ANGLIA RUSKIN UNIVERSITY

THE BEHAVIOUR OF FREE-ROAMING HERDS OF HIGHLAND CATTLE AND KONIK POLSKI AT WICKEN FEN NATURE RESERVE.

CAROL LAIDLAW

A thesis in partial fulfilment of the requirements of Anglia Ruskin University for the degree of Master of Philosophy

Submitted September 2018

Acknowledgements

Firstly, and with much gratitude, my sincerest thanks go to my first supervisor, Dr. Dawn Hawkins, for her support, expertise and statistical skill. I owe a debt of gratitude also to my second supervisor, Dr. Olivia Norfolk, who helped to order my harems. Thanks are additionally due to Dr. Nancy Harrison, Dr. Francine Hughes and Dr. Mark Kennedy.

Sincere thanks go to the National Trust for providing the funding to complete this research, and to Jon Megginson for thinking of the opportunity. Especial thanks to my managers and colleagues at Wicken Fen NNR, who provided me with the time and support to conduct this research. Appreