sites with higher diversity of plant species also had higher diversity of Carabids.

Table 5.8: Relationship between the diversity of species of Carabids and total vegetation volume, bare ground and diversity of plant communities of lowland heath and. (*) indicate the only significant relationship ($P < 0.05$).

Dry heath			Wet heath		
Volume	Bare Ground	Plant diversity	Volume	Bare Ground	Plant diversity
$R^2 = 0.04$	$R^2 = 0.03$	$R^2 = 0.03$	$R^2 = 0.04$	$R^2 < 0.01$	$R^2 = 0.18^*$

No significant relationship was found between the ordination of sites by their communities of species of Carabids and the ordination of sites by their plant communities on dry or wet heath for any of the possible combinations between the DCA axes.

DISCUSSION

This study has investigated the impacts of Sika deer on plant and animal communities of lowland heath for a range of density of Sika deer actually utilising the heath of 0.005 to 0.36 deer/ha. However, this range of densities needs to be understood as a scoring of locations by their local population of Sika deer instead of an exact measurement of the true density, which was not directly determined in this study. Differences in the response of plant or animal communities of lowland heath at higher levels of local density of deer cannot be predicted based on extrapolation of results from this thesis. Also it should be noted that although 0.36 deer/ha was the maximum interpolated density of deer actually utilising the heath, overall population densities of Sika deer in the study area can differ (e.g. 1.18 deer/ha at Arne and 0.26 deer/ha at Hartland).

This research has demonstrated a relationship between the local density of Sika deer and differences in the plant communities of lowland heath. In particular, higher local density of deer was related to the decline in quality of dry heath plant communities. This decline in quality was chiefly due to a reduction in total vegetation volume, particularly the abundance of *C. vulgaris*; an increase in bare ground, dead vegetation and disturbed areas; the establishment of opportunistic species (i.e. *P. aquilinum*, lichens and bryophytes). By contrast, on wet lowland heath, only a decrease in the abundance of *M. caerulea* and an enhancement of plant diversity were related to higher local density of Sika deer.

No consistent pattern was found in the response of the diversity of surface-active invertebrates across taxonomic levels to higher local density of deer on either of the heath types by deer. However, the community composition of surface-active invertebrates differed significantly with levels of local density of Sika deer. This was detected as a direct relationship on wet heath and indirectly through an effect on vegetation community composition (but not structure) on dry heath. No consistent pattern was found across taxonomic levels or heath types in the response of the diversity or composition of communities of surface-active invertebrates to differences in the vegetation structure (i.e. vegetation volume and percentage of bare ground) or plant diversity.

Effects of Sika deer on plant communities of lowland heath

There is a clear trend in the results showing that the combined effects of grazing and trampling by Sika deer were related to the structural configuration of plant communities of dry lowland heath despite the limited percentage of the variability in the vegetation structural parameters that was explained by the predictive models (33-46%). Higher local density of Sika deer on patches of dry heath was related to i) a decrease in the vegetation volume, ii) an increase in the area physically damaged by deer, iii) an increase in the amount of dead vegetation and iv) the creation of patches of bare ground. The consumption of *C. vulgaris*, a main component of Sika deer diet in the same geographic region of this research (Mann and Putman, 1989a) might have also contributed to the decline of the communities of dry lowland heath (i.e. decline in plant volume). Results of this research concur with previous work conducted across heaths of Western Europe demonstrating that heathland declines under heavy grazing (e.g. Bakker *et al.*, 1983, Welch, 1984a, Welch, 1984b, Welch and Scott, 1995, Palmer, 1997, Hester and Baillie, 1998, Hester *et al.*, 1999). Particularly on lowland heath, it has been proved that heavy grazing by sheep, cattle and rabbits leads to a decrease in cover and an increase in bare ground (Bullock and Pakeman, 1997).

Sika deer activity modifies the plant community composition of dry lowland heath. A decrease in cover and increase in bare ground related to higher local density of deer might have allowed other species and groups, such as *P. aquilinum*, lichens or bryophytes to take advantage of more open heaths and establish locally, as suggested by the community ordination analysis in the present study. *P. aquilinum* has been recognised as an opportunistic and invasive species in heath habitats (Gimingham, 1972, Gimingham, 1992), whilst some lichens such as *Cladonia arbuscula* are able to occupy gaps partially occupied by dead stems in the heather (Gimingham, 1972). With regard to bryophytes, individual species are known to show different responses to grazing (Welch, 1984b) but this study has considered bryophytes as a habitat component for invertebrates rather than as individual species. The establishment of opportunistic species and plant groups, together with the removal of *C. vulgaris* that otherwise would become dominant might have resulted in a higher diversity of vascular plant in areas under higher local densities of Sika deer. An increase in the species diversity of vascular plants related to grazing has also been found

elsewhere in heaths of Western Europe (e.g. Bakker *et al.*, 1983, Heil and de Smith, 2001, Lake, 2002).

The present study has not found higher abundances of grass species related to higher local density of deer that could indicate a shift of dry heath to more open, grass-dominated communities. In upland heath, heavy grazing by sheep and other large herbivores has been shown to result in a reduction in heaths and its replacement by grasses (Welch, 1984b, Welch and Scott, 1995). The same result has been obtained in lowland heath, both in the UK (Bullock and Pakeman, 1997) and the Netherlands (Bakker *et al.*, 1983). The lack of signs of a replacement of heaths by grasses in the present study might be attributed to three different reasons. Firstly, the grazing pressure might not have raised the level at which the decline in heath (i.e. decrease in volume and the opening of patches of bare ground) allows the colonization of grass species. A prime factor controlling the balance between *Calluna* and other species is the dense shade cast by the canopy of the dwarf-shrub if height and spread are not sufficiently affected by grazing (Gimingham, 1972). Secondly, high levels of usage of lowland heath by Sika deer and plant communities of lowland heath might have not interacted long enough to result in a decline of heath that allow the colonization of grass species. Thirdly, the surrounding communities of grass species in the area might not be able to colonize open patches of heath on poor soils. *Agrostis curtisii* is an example of one of the grasses linked to communities of dry heath in the region as part of the *C. vulgaris* - *U. minor* and *U. minor* - *A. curtisii* heath communities (see Elikington *et al.*, 2002 for a complete description of this heath communities classified as H2 and H3 in the National Vegetation Classification). *A. curtisii* and *M. caerulea* were the only grasses recorded by Mitchell *et al.* (1997) in 10 heathlands of the Poole Basin that included Arne. The presence of *A. curtisii* has been recorded in both study areas (in 1984 at Arne and 1994 at Hartland, source: Dorset SSSI Species Records 1952 – 2004, © Natural England). However, this species has not been detected in the present study during the vegetation survey and therefore it might not be abundant in the vicinity of the sampled sites. In fact, Mitchell *et al.* (1997) also failed to detect *A. curtisii* in heathland or successional stages at Arne and Diaz and Moody (2009) found only a very small mean abundance of this species across the site. Only one of the three reasons described above, a combination of them, or other factors might explain why grasses have not increased in abundance in areas that were used more extensively by Sika deer.

Results of this research suggest that there is a threshold in the level of local density of Sika deer above which there is a significant decline in dry lowland heath in terms of a decrease in total vegetation volume, increase in bare ground and a decrease in the abundance of *C. vulgaris*. This is also the threshold in the level of local density of Sika deer at which the diversity of plant species significantly increased. However, results showed a higher threshold in the level of the local density of Sika deer above which the area of vegetation damaged significantly increased. In upland heath, levels of shoots consumption higher than about 40% have been considered likely to result in a decline of cover (Grant *et al.*, 1982), although Palmer (1997) estimated that percentage as too high and suggested a value closer to 20%. A decline in heathland has been also directly linked to stocking rates of herbivores. Welch (1984a) considered that grazing pressures of 2.7 sheep/ha or 0.23 cattle/ha to be the limit above which upland dry heath will change to grassland communities. The present study has found a threshold of 0.04 to 0.09 Sika deer/ha above which dry lowland heath declines. However, results of this research related to the specific level of local density of Sika deer above which dry lowland heath declines need to be considered cautiously. The range of local densities obtained by interpolation needs to be interpreted as a scoring of locations by their local population of Sika deer instead of an exact measurement of the 'true' or 'absolute' density value, which has not been directly obtained in this study. Also, the local density of Sika deer referred to in this study is the local density of Sika deer on patches of dry heath, which can differ from the overall density of deer (i.e. population density) found at higher scales. For instance, at Hartland the population density over the whole area was 0.265 deer/ha) while the range of local densities on patches of heath was 0.01- 0.12 deer/ha; at Arne the overall population density was 1.18 deer/ha while the range of local density on heath was 0.03- 0.37 deer/ha. This difference between the local density of deer on patches of heath and the overall population density of Sika deer within a particular area should be considered when management policies involve controlling levels of deer population to conserve areas of interest (i.e. lowland heath). Intervention on deer populations to conserve a particular area of interest should require an assessment of the deer use of the area and the existent/expected local density.

In contrast to the generally strong evidence highlighting the relationship between plant communities of dry lowland heath and the local density of Sika deer, this research has only found weak marginally significant relationships on wet heath between the local density of Sika deer and the percentage of dead vegetation. Results of this research also showed that

although higher local density of deer was significantly related to a decrease in the abundance of *M. caerulea*, the total vegetation volume was not affected by the extent to which areas of wet heath are used by Sika deer. An important part of the community of lowland wet heath is formed by *M. caerulea*. Grasses are more resistant to grazing processes than dwarf shrubs, such as heather, (Grant and Armstrong, 1993, Stewart and Hester, 1998). Also, *Calluna* may be more damaged by trampling than *Molinia* (Lake *et al.*, 2001). The present research suggests that grazing by Sika deer are able to decrease the abundance of *M. caerulea* and there is some evidence (a weak, but still significant relationship) that this decrease in *Molinia* might allow *E. tetralix* to increase its abundance conserving patches of wet heath that otherwise would be turned into wet heaths dominated by *Molinia*. This depleting effect upon *M. caerulea* that otherwise could become dominant on wet heath seems reflected in an increase in the diversity of plant species. Whether the lack of a significant relationship between vegetation structural parameters and the local density of Sika deer on wet heath might be a result of a higher resistance of other species such as *E. tetralix* or *E. ciliaris* to physical disturbance needs to be addressed by further research.

It is accepted that causality can never be ascribed with certainty from correlation studies and that there is the potential for some circularity in this relationship. However, results of this research and previous research based on enclosure experiments and experiments controlling the density of grazers in which differences in composition and vegetation structure were related to the level of grazing by herbivores (e.g. Hulme *et al.*, 2002, Lake, 2002, Pakeman *et al.*, 2003, Jauregui *et al.*, 2008) suggest that at least some of the correlations found in this thesis between higher density of Sika deer and ecological impacts may be causal. Enclosure plots located on both wet types in one of the study areas (Arne) as a part of a different research have shown visible increase in the volume of *C. vulgaris* and *M. caerulea* after Sika deer had no access to the plots, although detailed data are still being collected.

Effects of Sika deer on animal communities of lowland heath

No strong evidence was found of a pattern across taxonomic levels of surface-active invertebrates in the direct relationship between the diversity of invertebrates and the local density of deer on either of the heath types. The only significant relationship between the diversity of invertebrates and the level of local density of deer was found on dry heath at the level of families of beetles. A heterogeneity of relationships between diversity of invertebrates and grazing pressure depending on the group of ground-dwelling invertebrates considered was also found by Garcia *et al.* (2009) in the Cantabrian upland heaths; the diversity of beetles increased under higher grazing pressure by goats, while the diversity of a family of spiders (i.e. Lycosidae) and Opiliones showed no significant differences under low or high grazing pressure. Moreover the present study has found no significant relationships between the diversity of surface-active invertebrates and vegetation structure. The lack of a pattern found in the present study in the relationship between vegetation structure and/or plant diversity and the diversity of surface-active invertebrates was a surprising result. It has been assumed that large herbivores, by their presence and activities, do contribute positively to invertebrate diversity, mainly by increasing habitat heterogeneity (van Wieren and Bakker, 2008). If grazing pressure increases, however, vegetation structure will be affected, direct competition for food among the invertebrate community might increase and other important micro habitats may disappear, which can result in a decrease in invertebrate diversity (van Wieren and Bakker, 2008). On heaths, such relationships between vegetation structure and invertebrate diversity have been described for different groups of invertebrates including Hemiptera and Coleoptera (e.g. Gardner, 1991, Gardner *et al.*, 1997, Hartley *et al.*, 2003). Finally, little evidence was found of a relationship between the diversity of surface-active invertebrates and plant diversity (i.e. direct relationship with grazing/trampling): only the diversity of families of beetles was related to plant diversity on dry heath, while on wet heath only the diversity of species of Carabidae was related to plant diversity.

Two main reasons may be proposed for the little evidence of direct or indirect effects of local density of deer on the diversity of surface-active invertebrates. The first reason may be that pitfall trapping was not adequate for sampling some groups of invertebrates. Some of the orders found in the samples such as spiders, Dermaptera and Hemiptera are probably better sampled by extracting turves or by vacuum netting (see e.g. Morris and Rispin,

1987). The second reason might be that the pitfall samples were identified at higher taxonomic level than at the species level (apart from the Family Carabidae). As species differ in ecological requirements they may therefore show contrasting responses to different local densities of Sika deer and vegetation parameters. The overall effect at higher taxonomic level might be then reduced because of species effects cancelling one another out (Vries *et al.*, 2007). Therefore, results highlight that an order-based approach to link the effects of grazing and trampling by deer to differences in surface-active invertebrates might not be adequate and might only reflect local abundances of particular species with specific habitat requirements. Further examination of the samples at species level could shed more light on this issue.

Despite the lack of a strong trend in the relationship between the diversity of surface-active invertebrates and the local density of Sika deer on lowland heath, results of this research showed some evidence that the composition of communities of surface-active invertebrates on dry heath was related to the composition of the vegetation community. This relationship between the composition of communities of surface-active invertebrates on dry heath and the composition of the vegetation community can be considered as an indirect effect of the local density of deer as results showed a significant relationship between the local density of Sika deer on dry heath and the composition of plant communities. On wet heath the composition of communities of surface-active invertebrates were directly related to the local density of Sika deer. The response to direct or indirect effects of the local densities of Sika deer were found across the different taxonomic levels with the exception of the species-level of Carabidae, where the low number of samples did not allow the community composition analyses on dry heath. Results of the present research concur with previous studies on the effects of grazing and vegetation structure on invertebrate communities of upland heath. Heavy grazing levels in the Scottish moorlands had a significant impact in the vegetation structure of *Calluna* communities and resulted in a significant change in the composition of the Carabid community (Gardner *et al.*, 1997). Also, Usher (1992) found a relationship between the vegetation structure (i.e. vegetation height) and the species composition of the invertebrate assemblages. However, the former authors also found a strong relationship between the community composition of invertebrates and soil characteristics, in particular a wet-dry gradient. Although the present research already accounted for differences between dry and wet areas by splitting the analyses between dry and wet heath it is possible that fine scale gradients between wetter and drier areas might

have affected the results. Further work involving the analysis of other factors such as soil properties within the two types of lowland heath could better explain differences in the community composition of lowland heath invertebrates.

In conclusion, this research has found that plant communities of dry heath seemed to be more sensitive than those on wet heath in their response to the level of local density of Sika deer; higher levels of local density were related not only to a modification in the vegetation structure of dry heath as a result of disturbance but were also related to a modification in the composition of the plant communities. Also this research has detected a threshold level of the local density of Sika deer above which there is a significant decline in the quality of lowland dry heaths. The diversity of different taxonomic levels of surface-active invertebrates responded differently to higher local densities of deer, higher plant diversity or to differences in the vegetation structure, and that response also differed between heath types. Moreover, the community composition of surface-active invertebrates differed significantly with the level of local density of Sika deer; this was detected as a direct relationship on wet heath and indirectly through an effect on vegetation community composition (but not structure) on dry heath. This research, therefore, has found a different response of dry and wet heath plant and animal communities to the local density of Sika deer. These differences highlight the need for a differential management of wild grazers on dry and wet lowland heath to meet the conservation targets within each of these habitats.

CHAPTER 6: GENERAL DISCUSSION AND CONCLUSIONS

This thesis aimed to study the factors affecting the distribution and habitat use of Sika deer in habitat mosaics including lowland heath, and the effects of Sika deer on plant and animal communities of lowland heath. The thesis had three main objectives. The first objective was to investigate the ecological factors affecting the distribution and habitat use of Sika deer. The second objective was to explore the consistency of Sika deer habitat associations across landscapes with similar or different characteristics. The third objective was to study the ecological impacts of Sika deer on plant and animal communities of lowland heath. This chapter provides an integrated discussion of results obtained for each of these objectives and considers the management consequences of the new scientific knowledge acquired. This chapter also addresses the ways in which the present research could be improved and how different modelling approaches could contribute to a better understanding of the interaction of Sika deer with their environment.

What are the ecological factors affecting the distribution and habitat use of Sika deer?

Habitat availability, the spatial distribution of habitats and the avoidance of perceived risk (i.e. human disturbance) have been identified as key ecological factors for influencing the distribution and habitat selection of Sika deer at both the landscape and home range scale. Habitat selection by Sika deer was found to differ at the two spatial scales which supports previous studies suggesting that analyses to determine the ecological factors affecting habitat selection by deer and the relationship between forage consumption and availability should follow a multi-scale approach (e.g. Myrnerud and Ims, 1998, Dussault *et al.*, 2005, Månsson *et al.*, 2007, Herfindal *et al.*, 2009, Zweifel-Schielly *et al.*, 2009). When used in previous studies, a multi-scale approach to investigating the habitat selection by deer has allowed comparison of criteria in the selection of resources across spatial scales. For instance, studies on moose (*Alces alces*) have found that the use of resources can be based on different criteria at different spatial scales. Herfindal *et al.* (2009) found that moose selected habitat types that provided both good forage and cover at the landscape scale, while at the home range scale it was habitat types that provided cover and low human

impact which were selected. The authors explained this result as a compromise between protective cover, forage quality and avoidance of human presence in their habitat selection. Månsson *et al.* (2007) also found that the foraging patterns of moose were affected by the spatial scale, which supported a hypothesis of different foraging goals for large herbivores at the different spatial scales formulated by Senft *et al.* (1987). Senft's hypothesis proposed that at the landscape scale the foraging goal for large herbivores would be the maintenance of biomass intake and avoidance of physical stress, while at the feeding site the goal would be toxin minimization and nutrient maximization (Senft *et al.*, 1987).

At the landscape scale, the results of the present study suggest that Sika deer placed their home ranges with a trade-off between key resources (i.e. food and cover) and a perceived risk linked disturbance. There is a similarity between the results of this research and those described above obtained by Herfindal *et al.* (2009). In landscapes in which good quality food resources were limited and fragmented, the Sika deer studied in this thesis were found to place their home ranges in areas with more surrounding cover and with some cover between pasture areas, which allows Sika deer to avoid perceived risk in the form of human disturbance when moving between feeding areas. These habitat associations were found to be consistent between areas with similar landscape structure. The opposite situation was found in a landscape where high quality pastures were abundant and formed large patches and where cover was found adjacent to pastures and the intensity of human disturbance was lower. In this landscape, pastures seem to become more selected than cover by Sika deer. The present study has therefore found that Sika deer seemed to use the requirement for safe access to pastures as the main criteria for their habitat selection at the landscape scale. Aurélie *et al.* (2008) studied the movements of Roe deer in relation to sources of disturbance and found that the distances to roads and buildings were the most influential factors determining Roe deer movements. They concluded that the avoidance of potential sources of disturbance may be a key factor in determining the movements of Roe deer. The results from the present study suggest similar relationships for Sika deer in habitat mosaics of lowland England. It has been proposed that those factors with highest fitness impact have the highest influence on the habitat selection at larger scales (Senft *et al.*, 1987, Dussault *et al.*, 2005).

At the home range scale, the selection of pastures and cover were inversely related to their relative availability. This suggests that the criteria of choice in the use of resources by Sika

deer seemed to be related to a requirement for an appropriate balance of food and cover. A general trade-off between foraging and predation risk has been described for Roe deer in Norway (Mysterud *et al.*, 1999b) as Roe deer selected more open habitat and feeding sites closer to sources of human disturbance at night. Results of this thesis also suggest a trade-off between access to good quality food and perceived risk both directly and indirectly through the selection for cover, as deer on pasture were found to be closer to cover and further from areas of human disturbance during the day than during the night. Similar results related to the existence of a temporal pattern in the habitat use and activity by deer in response to human disturbance have been described for different species, such as Red deer (Georgii, 1981), mountain elk (Green and Bear, 1990) and Sika deer (Mann and Putman, 1989b). The present study, using radio tracking and GIS, has not only related the animals to the habitat where they were found, but also has related the geographic position of individuals to their proximity to cover. This has allowed finding that despite day/night differences in the distance to cover and areas of human disturbance found in the present study, Sika deer maintained a “safety” distance from cover during both day and night. This result concurs with those obtained by Takatsuki (1989), who found that the number of faecal pellets deposited by Sika deer decreased suddenly after 150 m out of the forest. Results of this thesis indicate that human disturbance, as a form of perceived risk, may have been a limiting factor of habitat use at the home range scale as it affected the daily and spatial pattern in the exploitation of key resources. Also this thesis has found indications of consistency in the habitat associations across areas with similar landscape structure. This suggests that criteria of choice in the habitat use by Sika deer might be, at least, consistent between areas of similar landscape characteristics. However, these findings are based on comparison of habitat selection of Sika deer in only three study areas. The extent to which the criteria of choice in the habitat use by Sika deer at landscape and home range scale found in this thesis can be extrapolated to new areas is difficult to evaluate without more studies over a wider geographical range.

Sika deer make choices at both landscape and home range scale not only related to the exploitation of those habitats offering good quality food resources (i.e. grassland) and cover but also other habitats that might offer alternative food and/or cover resources, such as saltmarshes, reedbeds or lowland heath. In particular, results of this research have found that the extent to which Sika deer use patches of lowland heath was affected by both the availability of pastures (as preferred foods) and the distribution of heath patches in relation

to cover and pastures. *C. vulgaris*, which is found in patches of lowland heath, is a food resource for Sika deer that has been found to be especially important during late autumn and winter (Mann, 1982, Mann and Putman, 1989a). The importance of the distribution of heath patches to wild grazers has also been suggested by other studies which found that the extent to which Red deer utilize upland heath (and consequently the grazing pressure) is strongly related to vegetation distribution within a heather/grass landscape (Clarke et al., 1995b, Hester and Baillie, 1998, Palmer and Hester, 2000). This thesis has shown that Sika deer also made more extensive use of lowland heath when it was located between areas of pasture and cover. Sika deer are considered to be intermediate /opportunistic feeders due to the contribution of graminoids and woody plants to their diet (e.g. Mann and Putman, 1989a, Asada and Ochiai, 1996, Yokoyama *et al.*, 2000). This is reflected in a wide range of feeding behaviour across their Japanese distribution, from specialist grazing to seasonal or continuous browsing (e.g. Jayasekara and Takatsuki, 2000, Ueda *et al.*, 2003, Campos-Arceiz and Takatsuki, 2005, Takatsuki, 2009a). The present study has shown that Sika deer used lowland heath more intensively in areas in which the availability of high quality food resources (i.e. pasture) were more limited and during seasons when the availability of high quality food was lower (i.e. winter). These results seem to agree with studies which have shown that Sika deer are capable of exploiting alternative food resources when their preferred food becomes scarce, best demonstrated when after a crash caused by food shortage Sika deer switched from a diet of fresh vegetation to a diet of litterfall (Takahashi and Kaji, 2001, Miyaki and Kaji, 2009). The exploitation of a wider variety of plant species under food limitation is a process that has also been described for other cervids such as reindeer *Rangifer tarandus* (e.g. Leader-Williams *et al.*, 1981, Terje, 1984). When alternative foods are found in areas of conservation interest, such as lowland heath, the availability and spatial distribution of cover and grassland in relation to alternative foods may be key factors in predicting the possible impacts of grazing and trampling by Sika deer as impacts are related to the level of habitat usage.

Is there a between-area consistency in the habitat associations of Sika deer?

A large number of studies have modelled the spatial distribution and habitat associations of deer (e.g. Dettki *et al.*, 2003, Plante *et al.*, 2004, Shi *et al.*, 2006, Vospernik *et al.*, 2007, Vospernik and Reimoser, 2008 among many others). The value of habitat association models as a conservation tool is based on the assumption that organisms exhibit the same patterns of selection across different regions. However, the potential transferability of predictive species distribution models has not received enough attention (McAlpine *et al.*, 2008). If habitat associations derived in one area can be used to predict or understand Sika deer distribution (and hence potential impacts) in others, this knowledge could be used as a conservation tool for lowland heath managers. In this thesis the consistency in Sika deer habitat associations was investigated as a first stage in the development of a future empirical model to predict the distribution and abundance of Sika deer. Habitat selection by Sika deer at the landscape scale was similar in areas with similar landscape characteristics measured in terms of habitat availability and the distribution of habitats. In contrast, habitat selection by Sika deer differed between areas of different landscape characteristics. These results suggest that habitat association models built in one area should only be used to predict Sika deer distribution and abundance in areas with similar landscape characteristics.

This thesis has shown the importance of different spatial scales in the response of Sika deer to their environment as they showed different criteria in their habitat associations at different spatial scales. This suggests that predictive models focused on relating resources at a small scale to the distribution and abundance of Sika deer might not account for differences in how resources are used at different spatial scales. Previous research has shown that deer respond to their environment at the landscape scale; the distribution and habitat use of deer is related to the availability of food and cover at the landscape scale (e.g. Myrnerud *et al.*, 1999a, Godvik *et al.*, 2009), landscape structure (e.g. Kie *et al.*, 2002, Said and Servanty, 2005, Lamberti *et al.*, 2006, Aurélie *et al.*, 2008) and human disturbance (e.g. Czech, 1991, Rowland *et al.*, 2000). Based on the findings of this thesis, a multi-scale approach is recommended not only for studies of habitat selection by deer but also for habitat models predicting their distribution and abundance.

What are the ecological impacts of Sika deer on plant and animal communities of lowland heath?

Effects of Sika deer on plant communities of lowland heath

In this thesis, the interaction of Sika deer with plant and animal communities of lowland heath has been studied by relating the extent to which lowland heath patches are used by Sika deer to the characteristics of their plant and animal communities. This study has investigated the impacts of Sika deer on plant and animal communities of lowland heath for a range of density of Sika deer actually utilising areas of heath of 0.01 to 0.36 deer/ha. However, this range of densities needs to be understood as a scoring of locations by their local population of Sika deer instead of an exact measurement of the true density, which was not directly determined in this study. Differences in the response of plant or animal communities of lowland heath at higher local densities of deer cannot be predicted based on extrapolation of results from this thesis. Also it should be noted that although 0.36 deer/ha was the maximum interpolated density of deer actually utilising the heath, overall population densities of Sika deer can differ at the study area scale.

Overall, findings on the effect of the ecological impacts of Sika deer on plant communities of lowland heath concurred with previous work, conducted across heaths of Western Europe, demonstrating that heathland declines under heavy grazing (e.g. Bakker *et al.*, 1983, Welch, 1984a, Welch, 1984b, Welch and Scott, 1995, Palmer, 1997, Hester and Baillie, 1998, Hester *et al.*, 1999). The findings also concur with research based on enclosure experiments and experiments controlling the density of grazers which have shown the importance of grazing in determining the composition and/or vegetation structure of heathlands (e.g. Hulme *et al.*, 2002, Lake, 2002, Pakeman *et al.*, 2003, Jauregui *et al.*, 2008). Pakeman *et al.* (2003) and Jauregui *et al.* (2008) found differences in composition and vegetation structure of patches of heath enclosure related to the level of grazing by sheep, which concurs with results of this thesis relating the level of dry heath usage by Sika deer to the vegetation structure and plant composition. Hulme *et al.* (2002) concluded that the lack of grazing within enclosure plots of wet heath was responsible for increases in the abundance of *C. vulgaris* while Lake (2002) found a significant increase of *Molinia. caerulea* in non grazed plots of wet lowland heath. Also, enclosure plots located on both wet types in one of the study areas (Arne) as a part of a different research have

shown visible increase in the volume of *C. vulgaris* and *M. caerulea*, although detailed data are still being collected. These previous studies suggest that at least some of the correlations found in this thesis between higher density of Sika deer and ecological impacts may be causal. However, it is accepted that causality can never be ascribed with certainty from correlation studies and that there is the potential for some circularity in this relationship. Circularity may occur if changes in the quality of lowland heath as a result of increasing levels of usage by Sika deer result in habitat changes (i.e. habitat fragmentation or changes in the availability of heath as an alternative food resource) that lead to changes in the distribution and habitat use by Sika deer at the landscape scale

Analysing the ecological impacts of Sika deer on plant communities of dry and wet lowland heath separately showed that plant communities of dry heath seemed to be more sensitive than those of wet heath in their response to local densities of Sika deer. Higher local densities of deer were related to decline in the quality of plant communities of dry heath. This was characterized by a reduction in vegetation volume and abundance of *C. vulgaris*, increase of bare ground, dead vegetation and area disturbed and the establishment of opportunistic species. A decrease in cover as a result of heavy grazing is a typical response of heather that has been found both in upland heaths (e.g. Welch, 1984a, Hester and Baillie, 1998) and also in lowland heaths (e.g. Bakker *et al.*, 1983). An increase of bare ground as a result of heavier grazing was found by Bullock and Pakeman (1997) on lowland heath in England, while an increase in the dead matter cover as a result of higher grazing pressure has been described in the Cantabrian heaths (Jauregui *et al.*, 2008). The establishment on dry heaths of species more resistant to grazing as a response to high levels of grazing is also a process described in both upland and lowland heaths (e.g. Bakker *et al.*, 1983, Welch, 1984b, Welch and Scott, 1995).

By contrast to the responses of dry lowland heath, the only significant response to higher local densities of Sika deer detected on wet lowland heath was a decrease in the abundance of *M. caerulea*. This contrasting response of the plant communities of dry heath to those of wet heath has been linked to potential differences in the capability of different plant species within the community for recovery after disturbance. Grasses are more resistant to grazing processes than dwarf shrubs, such as heather (e.g. Grant and Armstrong, 1993, Stewart and Hester, 1998). *C. vulgaris* is more vulnerable to long-term damage than are grasses because the growing points of *C. vulgaris* are located at the tips of their shoots

instead of at the ground level as in grasses, which are more protected from grazers (e.g. Grant and Armstrong, 1993). Also, *C. vulgaris* may be more damaged by trampling than *M. caerulea* (Lake *et al.*, 2001). Despite the differences in responses of dry and wet heath communities to the level of heath usage by Sika deer, both heath types showed an increase in plant diversity (species richness and evenness) up to the maximum local density of deer estimated on areas of heath (0.36 deer/ha). Other studies have found that different grazing intensities have shown a variety of effects on plant diversity (i.e. increase, decrease or no effects) depending on the habitat and the precise grazing regimes (reviewed in Lake *et al.*, 2001). Results of this thesis suggest that on dry heath the increase in diversity might be related to an improvement of the conditions for the establishment of opportunistic species as a result of a decrease in the abundance of *C. vulgaris* and the creation of a diversity of gaps in the vegetation. This is a process described for other heath systems (e.g. Bullock and Pakeman, 1997). On wet heath *M. caerulea* becomes dominant in the absence of grazing or under low grazing pressure (Berendse, 1985). A decrease in the abundance of *M. caerulea* at the sites surveyed by this thesis might have resulted in an improvement in the conditions for other less competitive species, such as *E. tetralix*, whose abundance increased as a result of higher wet heath usage by Sika deer.

Results from this thesis suggest that there is a threshold level of local density of Sika deer above which there is a significant decline in the quality of dry lowland heath in terms of a decrease in the abundance of *C. vulgaris* and total vegetation volume, and an increase in the percentage of bare ground and the area of vegetation damaged. This is also the threshold in the level of density of heath utilisation by Sika deer at which the diversity of plant species significantly increased. In upland heath, levels of shoots consumption higher than about 40% have been considered likely to result in a decline of cover (Grant *et al.*, 1982), although Palmer (1997) suggested that this percentage was too high and suggested a value closer to 20%. This thesis has not investigated the shoot consumption by Sika deer although comparisons with other studies are possible as a decline in heaths has also been also directly linked to stocking rates of herbivores. Welch (1984a) considered that grazing pressures of 2.7 sheep/ha or 0.23 cattle/ha to be the limit above which upland dry heath will change to grassland communities. However, the levels of grazing pressure calculated by Welch (1984a) as sustainable levels for sheep grazing of heather moorland were considerably higher than those suggested to restore degraded dry and wet heath by Pakeman *et al.* (2003) and Hulme *et al.* (2002). Pakeman *et al.* (2003) considered that an

annual level of sheep grazing of 0.8/0.9 sheep/ha allows an increase in the extent and condition of dwarf shrubs present on a degraded dry heath within four years of initiating the treatment; Hulme *et al.* (2002) found that the best results to recover a degraded wet heath were obtained with an annual level of sheep grazing of 0.7 sheep/ha. Thresholds obtained above were based on sheep grazing, which was managed to limit the stock numbers. The present study was based on wild populations of deer, therefore deer numbers were more difficult to control precisely. The specific level of habitat usage by Sika deer above which dry lowland heath declines in quality need to be considered cautiously as they reflects the local density of Sika deer, which is different to the overall density of deer (i.e. population density) found at the study area scale. Also, the specific levels of local density of deer at each site were obtained as a spatial interpolation of the level of habitat usage by deer, therefore they were an estimation of the level of local density of deer in the surroundings (i.e. a scoring of different areas by their local density of deer) rather than an exact measurement of the 'true' or 'absolute' value of the local density of deer at each site.

Sika deer have been shown to adapt their diet to alternative foods after a food shortage (Takahashi and Kaji, 2001, Miyaki and Kaji, 2009). If Sika deer use lowland heath as an alternative or contributing part of the diet it is likely that depletion of lowland heath as a result of Sika deer over-abundance would result in a search for other food sources. A search for alternative food resources by Sika deer in mosaics of lowland heath, woodlands and grassland might result in a modification of the habitat associations and spatial distribution of deer that could provoke a cascade effect affecting other protected habitats. Impacts on other habitats as a result of Sika deer depleting resources have been described in Japan by Takashi and Kaji (2001) where Sika deer first depleted tall herbs used as summer foods and other woodland herbs used as winter foods, then started eating the saplings of deciduous trees and bark stripping palatable tree species and finally, after a population crash, Sika deer started eating fallen leaves of deciduous trees and previously unpalatable plants. Changes to saltmarshes and fenland communities in Poole Harbour in England as a result of their use as an alternative food resource by Sika deer have been documented by Hannaford *et al.* (2006).

Effects of Sika deer on animal communities of lowland heath

Evidence found by this thesis suggests that Sika deer, through grazing and trampling, affect vegetation structure and the composition of plant communities of dry heath and the plant diversity of both heath types. The relationships between vegetation structure and invertebrate diversity on heath ecosystems have been described in previous studies for different groups of invertebrates including Hemiptera and Coleoptera (e.g. Gardner, 1991, Gardner *et al.*, 1997, Hartley *et al.*, 2003). Gardner (1991) and Gardner *et al.*(1997) suggested that an enhancement in the diversity of Coleoptera on moorland was expected in areas of a high degree of vegetation structural heterogeneity. Hartley *et al.* (2003) found that grazing was an important indirect driver of the hemipteran community diversity through its effect on the shoot and canopy structure of *Calluna*. Consequently, the diversity of surface-active invertebrates was expected to be related to the extent to which areas of lowland heath is used by Sika deer. However, no consistent pattern was found in this thesis in the response of the diversity of surface-active invertebrates to either higher local density of Sika deer or to differences in the vegetation structure or plant diversity.

Despite the lack of a relationship between diversity of invertebrates and direct or indirect effects of the local density of Sika deer, this research has detected a relationship between the composition of communities of surface-active invertebrates and the composition of the vegetation community on dry heath. This was considered as an indirect effect of the local density of deer as a relationship between the local density of Sika deer and vegetation structure had been already established by this thesis. This indirect effect of the extent to which herbivores use areas of heath on the composition of communities of invertebrates through their effects on the vegetation structure has been also found in the Scottish moorlands by Gardner *et al.*(1997). These authors found that heavy grazing by sheep and deer had significant impacts on the vegetation structure and resulted in changes in the composition of the Carabid community. In a more general context, indirect effects of deer activity can be related to modifications of the availability of suitable microhabitats for invertebrates, as has been shown after the introduction of non native deer in new areas (e.g. Allombert *et al.*, 2005b, Martin *et al.*, 2010). These authors found that the introduction of deer in some Canadian islands produced a simplification of vegetation structures and communities, which was reflected up the food chain resulting also in a simplification of understory invertebrates and shrub-dependent song bird communities. Therefore, the

evidence suggests the potential for indirect effects of Sika deer on animal communities through their effect on the composition and structure of vegetation.

On wet heath, where this thesis found a general lack of significant responses of the vegetation structure or composition of plant communities to higher local density of Sika deer, the composition of communities of surface-active invertebrates were directly related to the level of local density of Sika deer. This might be a reflection of a creation of microhabitats for invertebrates as a result of the deposition of dung or as an effect of trampling. Some species of invertebrates found in lowland heath are directly dependant on animal dung as a food resource, others although not directly dependant on dung, prey on insects that feed on dung, while other species of invertebrates are affected by the destruction of nests as a result of trampling (Lake *et al.*, 2001). However, based on this evidence, the same direct response to Sika deer by both communities of dry and wet lowland heath would be expected. No direct response to the local density of Sika deer was detected on dry lowland heath. A different response between the animal communities of dry and wet lowland heath to the local density of Sika deer was therefore obtained by this thesis. This conclusion concurs with the heath type-specific response of the plant communities of lowland heath described earlier.

IMPLICATIONS FOR MANAGEMENT

Results of this thesis have shown that the distribution and availability of key resources (i.e. food and cover) and human disturbance affect the distribution and habitat use of Sika deer populations. Landscape management, such as fencing or road development, might produce habitat fragmentation or a decrease in the availability or accessibility to preferred food resources or cover. If alternative food resources are found in protected or commercial habitats Sika deer might cause damage to these new areas. By contrast, management decisions might also result in new resources of food or cover becoming available. In this case, habitats surrounding these alternative resources might also be affected by Sika deer, as the extent to which habitats such as lowland heath are used by deer depend on both the availability and distribution of surrounding food and cover. Where modifications of

landscape features might produce a decrease in food resources for Sika deer, managers would be recommended to aim to provide alternative foods to avoid the exploitation of protected or commercial areas, although this could be costly over a long period. If modifications of landscape features increase the attractiveness of the area for Sika deer, managers could consider measures to protect surrounding habitats.

An increase in human disturbance is likely to produce changes in deer behaviour that could produce impacts on protected habitats. Results of this thesis have shown a higher selection for cover in areas with a higher level of human disturbance. If habitats offering cover are protected or commercially valuable, a higher selection for those habitats could result in conservation or financial losses. Managers need to make visitors aware that their activities might affect the behavior of animals. Taylor and Knight (2003) during their work on the response of Mule deer to visitors found that approximately 50% of recreationists felt that recreation was not having a negative effect on wildlife. Information packs should therefore include advice on how to limit their impact on the behavior of deer. This advice should be based on scientific knowledge. For instance, Pépin *et al.* (1996) after studying the influence of visitors on the diurnal habitat patterns of the Pyrenean chamois (*Rupicapra pyrenaica*), advised people on foot to remain on established hiking trails as their activities might be perceived as predictable by Pyrenean chamois and thus more acceptable.

Human disturbance might be considered in certain situations as positive to avoid damage caused by deer. This thesis has found that the extent to which areas are being used by Sika deer might be related to an avoidance of perceived risk. Based on this finding, it is suggested that managers should consider the possibility that certain modifications of landscape features might reduce the attractiveness of areas such as agricultural fields, as an alternative to culling. Landscape management to reduce the incidence of deer might be valuable for managers of areas where the public opinion is against hunting deer or where resources are too limited to seek the help of professional stalkers. For instance, creating conservation headlands by crops to increase the distance to cover might reduce commercial losses as a result of an increase of the exposure of the field, which makes it less attractive for deer. These conservation headlands would also be beneficial to other wildlife (Cole *et al.*, 2007). However, this might only be financially practical for large crops field, as results of this thesis suggest that deer prefer areas within 100-110 metres from cover, therefore the conservation headland would need to have this size. Another management strategy could

be to encourage the use of existing footpaths across agricultural areas, by improving the knowledge of their existence among the public. This might not decrease the level of grazing at night, but could decrease the utilization of the fields for bedding/resting during the day and hence decrease commercial losses as a result of trampling.

The difference between the local density of deer and the overall population density within a particular area (as shown on lowland heath patches in this thesis) should be considered when management policies involve controlling deer population densities. Intervention to conserve a particular area of interest by manipulating the incidence of deer should require an assessment of the current/expected local density rather than just the population density of deer within an estate or reserve as a base to predict potential ecological impacts of deer on protected areas. Although the management of the local area in which Sika deer may be affecting the ecosystem is important, interventions at a landscape scale might also need to involve a management of the surrounding areas. For instance, land and culling management should target those areas of lowland heath more prone to suffer from deer activity, such as heath close to pastures or those patches of heath located in between areas of cover and good quality pastures. As areas of heath and surrounding cover or pastures might be owned by different stakeholders, a coordinated management across neighbouring estates or reserves to protect areas of lowland heath might be required.

This thesis has highlighted the different response of dry and wet lowland heath to the level of local density of Sika deer. Therefore it is possible that under the same levels of local density Sika deer cause a decline in the quality of dry heath, which is negative from the point of view of conservation aims, while the effects on wet heath might be considered as positive through the control of the abundance of *M. caerulea*. This different response of dry and wet heath to local densities of deer makes it challenging to manage lowland heath to meet conservation objectives. Grazing management of lowland heath for nature conservation generally aims to maintain open shrub vegetation with high diversity of heath species and at the same time to control scrub and other unwanted species (Bullock and Pakeman, 1997). However, Lake *et al.* (2001) identify fundamental differences in the main conservation aims in grazing for dry and wet lowland heath; the main conservation aim in grazing on dry heath is to increase structural diversity, while on wet heath the aim is to avoid the dominance of *M. caerulea*. However, wet and dry lowland heath are of course just extremes of a floristic composition and soil drainage gradient and patches of dry and

wet heath are often distributed as a mosaic in which the limits between one heath type and the other are not clear. Although ideally managers should consider the variation in the sensitivity of lowland heath to Sika deer grazing and trampling and conduct a differential management on dry and wet heath in reality both heath types are often too closely located to allow for a direct intervention on the incidence of Sika deer on one specific heath type. Managers therefore might need to consider which levels of heath usage by Sika deer might result in a “best possible scenario” for the balance of conservation aims of both dry and wet lowland heath.

RECOMMENDATIONS FOR FUTURE WORK

The investigation of the ecological factors affecting the distribution and habitat selection by Sika deer in this thesis has been based solely on monitoring female Sika deer. Therefore further work into the factors determining the distribution and habitat use of males is required to better understand the response of Sika deer to their environment at different spatial scales. An attempt to study the ecology of male Sika deer was conducted during the development of this thesis. The objective was to monitor 15 male Sika deer by GPS tracking in order to gather location and activity data to explore the environmental factors affecting male Sika deer distribution and habitat use. Attempts to tag male Sika deer during the winter 2008 were only successful in two occasions whilst during the winter 2009 six more males were GPS tagged. However, the GPS equipment was unreliable. Only two GPS devices provided regular readings of location and activity of male Sika deer and the longest period during which a male was monitored by GPS was eight months. The poor results of this part of the project made it impossible to fit the data obtained to the objectives of this thesis. Future evaluations into the statistical and ecological significance of the data obtained to address different research objectives are required. The main limitations to investigating different aspects of the ecology of male Sika deer (e.g. home range size, habitat associations or patterns of movement) seem to be the low number of individuals monitored and the short periods covered by the data.

Results of this research have identified a threshold in the local density of Sika deer above which there is a significant decline in dry lowland heath. However, it has failed to obtain

similar output in wet heath. Research efforts should be invested in detecting the threshold in the level local density of Sika deer in areas of wet lowland heath above which the conservation objectives cannot be met. This could help heath managers to control the incidence of Sika deer considering thresholds for both heath types in order to balance positive and negative effects of the same levels of grazing and trampling on both heath types.

This thesis has found consistency in the habitat associations of Sika deer across areas with similar landscape configuration. This could be the first step towards developing models to predict Sika deer distribution and abundance at a landscape scale. Models to predict the distribution of deer are usually habitat based, as they attempt to relate measurable environmental variables to the suitability of a site for a species. This type of model is based on habitat associations and therefore they assume that organisms exhibit the same patterns of selection across different regions. However, the transferability in distribution models based on habitat associations between areas has proven sometimes successful (e.g. Vanreusel *et al.*, 2007) but other times has failed (e.g. Whittingham *et al.*, 2007, McAlpine *et al.*, 2008, Bamford *et al.*, 2009). Also, as the environment changes, models to predict deer densities need to adapt to the new situation. Models based on habitat might not be sufficiently adaptable to environmental changes. An alternative to these limitations is the application of individual-based ecology (IBE, Grimm and Railsback, 2005), in which individual-based models (IBMs, Huston *et al.*, 1988) are the primary tools. Rather than being based on habitat associations, individual-based models (IBMs) derive their predictions from an understanding of the resource requirements, behaviour and physiology of animals. They assume that a constant, no matter how much landscape structure changes, is that animals will behave in order to maximise their chances of survival and reproduction (i.e. their fitness) (Goss-Custard, 1996). IBMs have been designed to predict how individuals within a population will alter their behaviour in response to environmental change (e.g. different management regimes of animal populations and landscape structure). By following the behaviour and fates of the individuals IBMs are able to predict the population consequences of the optimal decisions of individuals (Stillman, 2003). Future work should be invested in exploring the potential for individual-based models to predict Sika deer behaviour in response to environmental change as a conservation/management tool to foresee potential impacts on protected habitats.

CONCLUSIONS

What are the ecological factors affecting the distribution and habitat use of Sika deer?

The habitat availability, the spatial distribution of habitats and the avoidance of perceived risk (i.e. human disturbance) have been identified as key ecological factors affecting the distribution and habitat selection of Sika deer at both the landscape and home range scale.

Habitat selection by Sika deer was found to differ at the two spatial scales. At the landscape scale Sika deer placed their home ranges with a trade-off between key resources (i.e. food and cover) and a perceived risk linked to human disturbance. Sika deer seemed to use the requirement for safe access to pastures as the main criteria for their habitat selection at the landscape scale. At the home range scale, the criteria of choice in the use of resources by Sika deer seemed to be related to a requirement for an appropriate balance of food and cover as the selection of pastures and cover were inversely related to their availability. Human disturbance, as a form of perceived risk, was a limiting factor at the home range scale as it affected the daily and spatial pattern in the exploitation of key resources.

The extent to which Sika deer use patches of lowland heath was affected by both the availability of pastures (as preferred foods) and the distribution of heath patches in relation to cover and pastures. Sika deer made more extensive use of lowland heath when it was located between areas of pasture and cover and in areas in which the availability of high quality food resources (i.e. pasture) were more limited and during seasons when the availability of high quality food was lower (i.e. winter).

Is there a between-area consistency in the habitat associations of Sika deer?

Habitat selection by Sika deer at the landscape scale was similar in areas with similar landscape structure (i.e. areas with similar habitat availability and similar distribution of habitats). In contrast, Sika deer habitat selection differed between areas of different

landscape structure. These results indicate that habitat association models built in one area should only be used to predict Sika deer distribution and abundance in areas with similar landscape structure.

Based on the findings of this thesis, a multi-scale approach is recommended not only for studies of habitat selection by deer but also for habitat models predicting their distribution and abundance. Moreover, it is suggested that in order to overcome the limitations of predictive models based on habitat associations, future work should be invested in exploring the potential for individual based models to predict Sika deer behaviour and subsequent ecological impacts on protected habitats.

What are the ecological impacts of Sika deer on plant and animal communities of lowland heath?

Effects of Sika deer on plant communities of lowland heath

Plant communities of dry heath seemed to be more sensitive than those of wet heath in their response to local densities of Sika deer. Higher local densities were related to a decline in the quality of plant communities of dry heath, which is characterized by a reduction in vegetation volume and abundance of *C. vulgaris*, increase of bare ground, dead vegetation and area disturbed and the establishment of opportunistic species. By contrast, on wet lowland heath, only a decrease in the abundance of *Molinia caerulea* and an enhancement of plant diversity were related to higher local density of Sika deer. Despite the differential responses of dry and wet heath to higher local densities of Sika deer, both heath types showed an increase in plant diversity with increased heath usage by Sika deer. However this study has been limited to investigating the impacts of Sika deer on plant and animal communities of lowland heath for a range of spatially interpolated density of Sika deer actually utilising areas of heath of 0.005 to 0.36 deer/ha.

A threshold in the level of local density of Sika deer above which there is a significant decline in the quality of dry lowland heath was identified. This is also the threshold in the level of local density of Sika deer at which the diversity of plant species significantly

increased. However, this increase in diversity was linked to the addition of opportunistic species.

Effects of Sika deer on animal communities of lowland heath

No consistent pattern in the response of the diversity of surface-active invertebrates to higher local density of Sika deer or to differences in the vegetation structure or plant diversity was found across the taxonomic levels considered in this research or between heath types.

A relationship was found between the composition of communities of surface-active invertebrates and the composition of the vegetation community, which was considered as an indirect effect of the local density of deer as results showed a significant relationship between the local density of Sika deer in areas of dry heath by Sika deer and the composition of plant communities. On wet heath the composition of communities of surface-active invertebrates were directly related to the level of habitat usage by Sika deer.

FINAL REMARKS

As a final brief summary of this thesis, this research has found that the habitat availability, the spatial distribution of habitats and the presence of human disturbance all affect how Sika deer are distributed and their habitat associations. Those ecological factors also determine the extent to which areas of lowland heath is used by Sika deer and the subsequent ecological impacts of Sika deer on plant and animal communities of lowland heath. Consistency in the habitat associations of Sika deer have been found between areas with similar landscape structure and therefore it is likely that in those areas the ecological impacts of Sika deer will be also similarly distributed.

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APPENDIX 1: ESTIMATING THE SPATIAL VARIATION OF LOCAL DENSITY OF DEER IN OPEN HABITATS: A METHOD COMBINING A ROUTE OF VANTAGE POINTS AND A SPATIAL INTERPOLATION OF LOCAL DENSITY OF SIKA DEER

Abstract

In this appendix, a method to estimate spatial and seasonal variation in the local density of deer in areas of open habitats is described. The method consisted of a survey method, based on a route of vantage points, coupled to a spatial modelling technique to interpolate the spatial variation of usage of area by Sika deer (*Cervus nippon*) around those instantaneous observations. The field technique used was able to cover adequately the majority of the open habitats. Deer were observed and located independently of differences in vegetation and terrain between the open habitats surveyed in the study areas. Observations were spread during a month in each season and were also obtained at different times of the day. The observer minimized disturbance to the deer while making observations. The spatial modelling was based on a kernel smoothing with a decay-rate function related to the movement abilities of Sika deer. The modelling technique, performed using open source software, allowed an estimation of the local variation in density of deer usage around specific locations as well as easy visualization of the spatial variation in local density of deer in open areas. The limitations of this method were: (i) the lack of an estimate of the probability of detecting deer; (ii) the movement abilities of Sika deer were only based on data of female home ranges. Further use of this technique should consider: (i) differences related to the specific landscape of the study area and seasonal variations in the vegetation; and (ii) differences related to deer species as the movement abilities will be species, habitat and season-specific.

Key words

Spatial usage, modelling, *Cervus nippon*, heathland, deer survey

Introduction

Methods to measure the relative or absolute density of deer have been broadly divided into direct and indirect methods (Mayle and Staines, 1998, Mayle *et al.*, 1999, Smart *et al.*, 2004, Putman and Watson, 2009). In open habitats the most suitable methods are those based on direct observations and therefore are commonly used (Mayle and Staines, 1998, Marques *et al.*, 2001, Smart *et al.*, 2004, Daniels, 2006), whilst in concealed habitats indirect methods are more widely used (Mayle *et al.*, 1999, Campbell *et al.*, 2004, Smart *et al.*, 2004). Direct methods such as the use of helicopters combined with digital photography or the use of thermal imaging are expensive but capable of minimize errors in accuracy and precision (Focardi *et al.*, 2001, Daniels, 2006) and the labour required to count deer (Daniels, 2006). Probably the most widely used method for analysing censuses of ungulates throughout the world is the distance sampling technique (DST, Buckland *et al.*, 2001). DST has been applied to both direct and indirect observations of the density of deer (e.g. Mandujano and Gallina, 1995, Marques *et al.*, 2001, Focardi *et al.*, 2002, Koenen *et al.*, 2002, Smart *et al.*, 2004, Focardi *et al.*, 2005, Acevedo *et al.*, 2008) and has been successfully employed to monitor deer populations such as Roe deer *Capreolus capreolus* (Focardi *et al.*, 2005).

The suitability of any given method to estimate deer densities depends not only on the ecology and behaviour of the species of interest or the type of habitat the deer inhabit, but also depends on the management questions to be answered (Marques *et al.*, 2001). The importance of estimating the density of deer at a study area scale of hundreds to a few thousand hectares or at a higher landscape scale corresponding to the estimated population range has been recognised within the context of measuring deer impacts on ecosystems (e.g. Putman and Watson, 2009). However, as several studies have shown that deer habitat use varies spatially and temporally (e.g. Georgii, 1981, Mann and Putman, 1989b, Yeo and Peek, 1992, Benhaiem *et al.*, 2008), researchers and managers might be also interested in estimating the spatial variation of deer occupancy within smaller areas of a few tens of hectares in order to reflect the extent to which patches of habitat are being used by deer. Methods to estimate deer numbers described earlier usually aim to obtain deer densities for geographical blocks or habitat types rather than obtaining the spatial variation of the local density of deer at a finer scale in areas containing one or more different habitats.

Within the context of a wider research project linking the spatial variation in the local density of Sika deer (*Cervus nippon*) in areas of lowland heath to differences in plant and animal communities of lowland heath, a method was required to estimate spatial variation in local density of deer in areas of lowland heath. The surveying methods described above, which are designed to estimate the overall density of deer for a given area or habitat, were considered not to be suitable as they could not provide data at the fine spatial scale required. As a response to this need, the aim of this study was to estimate the spatial variation of local density of Sika deer in a mosaic of lowland heath, woodlands and grassland based on direct observations. The method can be repeated by management personnel after a period of training. The specific objectives of this research were: 1) to develop a field technique to obtain direct observations of deer which can represent the variation in the spatial usage by deer of open areas; 2) to obtain a visual representation of the spatial variation of local densities of deer in open habitats and an estimation of the level of local density of deer around specific locations, which could represent, for instance, areas of particular conservation interest.

The method consisted of a non-intrusive survey method, based on a route of vantage points, coupled to a spatial modelling technique to interpolate the spatial variation of deer density. The method was designed to be as cost effective as possible; the field technique is designed to minimize labour and equipment costs while the modelling technique is based on open source software. As a demonstration, the method is used to estimate the variation in local density of Sika deer across two study areas in a lowland landscape, comprising open habitats including grassland, heathland and saltmarsh. Advantages and disadvantages of the method are discussed.

Study Areas

The study was conducted in two nature reserves in the district of Purbeck, southwest England. Purbeck, as a part of the Poole Basin, contains one of the largest populations of wild Sika deer in England (Putman, 2000). The region is a mosaic of pastures, lowland heaths, deciduous and coniferous woodlands and wetland habitats such as saltmarshes and reed-beds. Lowland heath, an international priority conservation area (i.e. Habitats Directive 92/43/EEC), is an open habitat dominated in the area by low growing ericaceous shrubs such as *Calluna vulgaris* and *Erica* species. Field observation and radio tracking data (Chapter 3) indicate that Sika deer make extensive use of the Purbeck lowland heaths.

Arne RSPB reserve (henceforth termed 'Arne') is a 608 ha protected area located on the west coast of Poole Harbour (50° 41' 20" N, 2° 2' 20" W). Hartland Moor and Middlebere Heath Natural Nature reserve (henceforth termed 'Hartland') is a protected area of 550 ha situated 3 km south of Arne (50° 39' 58" N, 2° 4' 26" W). Population density of Sika deer differed between these areas; the estimated density in October 2007 obtained by direct observation during a deer survey at Arne was 118 deer/km², while at Hartland was 26.5 deer/km² (source: The Royal Society for the Protection of Birds and The National Trust respectively). The open habitats at Arne and Hartland were pastures, heath and open wetlands. Both areas differed in the relative abundance of coniferous and deciduous woodland, lowland heath, pastures and wetland habitats such saltmarshes and reed-beds. At Arne, the most abundant habitat was heath (33% cover) followed by saltmarshes (14% cover) and coniferous woodland (13% cover), while at Hartland the most abundant habitat was improved grassland (35% cover) followed by heath (33% cover) and mires (11% cover).

Methods

The method described in this section was divided into two steps. The first step involved conducting a field survey based on a direct observation technique that used vantage points to obtain observations of deer throughout the day and across seasons. The second step involved a modelling technique that used the field observations and data on the extent of movement of Sika deer to interpolate the spatial variation in the local density of deer around the actual recording points. The modelling technique converted the point-based deer observations into the two dimensional variation of local densities of deer throughout the study areas, which allowed to extrapolate the local density of deer into the gaps between the observations of deer.

Field technique

The direct observation technique uses vantage points from which to survey deer, and so it is similar to the established point transects method (e.g. Mack and Quang, 1998, Mayle and Staines, 1998, Koenen *et al.*, 2002, Koenen and Krausman, 2002). However, although in this technique animals are recorded from a number of fixed stations as in the established point transect (see e.g. Buckland *et al.*, 2001, Buckland *et al.*, 2006), the detection distance is not measured, and therefore the statistical analysis differs. A number of vantage points were used along a route that covered the majority of the open habitats of each of the study areas. Vantage points were surveyed at regular intervals during the day and night instead of being restricted to only those periods when deer are most active (i.e. sunset or sunrise). This technique allowed a single researcher to cover a whole study area that could not be surveyed from a single vantage point. A powerful spot-light was used to assist night time observations. Observations were carried out by a single researcher with a basic knowledge of deer observation and identification. The required equipment was an off-road car, binoculars (Nikon Monarch 8x42), telescope (Kowa TS-612 20x60) and a powerful (five million candles) spot-light.

The number and location of vantage points depended on the terrain and aimed to cover the majority of open habitats in the study area during day and night. Eleven vantage points were used at Arne (increased to twelve during the night due to a more restricted visibility

of a particular area during the night) and nine at Hartland (Figure A1.1). In other studies the location of vantage points may need to be changed through the year in response to changing visibility (i.e. due to deciduous trees and seasonal vegetation changes). However this was not required in this study because no changes of visibility related to vegetation changes were detected. In order to access the vantage points, a route was designed in each study area following off-road tracks covering the main part of both study areas from where it was possible to observe Sika deer activity and minimize disturbance. Routes were designed to be completed in less than 1.5 hours in order to reduce double counts and to minimize changes in environmental conditions (e.g. sunrise or sunset) that may affect Sika deer behaviour.



Figure A1.1: Route through Arne (left) and Hartland (right). The black line represents the route, the stars the vantage point locations during the day and night and the square the added vantage point during the night at Arne. The grey polygons are the open areas surveyed, and the diagonally shaded patches open areas not visible. Other habitats are shown in white and the sea surrounding Arne is shown as stippled shading.

Direct observations were carried out from November 2007 to September 2008 and were classified into one of four seasons: winter (November-December 2007), spring (March-April), summer (June-July) and autumn (September 2008). Observations were made throughout the day to account for any circadian rhythm in patterns of habitat use by deer. Radio tracking (Chapter 3) and direct observations at Hartland and Arne showed deer grazing at different times of the day on improved grassland and saltmarshes or standing on the heath in the early hours of the morning. Also, human disturbance has been linked to differences in the habitat use of Sika deer in the area (Chapter 3), forcing deer to graze on the patches of improved grassland during the night. Consequently, a survey conducted during daytime would underestimate deer densities on the patches of grass, whilst a survey conducted during the night would overestimate average deer densities on the grass and underestimate average deer densities on the heath as a result of the aggregation of animals in patches of grass during the night. To account for such differences in the habitat use, each 24 hours period was divided into 12 periods of two hours. Twice per season, each route was surveyed within each of these two hours period, with a minimum of nine days between them. The following sampling restrictions were applied in each study area to avoid fatigue of the observer, to provide deer with enough time to change location and to avoid bias related to weather conditions: i) within any 24 hours period no more than four routes were conducted; ii) a minimum 3.5 hours were left between the beginning of the routes; iii) if more than 2 routes were carried out within 24 hours, a minimum of 12 hours was left between the completion of the second route and beginning of the third route. An example of the sampling restriction is given in Figure A1.2, where a 24 hours period for one site is shown. Fieldwork was not conducted under extreme weather conditions such heavy rain or fog that could affect visibility and/or deer behaviour.

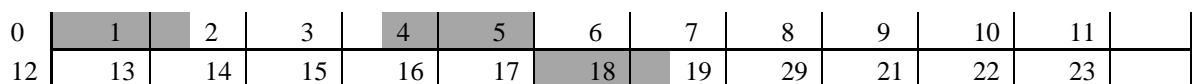


Figure A1.2: Example of radio tracking sampling restrictions within 24 hours period at one site. The number in each box represent hours. Survey periods are shaded in grey. No more than four routes were conducted within a 24 hours period (first restriction). The first route was surveyed from 0:00 to 01:30 (lasting 1.5 hours, maximum surveying time), the second route was surveyed after 3.5 hours since the beginning of the first route (second restriction), starting at 03:30 and lasting 1.5 hours. The third route was surveyed from 17:00 to 18:30, 12 hours after the second route was completed (third restriction).

To test if the route design and location of vantage points allowed the majority of open habitats within the study area to be viewed, the area of habitat that could be observed from each vantage point was estimated (Figure A1.1). To do this, each vantage point was first marked with a two-metre post as a representation of the observer's body. To define the area covered by the vantage point, the researcher then moved to different locations and noted whether he could see the post from his position. The total area covered by the vantage points was compared to the total area occupied by open habitats to test if vantage points were covering the majority of open habitats of the study area. The areas occupied by open habitats at each study area were measured using habitat maps and aerial photography.

The accuracy of measuring the location of deer was estimated as follows. The location error (the straight-line distance between the estimated and real position) of deer observations was estimated by comparing the positions obtained by direct observation (following the protocol described below) of 40 objects (fence posts) placed at random in our study areas with their GPS positions obtained by a handheld unit (Garmin GPS V®, maximum estimated location error of 5 metres). Aerial photographs of the area (scale 1:10,000) were used to estimate the geographic coordinates (Transverse Mercator projection, Ordnance Survey of Great Britain Datum 1936) of the real and observed locations.

The field observations of deer were conducted as follows: a suitable off-road vehicle was driven at a speed of 10 to 15 km/h between vantage points to minimize disturbance to deer in an attempt to avoid flushing behaviour that could result in double counts. As the observer approached each vantage point, any deer very close to the vantage point were counted, as these would be disturbed by the observer. When individuals or groups of deer were separated by more than 100 m, separate geographic positions were recorded. Before leaving the vehicle, a quick 360 degree scan using binoculars (and a hand torch during night time) was conducted in order to avoid missing animals that could have been disturbed by the arrival of the observer. Another quick scan was conducted at the end of any short walk required to get from the vehicle to the vantage point. After these quick scans, a longer scan of the area was performed. If deer were observed, the observation lasted a maximum of 10 minutes (although usually lasted a much shorter period) to examine the number of deer, activity, the location of the geometric centre of the deer groups and the direction in which deer could flush in order to anticipate double counts.

Activity was classified as ‘bedded/resting’ when animals were lying down, ‘standing’ when animals were not moving nor feeding and their heads were up, ‘feeding’ when actively feeding and ‘travelling’ when animals were moving across the surveyed area in one direction. If the visibility was reduced or the distance from the observer to the group of deer was too great to use the binoculars, the telescope was used. Flushing behaviour as a result of the presence of the surveyor was recorded as it was whether animals were observed before fleeing.

The field technique recorded the number of deer at specific locations and times. The field observations provided a snapshot of the location of deer, but in reality deer were moving throughout the study sites daily and seasonally. Consequently, in order to estimate seasonal spatial variation of local density of deer in open habitats at each of the study areas it was required to conduct a spatial interpolation of deer densities.

Modelling technique

A spatial interpolation based on the Gaussian kernel (see Diggle, 1985 for an example of this kernel function) was applied to the deer data. The type of kernel determines how events within the neighbourhood will be weighted and although theoretically important, the kernel type has little impact on the output (Nelson and Boots, 2008). In the Gaussian kernel method, the central point of a Gaussian kernel curve with a distance-decay function is placed on each of the deer observations and weighted by the number of deer per observation. A smoothing factor (also referred to as the bandwidth or h statistic) controls the amount of smoothing of the kernel density estimate. In this case the smoothing factor was based on the seasonal standard deviation (σ) of the kernel distribution of the home ranges of 31 female Sika deer obtained by telemetry (see Section 2.3.1). 31 female Sika deer were caught with nets during drive-beating sessions between December 2003 and February 2006 at Arne and February –March 2007 at Hartland. Animals were fitted with VHF TW-3 radiocollars (Biotrack Ltd.). Radio locations were obtained by triangulation (Kenward, 2001b) using a Telonics TR-4 receiver (Mesa, USA) and a three element hand-held Yagi antenna. From February 2004 to October 2007 (Arne) and May 2007 to February 2009 (Hartland) 35-36 locations per deer were obtained during February, May, July and October. The seasonal home-ranges of female Sika deer ($N = 21$ at Arne and $N =$

10 at Hartland) were obtained using Ranges8 software (Kenward *et al.*, 2008). Following Borger *et al.* (2006), home ranges were defined using the kernel method (Worton, 1989) for the 90% isopleths. The average of the standard deviation of the kernels distribution fitted to the locations of each deer was used as smoothing factor to reflect the species local behaviour in terms of movement abilities and the size of the area that deer were using during a season.

Using a smoothing factor linked to the area occupied by Sika deer over a season was preferred to the option of using a number without any biological meaning. As the direct observations on which the deer data were based were obtained over a period of time spread during a month, other choices of smoothing factor based on data obtained over a much shorter period of time (e.g. the average distance of daily travel or the average distance between successive radio tracking fixes) were not considered appropriate. The statistical standard deviation around mean range size was selected because this measure takes account of the full range of data collected instead of using a mean value that could be highly affected by extreme values.

In biological terms, use of the standard deviation as the smoothing factor implies in effect that there is a 68% likelihood that, during a given season, deer will use an area within a distance of a standard deviation from the actual location of any single observation. The probabilistic nature of the standard deviation also means that in using it as a smoothing factor there is a higher probability that deer will be found closer to the observed location and that the probability will gradually be lower as the distance to the observed location increases up to the value of the standard deviation.

Although different values of the smoothing factor affect the specific value of the estimated local density at a given location, correlation analyses conducted during the development of this method showed that the scoring of local density across different locations within the study areas was not affected by the choice of the smoothing factor.

The raw data comprised cumulative counts of the numbers of deer at specific locations observed over 24 surveys per season. The required output of the analysis was predicted spatial variation in the local density of deer in open areas during an observation period (i.e. season). Therefore, prior to analysis, the deer numbers observed at each location were

divided by 24, to convert cumulative numbers to those expected during a single visit. Two possible outputs of the modelling technique were obtained. First, the contours of local densities of deer were mapped to a raster format (resolution 10 x 10 m), as may be required to identify hotspots of activity. The resolution was selected as it was considered the highest possible resolution considering the potential error in locating deer and mapping habitats using conventional GPS devices. Second, the level of local density of deer around fixed points within the landscape were estimated, as may be required to relate the local density of deer to particular conservation areas. 100 random locations within the areas covered by the vantage points in each study area were used (as an example of the potentiality of the method to estimate the local density of deer around specific locations), with a minimum distance between locations of 25 metres.

The spatial interpolation of habitat usage by deer was conducted using the free SPATSTAT package of R (Baddeley and Turner, 2005, www.jstatsoft.org), which has a range of methods for analyzing spatial point patterns (see Appendix 1 for the R code used in the analysis).

Results

Field observations covered the majority of the open habitats in both study areas. Observations were obtained from an area of 177 ha at Arne (70% of the open habitats in this study area) and 343 ha at Hartland (81% of the open habitats). The estimated error in locating deer was 31.85 ± 4.11 m S.E. for both study areas combined (29.20 ± 5.79 m S.E. for Arne, 34.50 ± 4.25 m S.E. for Hartland).

Totals of 12,048 deer (in 684 groups) and 4,363 deer (in 236 groups) were observed at Arne and Hartland respectively during the survey period (Figures A1.3 and A1.4), therefore some deer were counted more than once. Seasonal results (Table A1.1) showed a much higher number of deer observed at Arne than at Hartland. The highest number of deer was observed during autumn in both study areas, while the lowest number of deer observed was obtained during summer at Arne and winter at Hartland.

Table A1.1: Seasonal observations of Sika deer at both study areas (N groups = Number of deer groups, N deer = Number of deer, A = Arne, H = Hartland).

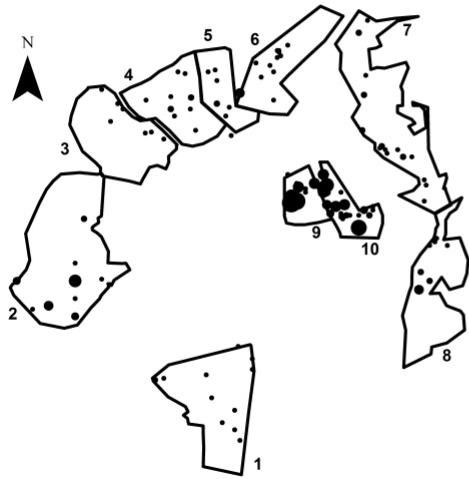
	Winter 2007		Spring 2008		Summer 2008		Autumn 2008	
	A	H	A	H	A	H	A	H
N groups	179	50	134	45	213	80	158	61
N deer	2761	518	2708	749	2608	1411	3971	1681

Observed deer activity was fairly consistent between study areas (Table A1.2). The most common deer behaviour observed at both study areas was ‘feeding’ and the least common ‘standing’. A total of 19.2 % of deer groups between both areas were disturbed as a consequence of the survey but 74.2 % of those groups were observed before the surveyor was detected and/or deer was alerted or flushed.

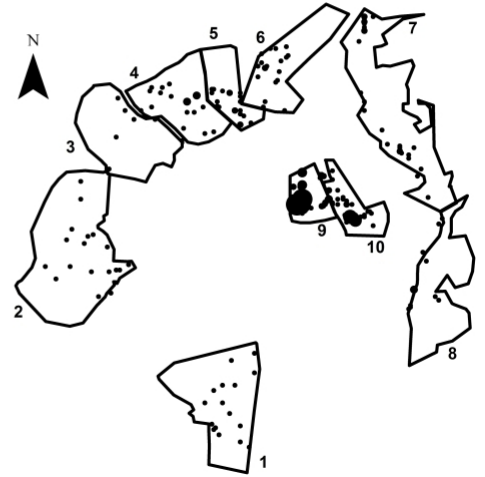
Table A1.2: Deer activity and response to survey recorded during the survey. Activity values indicate the percentage of deer groups in which the majority of members showed a particular behaviour.

		Arne	Hartland
Activity	Bedded/resting	16.4	14.8
	Standing	15.5	11.4
	Feeding	41.1	39.4
	Travelling/on move	17.3	24.6
	Unknown	9.7	9.8
Response to survey	Disturbed/flushed	18.1	20.3
	Seen before flushing	73.4	75.0

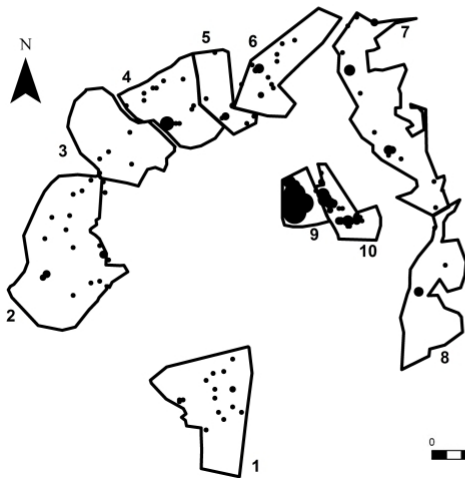
Winter 2007/2008



Spring 2008



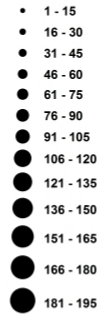
Summer 2008



Autumn 2008



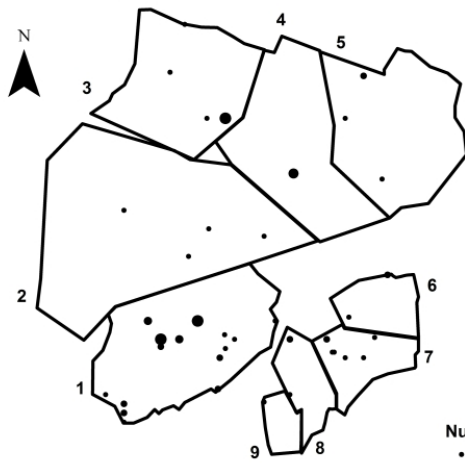
Number of deer observed



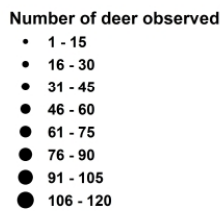
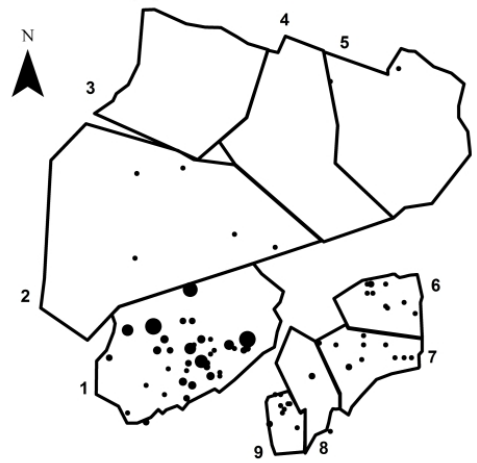
0 250 500 1,000 1,500 Meters

Figure A1.3: Observations of Sika deer at Arne. Polygons represent the areas surveyed from vantage points. Polygons 1 to 6 are areas of lowland heath; polygons 7 & 8 are saltmarshes; polygons 9 & 10 are areas of improved grassland.

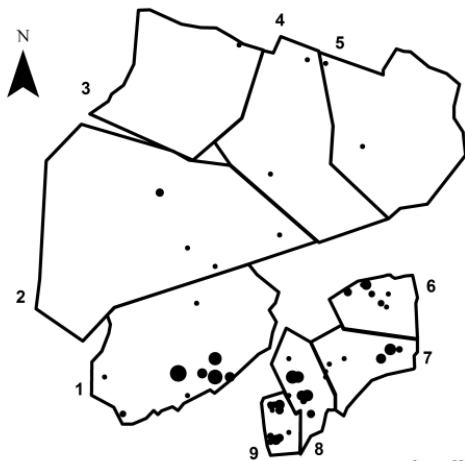
Winter 2007/2008



Spring 2008



Summer 2008



Autumn 2008

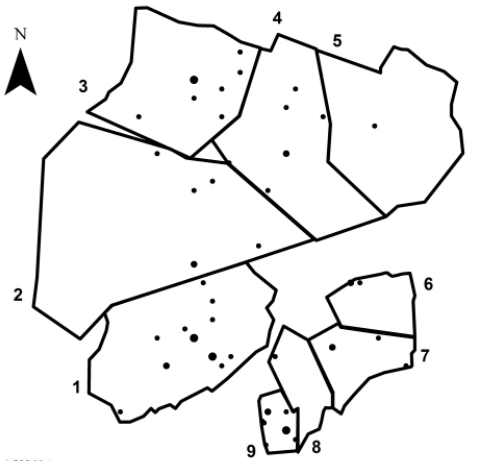


Figure A1.4: Observations of Sika deer at Hartland. Polygons represent the areas surveyed from vantage points. Polygons 2 to 5 are areas of lowland heath; polygons 1 & 6 to 9 are areas of improved grassland.

At Arne (Table A1.3), the highest number of deer observed in areas of lowland heath was found during winter and summer, whilst deer were observed in higher numbers in areas of saltmarshes during autumn. However, areas of improved grassland (polygons 9 and 10) showed overall the number of Sika deer throughout the year. At Hartland (Table A1.3), those areas of lowland heath showed the highest number of observed deer during winter. Areas of improved grassland showed the highest numbers of Sika deer throughout the year.

Table A1.3: Seasonal values of the number of deer observed in different open habitats at Arne and Hartland

		Heath	Grassland	Saltmarshes
Arne	Winter	618	1700	325
	Spring	441	1732	317
	Summer	637	2923	333
	Autumn	319	1677	736
Hartland	Winter	208	503	-
	Spring	9	1397	-
	Summer	69	1564	-
	Autumn	139	379	-

Home range analysis obtained an average annual value of the standard deviation (σ) of the kernels distribution fitted to the locations of each of the female Sika deer home range of 289.50 m at Arne and 306.86 m at Hartland. The average seasonal value of σ for each study area is showed in Table A1.4.

Table A1.4: Seasonal values of the standard deviation of the kernels distribution fitted to the locations of each of female Sika deer σ (m) derived from the home range analysis. A = Arne, H = Hartland.

Winter 2007		Spring 2008		Summer 2008		Autumn 2008	
A	H	A	H	A	H	A	H
302.43	354.92	269.80	281.52	282.38	348.35	298.50	202.96

A spatial interpolation of the seasonal habitat usage by Sika deer was obtained for each of the study areas. In agreement with the results showed in Table A1.3 at Arne, those areas of lowland heath (polygons 1 to 6, west part of the study area) seemed to show higher local densities of Sika deer during winter and summer, whilst areas of saltmarshes (polygons 7 and 8) seemed to hold higher local densities of Sika deer during autumn. Areas of improved grassland (polygons 9 and 10) showed the highest level of local density of Sika deer throughout the year (Figure A1.5).

At Hartland (Figure A1.6), those areas of lowland heath (polygons 2 to 5, west part of the study area) were more used by Sika deer during winter. Areas of improved grassland (polygons 1 and 6 to 9) showed the highest habitat usage by Sika deer throughout the year.

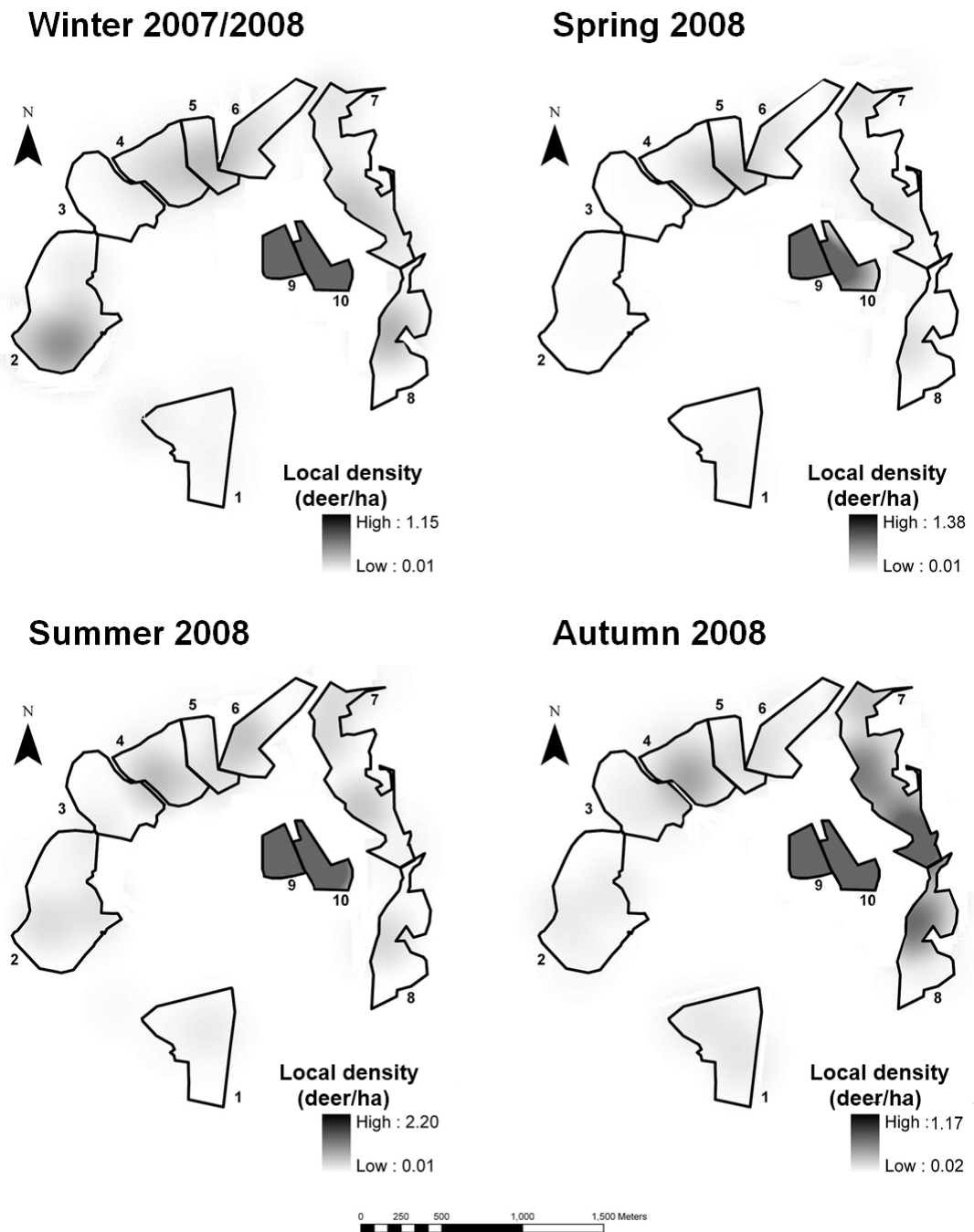
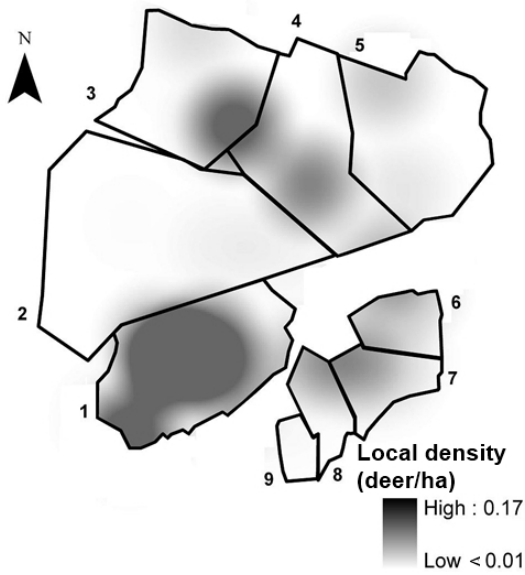
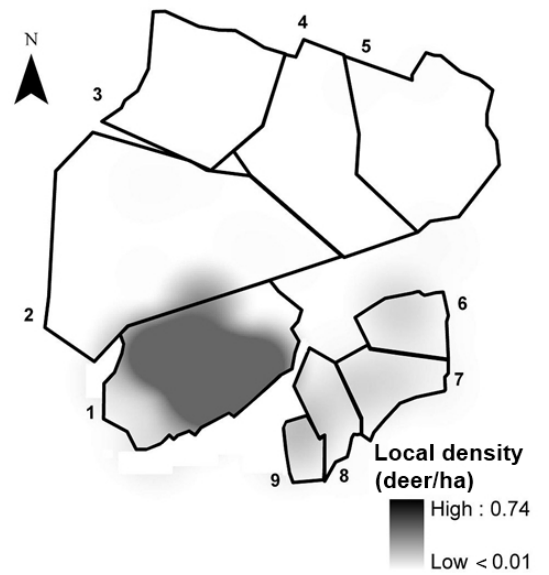


Figure A1.5 Spatial interpolation of local density of Sika deer at Arne across the seasons. Polygons represent the areas surveyed from vantage points. Polygons 1 to 6 are areas of lowland heath; polygons 7 & 8 are saltmarshes; polygons 9 & 10 are areas of improved grassland. Darker shading indicates higher local density of Sika deer.

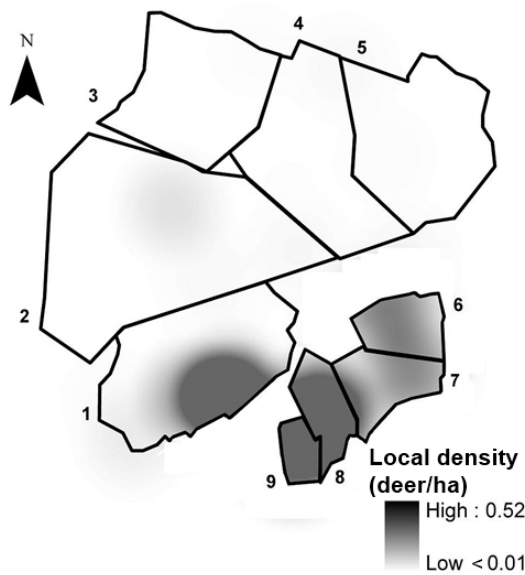
Winter 2007/2008



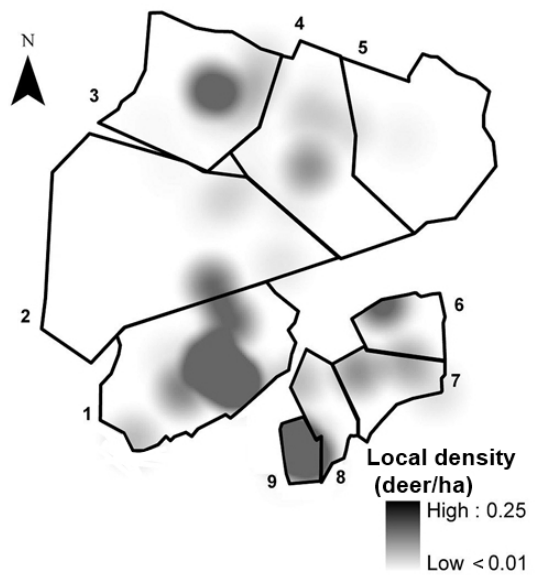
Spring 2008



Summer 2008



Autumn 2008



0 250 500 1,000 1,500 Meters

Figure A1.6: Spatial interpolation of local density of Sika deer at Hartland across the seasons. Polygons represent the areas surveyed from vantage points. Polygons 2 to 5 are areas of lowland heath; polygons 1 & 6 to 9 are areas of improved grassland. Darker shading indicates higher local densities of Sika deer.

The results of the interpolation of levels of local density of Sika deer at the random locations also differed depending on the season in which the direct observations were conducted (see an example of the results from two seasons in Figure A1.7 below).

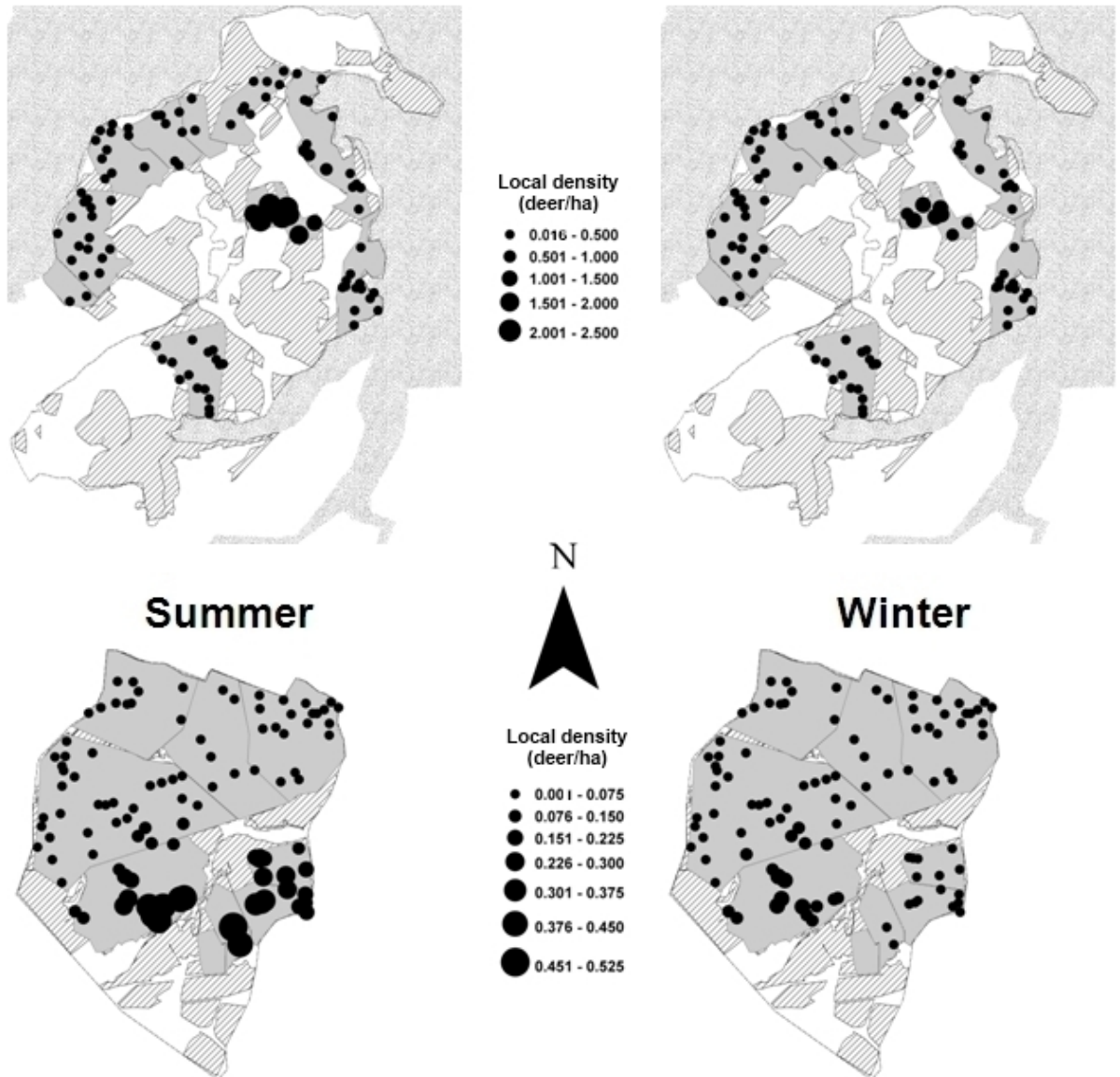


Figure A1.7: Interpolation of local density of Sika deer (deer/hectare) at Arne around 100 random locations (dots) in open areas during Summer and Winter. Increasing size of dots indicate higher local density in the proximity of the location. Arne (top), Hartland (bottom).

Discussion

The method presented in this study fulfilled the aim of this research as it was able to obtain an estimation of the spatial variation in the seasonal local density of deer. The field technique was able to cover the majority of the open habitats. Deer were observed and located independently of differences in vegetation and terrain between the open habitats surveyed in the study areas. Observations were spread during a month in each season, were obtained at different times of the day and night and the observer minimized disturbing deer while making observations. The modelling technique allowed an easy visualization of the spatial variation in the local density of deer and also estimated the local density of deer around specific locations, which could represent, for instance, areas of particular conservation interest.

Field technique

The method described in this section was able to obtain a seasonal estimation of the spatial variation in the local density of deer in open habitats by surveying at different hours during the night and day and averaging results. Estimates of deer numbers obtained over a short time period by vantage points or driven counts do not necessarily reflect the average seasonal or annual density and therefore the browsing pressure on vegetation (Palmer and Truscott, 2003) or other potential impacts related to deer use. This is due to differences in deer aggregation and habitat use on different areas depending on different factors such as season, time, weather and human disturbance. Direct surveys of deer numbers within an area of interest are usually concentrated around the hours before and after sunrise and sunset (e.g. Focardi *et al.*, 2002, Koenen *et al.*, 2002, Acevedo *et al.*, 2008). This is done to optimize deer observations and record the highest possible number of deer over a given area. However, as this research was focused on observing deer on open areas, limiting the observations to one singular period during the day or night would result in an overestimation or underestimation of the deer use of open areas. By conducting the surveys at different hours during the night and day the estimations of the local densities of deer were averaged, hence potential overestimations or underestimations of local deer densities were minimized.

The surveys were able to cover the majority of the open habitats in both study areas and observations had a limited observation error in terms of their geographical location. The potential disadvantage of a more limited sight range during the night was minimised when possible by adding another vantage point to the route conducted at Arne. The open habitats surveyed were grassland, lowland heath and saltmarshes, which in the study areas were heavily grazed, which minimize the chances of not detecting an animal when bedded down. A high percentage of the deer were located and counted prior to a change of behaviour (i.e. flushing) caused by the disturbance. This indicates that approaching the vantage point did not cause great disturbance to deer, while the following act of standing and watching the animals resulted in disturbance for deer. Direct observations allowed the observer to obtain data related to behaviour and population structure, which can be considered a supplementary advantage of this method.

The method described required 24 surveys per season to each of the study areas; this represents 48 h of field work per season and study area. The method presented here was less labour-intensive than other methods used to obtain the total population density, such as ground counts (60 to 178 h per area) or dung counts (66 to 185.5 h per area) as described by Daniels (2006). Also this method used limited equipment, which also reduces total costs compared to direct methods to estimate total population densities such as helicopter counts (see Daniels, 2006 for a description of costs associated with different methods).

In contrast to the established Distance Sampling method to estimate deer densities (Buckland *et al.*, 2001), the method described was not able to estimate the probability of detecting a deer, which might be the most important disadvantage of the present method. As a recommendation for future use of this field technique, it is advised that the number and location of vantage points should be carefully adapted to the particular characteristics of the study area so that the majority of the open habitats are surveyed during the day and night. Also, the location of vantage points might need to be changed through the year in other studies, given changing visibility due to deciduous trees and seasonal vegetation. Finally, the response of animals to observers when they are standing and watching should be assessed in the future and alternatives (such as selecting vantage points that can be viewed directly from an off-road vehicle) should be implemented.

Modelling technique

Most frequently, population size of wildlife is estimated from sample counts throughout a study area (Pople *et al.*, 2007). Obtaining population size is the aim of techniques such as Distance Sampling (Buckland *et al.*, 2001). By contrast, the pattern of distribution of wild populations is either ignored or considered subjectively (Pople *et al.*, 2007). In the present study, the field technique was designed to obtain deer observations, which are an example of point-based data that needs to be converted to surfacial data (i.e. two dimensions with assigned area) in order to estimate spatial variation in deer occurrences (e.g. Plante *et al.*, 2004). The modelling technique described in this section transformed those direct observations of deer locations in a surfacial estimation of the spatial variation in seasonal local density, which allowed obtaining both an easy visualization of the spatial variation in seasonal local density of deer and also an estimation of the local density of deer around random locations.

The modelling technique presented here is similar to some stages of the methods developed by Plante *et al.* (2004) to relate deer occurrences to landscape characteristics or the method developed by Nelson and Boots (2008) to detect spatial hot spots of mountain pine beetle infestation, in particular the choice of a kernel smoothing function to conduct a spatial interpolation of densities. The method described in this section used a value of the kernel smoothing function directly related to the home range of Sika deer in the study areas in an attempt to reflect the movement abilities of Sika deer and the size of the area that deer were using during a season and so smooth the distance between sampling locations. There is inevitably an element of subjectivity in choosing the appropriate value for the smoothing factor (Nelson and Boots, 2008). Consequently, although it is recommended to have knowledge of the home range of the specific species of deer to estimate their movement abilities and smooth the distance between locations, in the absence of such data it would be possible to use estimates of home range size derived from the literature for similar species in similar habitats

Only data from female Sika deer were used to estimate the smoothing factor. Studies on the deer home ranges of both sexes have shown that in some cases the size of home ranges among deer sexes do not differ (e.g. Inglis *et al.*, 1979, Tierson *et al.*, 1985). However, male deer often have larger home ranges than females (e.g. Catt and Staines, 1987,

Borkowski and Pudelko, 2007, Kamler *et al.*, 2008, Vila *et al.*, 2008). Consequently, it is possible that the movement abilities of Sika deer as a whole population in the study areas has been underestimated, and therefore the spatial influence of the deer observations might have been also underestimated. To overcome this potential disadvantage further use of this technique should consider obtaining the home ranges for both males and females to estimate their movement abilities.

The required analyses were performed using open source software; therefore this technique can be used by managers or researchers with limited resources, although some training is required for both the field and modelling method. Field training should involve developing deer recognition and time management skills, while modelling training should include the acquisition of basic R-language skills.

R-CODE

Part 1: Getting the data into R

```
rm(list=ls())
library(maptools)
library(rgdal)
library(spatstat)
Uploading the files
wd<-getwd()
setwd("FILES FOLDER LOCATION")
areas<-readShapePoly("SHAPE FILE WITH VANTAGE AREAS ")
deer<-read.csv("OBSERVATIONS FILE SPREADSHEET.csv")
sites<-read.csv("FILE WITH SELECTED LOCATIONS")
setwd(wd)
```

Part 2: Fitting a Kernel function with a smoothing factor ‘VALUE’ and weighting deer observations by the number of deer per observation ‘NUM’

```
sigmaVALUE<-density.ppp(deer.ppp,weights=deer[["NUM/number VISTS"]],sigma=VALUE,
  edge=FALSE)
```

Part 3: Extracting the values of deer density per visit at the selected locations (‘sites’)

```
sigmaVALUE<-as.SpatialGridDataFrame.im(sigmaVALUE)
sigmaVALUE@proj4string<-areas@proj4string
sites[["FIGURE_HEADING"]]<-overlay(sigmaVALUE,sites)@data$V*10000/NUMBER_OF_VISITS
sites<-data.frame(sites)
```

Part 4: Saving the results

```
setwd("FILES FOLDER LOCATION")
write.csv(sites,"OUTPUT TABLE.csv",row.names=F)
save(list=ls(),"output.rob")
setwd(wd)
library(xtable)
xtable(sites)
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APPENDIX 2: HOW ARE INDIRECT MEASUREMENTS OF LOCAL DENSITIES OF DEER IN OPEN HABITATS AFFECTED BY SEASON AND HABITAT TYPE?

Abstract

Methods to estimate deer numbers usually aim to obtain deer densities for geographical blocks or habitat types rather than obtaining the spatial variation of densities of deer at a finer scale (i.e. local density). Therefore, comparisons of methods to estimate population deer densities might not be applicable to estimations of local densities of deer, as the impact of habitat or seasonal variation on direct and indirect measures of the spatial usage of deer might have not been sufficiently accounted for. This study analysed the effect of habitat variability (dry heath versus wet heath) and temporal variability (season) upon relationships between four indirect indices of local density of deer. It also investigated whether incorporating a measure of the effect of such habitat and temporal variability might improve the relationship between a direct estimation of the spatial variation in local densities of deer and the indirect indices. The four indirect indices used were: the percentage of area trampled by deer; the number of tracks; the total number of pellets and the distance to first sign of deer presence. The strengths of the relationships between the direct estimation and indirect indices were investigated using bivariate and partial correlation analyses and found to vary in response to both habitat and seasonal changes. Analysis using general linear models (GLMs) showed that the best model for predicting the direct estimation of local density of deer from an indirect index incorporated both heath type and season. It is concluded that care should be taken when interpreting indirect indices to estimate the spatial variation of local densities of deer, taking into account the likely effects of habitat and season on these indices. An approach for deriving indirect indices that account for habitat and season is finally proposed.

Key words

Deer density, Sika deer, *Cervus nippon*, heath, deer signs, counting methods

Introduction

Many studies have compared methods for obtaining relative or absolute deer densities in terms of their accuracy, precision and cost (e.g. Mandujano and Gallina, 1995, Doney, 1996, Mayle, 1996, Mayle *et al.*, 1999, Mayle *et al.*, 2000, Focardi *et al.*, 2001, Campbell *et al.*, 2004, Smart *et al.*, 2004, Daniels, 2006, Acevedo *et al.*, 2008, Meriggi *et al.*, 2008). Such comparisons have been usually made between methods to estimate deer numbers which aimed to obtain deer densities for geographical blocks or habitat types rather than obtaining the variation in habitat usage by deer at a finer scale. However, several studies have shown that deer habitat use varies spatially and temporally (e.g. Georgii, 1981, Mann and Putman, 1989b, Yeo and Peek, 1992, Benhaiem *et al.*, 2008). Researchers and managers might be also interested in estimating the spatial variation of deer occupancy within smaller areas of few tens of hectares in order to reflect the extent to which patches of habitat are being used by deer. Therefore, comparisons of methods to estimate population deer densities might not be applicable to estimations of the spatial variation in the local density of deer as the impact of habitat or seasonal variation on direct and indirect measures of local density of deer might have not been sufficiently accounted for.

Variation in habitat type is an important component of spatial variability of a study area; the other is the distribution (juxtaposition) of habitats. Both components might affect the spatial pattern of habitat use of deer. For instance, it has been shown that the extent to which Red deer (*Cervus elaphus*) utilize patches of heath is strongly related to vegetation distribution within a heather/grass landscape (Clarke *et al.*, 1995b, Palmer and Hester, 2000). The non-random nature of deer habitat use and selection is reflected by different levels of aggregation of deer in patches of habitat and subsequently the amount of signs of presence. It has been argued that stratified sampling that accounts for this habitat type variability is required in deer monitoring programmes (Mayle *et al.*, 1999, Putman and Watson, 2009). Such stratification is usually based on habitat or ecological characteristics with which the density of deer might be related, such as resources available to deer (Mayle *et al.*, 1999). However, such stratification might not take into account habitat features related to vegetation and terrain properties that might affect the establishment, decay rates and detectability of signs of deer presence. For example, the amount and type of ground cover affects the detectability of pellets (Neff, 1968), while the decay rate is determined by moisture, substrate and canopy of the area (Harestad and Bunnell, 1987). Therefore, further

stratification within main habitats might be also required in order to account for differences in terrain or vegetation characteristics.

The extent to which deer use different habitats and locations varies temporarily through the day and across seasons due to changes in the availability of resources and/or frequency of disturbance as it has been shown for species including Sika deer *Cervus nippon* (e.g. Mann and Putman, 1989b), Roe deer *Capreolus capreolus* (e.g. Benhaiem *et al.*, 2008), Red deer (e.g. Georgii, 1981) and Sitka black-tailed deer *Odocoileus hemionus sitkensis* (e.g. Yeo and Peek, 1992) among an extensive number of other studies for different cervids. As a high percentage of studies and monitoring programmes require a single measurement of the population density of deer usually monitoring programmes and comparisons between methods for estimating population density of deer have recorded a single annual value of density (e.g. Mayle *et al.*, 2000, Focardi *et al.*, 2002, Campbell *et al.*, 2004, Daniels, 2006, Acevedo *et al.*, 2008). Far fewer studies have extended the period of data collection to two seasons (but see Agetsuma *et al.*, 2003). Therefore, comparisons between methods of measuring deer population density usually do not reflect seasonal changes in the spatial variation of local densities of deer.

Comparisons between direct and indirect methods to obtain deer population densities in open areas are available (Mayle and Staines, 1998, Mayle *et al.*, 1999, Daniels, 2006, Putman and Watson, 2009). Direct methods involve observing and counting animals while indirect methods relate the presence of deer signs (e.g. tracks, faeces) to deer numbers. Indirect indices are preferred in concealed habitats (Mayle and Staines, 1998, Mayle *et al.*, 1999, Marques *et al.*, 2001) where it is difficult to reliably observe deer. In open areas both direct and indirect methods can be used, although it has been postulated that the most suitable methods (in terms of effectiveness) are direct observations (Marques *et al.*, 2001). However, further study of the bias in estimates of deer population densities related to the habitat and temporal variations in deer distribution has been urged by Uno *et al.* (2006). Moreover, the effects of habitat and temporal variability on comparisons between indices to estimate the spatial variation of local densities of deer have not been investigated sufficiently. Therefore, these comparisons might be habitat and season-specific, limiting extrapolation of results to other sites, habitats and seasons.

The specific aim of this study was to investigate the extent to which differences related to habitat and temporal variability affects predictions of local densities of deer from indirect indices. To fulfil this aim the objectives of this research were: i) to analyse the effect of habitat and temporal variability upon comparisons between indices to estimate the spatial variation in local densities of deer; ii) to analyse whether incorporating habitat and temporal variability might improve the relationship between a direct, reference method and a range of indirect methods. In the light of the results obtained, the present research discussed whether integrating habitat and temporal variability might improve calibrations of indirect methods of estimating the spatial variation in local densities of deer.

Study areas

Two study areas were selected to determine how the effects of habitat and season on the estimated level of habitat usage by deer differed between sites. Both study areas were located in the region of Purbeck in Dorset, southwest England. Purbeck is part of the Poole Basin, which contains one of the largest populations of wild Sika deer in England (Putman, 2000). The landscape of Purbeck is a mosaic of farmland, deciduous and coniferous woodlands, reed-beds and open habitats such as lowland heaths and saltmarshes. Two study areas of contrasting population densities of Sika deer in this region were selected: Arne and Hartland. Arne Reserve ('Arne'), which is a 608 ha protected area located on the west coast of Poole Harbour in Dorset (50° 41' 20" N, 2° 2' 20" W) and Hartland Moor and Middlebere Heath National Nature Reserve ('Hartland'), which is also a protected area of 550 ha situated 3 km south of Arne (50° 39' 58" N, 2° 4' 26" W). Both areas contain coniferous and deciduous woodland, lowland heath, pastures and wetland habitats such as saltmarshes and reed-beds. Population densities of Sika deer differed between these areas; the estimated density in October 2007 at Arne was 118 deer/km² whilst at Hartland it was 26.5 deer/km². Numbers of Roe deer, the only other deer species in the area, were extremely low in both areas.

Methods

Experimental design

Lowland heath, an international priority conservation area (i.e. Habitats Directive 92/43/EEC), was chosen as an example of an open habitat abundant in the study areas. Previous field observations indicate that Sika deer make extensive use of lowland heath in the study areas. Although lowland heath is considered as a major habitat type, it is usually divided into two habitat types: dry and wet heath (Gimingham, 1992). Dry heath is found on freely drained soils while wet heath is found where soil drainage is impeded and peaty humus accumulates at the surface (Gimingham, 1992).

To evaluate the spatial variation in the local density of deer, a total of 90 sampling points were placed in the two study areas, 60 in Arne and 30 in Hartland, at random locations following two restrictions: i) a minimum distance between points of 25 m; ii) the random points were divided equally between the two different heath types. The difference in sample size between the two areas reflects the availability of wet heath in each area. A point was classified as located on dry heath when the 5 metres radius area around the centre of the site contained a composition of heath species dominated by *Calluna vulgaris* and/or *Erica cinerea* with a combined percentage higher than 50% of the total vegetation cover. Points classified as wet heath contained *Erica ciliaris* and/or *Erica tetralix* associated or not with *Molinia caerulea* with a combined percentage higher than 50% of the total vegetation cover. During the study, two points located on wet heath in Arne were accidentally removed due to land management changes therefore data from these two points were excluded from the analysis.

Indirect methods for estimating the spatial variation in local densities of deer

Four indirect indices to estimate the spatial variation in local densities of Sika deer were recorded (Table A2.1). The indices attempted to reflect the level of deer activity in the area: the percentage of area trampled by deer ('trampling') and the number of deer tracks ('tracks') reflected the physical damage caused by trampling by deer; the number of pellets ('pellets') was related to the abundance of deer in the area as it was assumed that higher

concentration of pellets would be related to higher local density. Finally, the first sign of Sika deer presence ('first sign') was selected as an index of probability of finding a sign of Sika deer presence as this index is based on all the Sika deer signs used in the indices described above.

Table A2.1: Name, abbreviated name used in the text and definition of the indirect indices used in this research.

Indirect Index	Acronym	Definition
Percentage of area trampled by deer	Trampling	Percentage of area trampled caused by deer activity
Number of deer tracks	Tracks	Number of paths created by deer
Number of pellets	Pellets	Total number of faecal pellets (faecal standing crop method)
Distance to first sign	First Sign	Distance to first sign of deer presence (hair, track or pellet)

Two plots were located at each sampling point. The first plot was placed 15 m from the centre of the point (which was marked with a 1.5 m post), using a random compass bearing, whilst the second plot was placed 15 m from the opposite side of the post (Figure A2.1). All indirect measurements were taken within a 5 m radius around the centre of a plot. The distance index was measured by walking in circles at 0.5 m increments up 5 m from the centre of the plot and noting the distance to the first sign of Sika deer presence. Results for each plot and indirect index were averaged for analysis, obtaining one data point for each indirect index per sampling point.

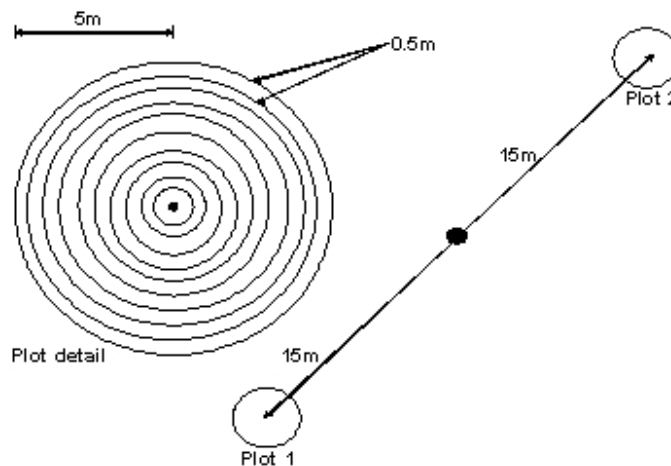


Figure A2.1: Design of indirect observation plots. Plots were located 15 m on either side of the centre of the site at a random angle. Within each plot five indirect indices were measured over the whole plot area or by walking in circles every 0.5 m increments up 5 m around the centre of the plot.

Direct method for estimating the spatial variation in the local densities of Sika deer

The spatial variation in the local densities of Sika deer was obtained by conducting a field survey based on the use of vantage points to obtain observations of deer throughout the day and across seasons followed by a modelling technique that used the field observations and data on the extent of movement of Sika deer to estimate the spatial variation in the local density of deer.

The spatial modelling was based on a kernel smoothing with a decay-rate function related to the movement abilities of Sika deer. Previous methods have used similar modelling technique to spatially interpolate densities of terrestrial mammals (e.g. Potvin *et al.*, 2005) or detect hot spots in landscape ecology (Nelson and Boots, 2008). In this case the value of the smoothing factor reflects the movement abilities and the size of the area that Sika deer were using during daily activities. The average of the standard deviation of the kernels distribution fitted to the locations of the home ranges of 31 female Sika deer obtained by radiotracking. Using a smoothing factor linked to the area occupied by Sika deer over a season was preferred to the option of using a number without any biological meaning. As the direct observations on which the deer data were based were obtained over a period of time spread during a month, other choices of smoothing factor based on data obtained over a much shorter period of time (e.g. the average distance of daily travel or the average distance between successive radio tracking fixes) were not considered appropriate. The statistical standard deviation around mean range size was selected because this measure takes account of the full range of data collected instead of using a mean value that could be highly affected by extreme values. In biological terms, use of the standard deviation as the smoothing factor implies in effect that there is a 68% likelihood that, during a given season, deer will use an area within a distance of a standard deviation from the actual location of any single observation. The probabilistic nature of the standard deviation also means that in using it as a smoothing factor there is a higher probability that deer will be found closer to the observed location and that the probability will gradually be lower as the distance to the observed location increases up to the value of the standard deviation.

Although different values of the smoothing factor affect the specific value of the estimated local density at a given location, correlation analyses conducted during the development of

this method showed that the scoring of local density across different locations within the study areas was not affected by the choice of the smoothing factor.

The modelling technique, performed using open source software, estimated the level of local density of deer around the specific locations. These areas could represent, for instance, areas of particular conservation interest. Analyses were performed using open source software. However, this technique was more labour intensive than any of the indirect indices. It was assumed that this direct method had no bias linked to effects of habitat or temporal variation upon the location and time/date of the deer observations. This assumption is considered to be sound because: i) observations covered all sampling points and vicinities of lowland heath in both study areas; ii) the locations of the vantage points allowed the researcher to observe and locate deer independently of differences in vegetation and terrain between different lowland heath types; iii) observations were spread during a month in each season and also were obtained at different times of the day and night; iv) the observer minimized disturbing deer while making observations. Although in itself an estimate of the number of deer present, and hence subject to errors, this method is believed to provide an appropriate estimate of the spatial variation of local densities of Sika deer in the study areas.

To evaluate the importance of seasonal variability upon the results, observations were carried out from November 2007 to November 2008 and classified into four seasons: winter (November 2007 to February 2008), spring (March to May 2008), summer (June to August 2008) and autumn (September to November 2008). Direct observations were conducted during the first 2 months of each season while indirect observations were made during the last month of each season. Due to the amount of fieldwork involved was not possible to conduct both methods at the same time.

Analysing effects of habitat type and season on indirect indices

To analyse whether the relationships between indirect indices were affected by differences in habitat type (dry and wet heath) and season, a seasonal Spearman correlation analysis between all possible pairs of indirect indices in both habitats and across all seasons was firstly carried out. Then, a Spearman partial correlation analysis (Iwata *et al.*, 2002), in

which the variable “heath type” was used as covariate in each season, was carried out. The partial correlation coefficient between one indirect index (A) and another (B) adjusted for heath type (C) was computed from the pairwise values of the correlation between variables A, B and C (ρ_{AB} , ρ_{AC} , ρ_{BC}):

$$\rho_{ABC} = \frac{\rho_{AB} - \rho_{AC}\rho_{BC}}{\sqrt{(1 - \rho_{AC}^2)(1 - \rho_{BC}^2)}}$$

where ρ is the coefficient of correlation, A is the first indirect index, B is the second indirect index and C is heath type.

The importance of heath type was determined by how much its incorporation decreased or increased the size of the correlation coefficient. This gave as an indication of the effect of heath type on the strength of the relationship between the indices. Values were obtained by applying the following formula:

$$\text{Importance of heath type} = [(\rho_h/\rho_w) \times 100] - 100$$

Where ρ_h is the coefficient of correlation considering the effect of heath type and ρ_w is the coefficient of correlation without considering the effect of heath type.

A univariate general linear model (GLM, Rutherford, 2001) was used to analyse how the relationship between an indirect index and the direct measure was related to the habitat type and season in which observations were made. The GLM used the direct measure as the dependent variable and each of the indirect indices as the main predictor. Study area, heath type and seasons were included as fixed factors to build the best possible model to predict the direct measure.

The following formula of GLM was applied:

$$D = \beta_0 + \beta_1 I + \beta_2 x_2 + \dots + \beta_i x_j + \varepsilon$$

where D is the dependent variable (direct measure), β are constants obtained by fitting the model, I is the predictor (indirect index) and x the fixed factors and their interactions.

The GLM was used to identify those fixed factors that together with each indirect index were significantly related to the direct measure. All possible combinations of fixed factors and their interactions were tested to determine the best model for predicting the direct measure from each indirect index.

Two-tailed statistical tests were performed with significance assumed wherever $P < 0.05$. SPSS 15.0 statistical software (SPSS Inc. 2006) was used for the analysis.

Results

Comparison between indirect indices

Table A2.2 shows the coefficients of correlation ρ and significance levels for the pairs of indirect index during each season. Table A2.3 shows the coefficients of correlation and significance levels between the pairs of indirect index controlling for the factor ‘heath type’ in a partial correlation. Seasonal analysis of the relationship between indirect indices showed important variability in results, with the weakest correlation coefficients during winter in both study areas (Table A2.2 and A2.3).

Table A2.2: Bivariate correlation coefficients (ρ) between indirect indices to measure the local density of Sika deer ignoring effects due to heath type. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$

	Index	Arne			Hartland		
		Trampling	Pellets	First sign	Trampling	Pellets	First sign
Spring	Tracks	0.72**	0.34*	-0.42**	0.61**	0.32	-0.28
	Trampling		0.54*	-0.58**		0.50**	-0.73**
	Pellets			-0.66**			-0.39*
Summer	Tracks	0.73**	0.39**	-0.43**	0.75**	0.27	-0.37
	Trampling		0.38**	-0.38**		0.12	-0.45*
	Pellets			-0.67**			-0.42*
Autumn	Tracks	0.79**	0.26	-0.50**	0.92*	0.36	-0.81**
	Trampling		0.25	-0.51**	-	0.39*	-0.59**
	Pellets			-0.72**	-	-	-0.38*
Winter	Tracks	0.65**	0.22	0.16	0.73**	0.08	0.30
	Trampling		0.29*	0.20	-	0.04	0.13
	Pellets			-0.25	-	-	0.44*

In both study areas, during all seasons, in both the bivariate and partial correlation analysis, the overall strongest significant relationship was between the track and trampling indices, while the weakest was between pellets and both tracks and trampling (Table A2.2 and A2.3).

Table A2.2: Bivariate correlation coefficients (ρ) between indirect indices to measure the local density of Sika deer accounting for effects due to heath type. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$

	Index	Arne			Hartland		
		Trampling	Pellets	First sign	Trampling	Pellets	First sign
Spring	Tracks	0.71**	0.31*	-0.37**	0.64**	0.36	-0.3329
	Trampling		0.52**	-0.056**		0.46*	-0.72**
	Pellets			-0.65**			-0.31
Summer	Tracks	0.73**	0.40**	-0.42**	0.77**	0.28	-0.36
	Trampling		0.38**	0.38**		0.21	-0.45*
	Pellets			-0.67**			-0.48*
Autumn	Tracks	0.74**	0.21	-0.41**	0.93**	0.38*	-0.63**
	Trampling		0.20	-0.42**		0.43*	-0.63**
	Pellets			-0.72**			-0.37*
Winter	Tracks	0.61**	0.17	0.10	0.66**	0.13	0.31
	Trampling		0.26	0.16		0.10	0.12
	Pellets			-0.28*			0.45*

The results seem to indicate that correlations among pairs of indirect indices were affected by the type of heath in which they were measured. When heath type was introduced as a covariate, the strength of the relationship between the indirect indices (measured by the coefficient ρ) changed in both study areas, making the relationship stronger or weaker depending on the pair of indirect indices and season (Table A2.4).

Table A2.3: : Difference in percentage between coefficients of correlation ρ with and without heath type as a covariate

	Index	Arne			Hartland		
		Trampling	Pellets	Distance	Trampling	Pellets	Distance
Spring	Tracks	-1.80	-9.12	-12.26	4.91	11.95	18.35
	Trampling		-3.71	-4.12		-6.85	-1.78
	Pellets			-1.36			-20.72
Summer	Tracks	0.27	2.80	-2.08	2.13	6.77	-2.19
	Trampling		0.52	-0.79		79.17	-0.44
	Pellets			1.05			14.83
Autumn	Tracks	-6.48	-18.25	-19.05	0.22	5.31	-22.09
	Trampling		-19.61	-18.91		9.64	6.44
	Pellets			0.00			-2.86
Winter	Tracks	-4.95	-22.77	-36.59	-9.62	69.74	3.00
	Trampling		-10.62	-18.59		188.89	-5.56
	Pellets			15.45			1.59

Predicting direct measure of local density of Sika deer from indirect indices

The best possible model to predict the direct measure from the pellet, track and distance indices included study area, heath type and season as fixed factors (Table A2.5). A square root transformation of the direct measure was used to obtain a better model fit. It was not possible to obtain a significant model to predict the direct measure from the trampling index.

Table A2.4: Best general linear model (GLM) to predict the direct measure of the local density of Sika deer from an indirect index. Fixed factors: ST = study area, H = heath type, S = season; P = predictor (indirect index), ^ = interaction between fixed factors. Asterisks indicate those factors or interactions used to generate the best linear model and the level of significance of their adding value to the general model: *P < 0.05; ** P < 0.01; *** P < 0.01

Predictor	ST	H	S	ST^H	ST^S	H^S	P^ST	P^H	P^S	R ²
Tracks	***	**	***							0.30
Pellets	***	***	**	**	*					0.33
Distance	***	**	**							0.30
Trampling	No significant GLM model using Trampling as a predictor.									

Discussion

In this section it has been demonstrated that the correlation between the indirect indices to estimate the local density of deer in open areas are affected by the habitat type and season in which measurements are taken. The effect of habitat and temporal variability (heath type and season) on the relationship between pairs of indirect indices has also been quantified. Finally, it has been demonstrated how to better predict the local density of deer from an indirect index by including the effects of habitat and temporal variability as factors.

The analysis has shown differences in the results obtained from indirect indices related to the type of heath where observations were made. Those differences might be related to detectability and decay rate of Sika deer signs. For instance, a more detectable effect of signs of trampling on wet heath than on dry heath under the same deer densities might have resulted in an overestimation of Sika deer abundance using the number of tracks or the percentage of area trampled by deer in this habitat. Also the distance to first sign of deer presence, which combines pellets and deer tracks, might show some bias related to a possible higher possibility of finding Sika deer tracks on wet/humid terrain. This probably is even more likely to occur during the more humid seasons. Pellet counts, on which the pellet and distance to first sign indices are at least partially based, are also affected by the amount and type of ground cover for two reasons. The first is that it affects the detectability of pellets (Neff, 1968, Putman, 1984, Forsyth *et al.*, 2009) and the second is that the decay rate is determined by moisture and substrate of the area (Harestad and Bunnell, 1987).

The results have shown that both the relationship between pairs of indirect indices were affected by the season in which the observations were obtained. As terrain and vegetation conditions change during the year (for instance the percentage of humidity or vegetation cover), the likelihood of finding signs of deer presence also change. For example, counting the number of pellets is subjected to bias due to the persistence period, which varies between times of year, habitat and individuals (Mitchell *et al.*, 1985, Mayle and Staines, 1998).

The results of this research indicate that further stratification within main habitats (such as heath in broad sense) might be also needed in order to improve the calibration of indirect

methods. Managers and researchers, when faced with the need for stratified sampling, should explicitly consider classifying habitats by differences in terrain and vegetation structure that might affect the detectability, deposition and decay of signs of deer presence. Clearly, endless sampling stratification is not practical but results presented here indicate that effective stratification is possible based on use of a few key factors such as vegetation structure (particularly vegetation height) and edaphic factors (particularly soil type and surface soil moisture). The results of this research recommend that future research involving the use of indirect indices to estimate local densities of deer should include a preliminary calibration of the method using a reference method that would allow the inclusion of habitat variability (e.g. related to differences of heath type). This could be a “one-off” calibration using a method that might require more labour and resources than indirect methods such as the direct method described in Appendix 1. This calibration should be area specific.

Based on the findings of this research, it is recommended that when the objective of research is solely to obtain a snapshot of the spatial variation of the local density of deer using a rapid method during a specific season, efforts should be focused on identifying the season in which the strongest relationship between the indirect and the reference indices can be obtained. For this, trials of reduced sample size should be conducted during the different seasons for both the indirect and reference method to select the season during which the strongest relationship between the indices is obtained by regression analyses. By contrast, if the objective of the research is to obtain seasonal changes in the local density of deer the efforts should be focused on calibrating the effect of each season upon the relationship between the indirect index and the true local density of deer. Therefore, it is recommended that researchers and managers carry out a preliminary calibration of their chosen indirect method(s) using a reference direct method and that they do this across seasons. This calibration would detect the season in which the best prediction of the local density of deer using the indirect method as predictor can be obtained, and also measure the effects of each season upon the prediction of the spatial variation in the local density of deer. Correlation analyses showed that overall indirect indices can be divided into two groups in terms of the strength of their correlation coefficients: i) indices related to physical disturbance of vegetation (number of tracks and proportion of area trampled) and ii) indices related to deer depositions (number of pellets and distance to nearest sign of presence). The recommendation based on these results is that researchers and managers

should not calibrate an indirect index to estimate the spatial variation in the local density of deer using another indirect index belonging to the same group as a reference method due to a potential autocorrelation related to the use of the same type of signs. Instead, the method should be calibrated with an indirect reference method belonging to a different group or a direct method.

In conclusion, this research has shown that habitat and temporal variability of signs of spatial usage by deer affect predictions of the density of deer. Effects of season and habitat type upon indices of local density of deer are especially important during winter. These effects most strongly affected predicted local density when pellet counts were used as the predictor. Therefore, the following steps should be adopted in studies designed to estimate the spatial variation in the local density of deer from an indirect method. i) Stratified sampling - habitats should be classified depending on vegetation and terrain conditions that might affect the deposition, detectability and decay rates of signs of deer presence. ii) Calibration of the indirect method - a one-off site-specific calibration using a reference method to directly estimate the local density of deer to allow inclusion of the effect of habitat and temporal variability. iii) Prediction of the spatial variation in the local density of deer - a model should be developed to predict the spatial variation in the local density of deer from the indirect method and the effects of habitat and temporal variability.

APPENDIX 3: HABITAT SELECTION BY SIKA DEER AT ARNE AND HARTLAND AS DETERMINED BY JACOB'S AND IVLEV'S INDICES

Table A3.1: Comparison between Arne and Hartland of habitat selection by Sika deer as determined by Jacob's index. AG, acid grassland; CS coniferous scrubland; CW, coniferous woodland; DH, dry heath; DS, deciduous scrubland; DW, deciduous woodland, G, gorse; IG, improved grassland; R, reed-beds; S, saltmarsh; U, urban-anthropic; WC, weed community; WH, wet heath. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ after conducting a t-test to determine habitat avoidance or preference.

Available habitat scale	Lower spatial scale	ARNE		HARTLAND	
		Habitats avoided	Habitats preferred	Habitats avoided	Habitats preferred
Study area (MCP100)	Home Range	IG*, S**, CW***, DS*, R***, WC*	DW**, DH*, G**	DH**, DS***	IG***, R*, AG**
	500 m radius	IG*, S***, CW**, DS*, R***, U***	DW*	DH**, DS**, U*	IG**
	250 m radius	IG**, S***, CW***, CS***, WH**, R***, WC*, U***		DH**, CW*, DS*, G***, U*	IG**
Buffer 750 m	Home Range	IG*, S*, CW***, CS*, DS**, R**, AG**, U***	DW*	DH*, U***	IG**, R**, AG**
	500 m radius	IG**, S***, CW**, CS**, WH*, R***, AG*, U**		DH*, DS*	IG*
	250 m radius	IG**, S***, CW***, CS***, DS**, WH**, R***, AG*, WC*, U***		DH**, CW*, G**, U*	IG**
Home range	Locations	CS*, DW*	DH*	IG*, AG**	DS**, R**

Table A3.2: Comparison between Arne and Hartland of habitat selection by Sika deer as determined by Ivlev's index.. AG, acid grassland; CS coniferous scrubland; CW, coniferous woodland; DH, dry heath; DS, deciduous scrubland; DW, deciduous woodland, G, gorse; IG, improved grassland; R, reed-beds; S, saltmarsh; U, urban-anthropic; WC, weed community; WH, wet heath. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ after conducting a t-test to determine habitat avoidance or preference.

Available habitat scale	Lower spatial scale	ARNE		HARTLAND	
		Habitats avoided	Habitats preferred	Habitats avoided	Habitats preferred
Study area (MCP100)	Home Range	IG*, S**, CW***, DS*, R***, WC*, U***	DW**, G**	DH**, DS***	IG***, R*, AG**
	500 m radius	IG*, S***, CW**, CS*, DS*, R***, U***	DW*	DH**, DS**, U*	IG**
	250 m radius	IG**, S***, CW***, CW***, DS*, WH**, R***, AG*, WC*, U***		DH**, CW*, DS*, G***, U*	IG**
Buffer 750 m	Home Range	IG*, S*, CW***, CS*, DS***, R**, AG**, U***	DW*	DH*, U***	IG**, R**, AG**
	500 m radius	IG**, S***, CW**, CS**, DS**, WH*, R***, AG*, U**		DH*, DS**	IG**
	250 m radius	IG***, S***, CW***, CS***, DS**, WH***, R***, AG*, WC*, U***		DH**, CW*, G**, U*	IG**
Home range	Locations	DW*, CS*	DH*	AG**	DS**, R**

Table A3.3: Comparison between Arne and Hartland of habitat selection of grouped habitats by Sika deer as determined by Jacob’s index. Cover (CO) was obtained by pooling CS, CW, DS, DW, G and R; Grazing (GR) was obtained by pooling AG, C, IG, S, and WC; Heath (H) was obtained by pooling DH and WH. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ after conducting a t-test to determine habitat avoidance or preference.

Available habitat scale	Lower spatial scale	ARNE		HARTLAND	
		Group of habitats avoided	Group of habitats preferred	Group of habitats avoided	Group of habitats preferred
Study area (MCP100)	Home Range	GR**	H**	H***	GR***
	500 m radius	GR**		H**	GR**
	250 m radius	GR**		H**	GR**
Buffer 750 m	Home Range	GR**		H*	GR**
	500 m radius	GR**	CO*	H*	GR*
	250 m radius	GR**		H**	GR**
Home range	Locations	CO**	H*	GR*	CO***

Table A3.4: Comparison between Arne and Hartland of habitat selection of grouped habitats by Sika deer as determined by Ivlev’s index. Cover (CO) was obtained by pooling CS, CW, DS, DW, G and R; Grazing (GR) was obtained by pooling AG, C, IG, S, and WC; Heath (H) was obtained by pooling DH and WH. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ after conducting a t-test to determine habitat avoidance or preference.

Available habitat scale	Lower spatial scale	ARNE		HARTLAND	
		Group of habitats avoided	Group of habitats preferred	Group of habitats avoided	Group of habitats preferred
Study area (MCP100)	Home Range	GR**	H*	H***	GR***
	500 m radius	GR**		H**	GR**
	250 m radius	GR***		H**	GR**
Buffer 750 m	Home Range	GR**		H*	GR**
	500 m radius	GR**	CO*	H*	GR**
	250 m radius	GR*		H**	GR**
Home range	Locations	CO**	H*	GR*	CO***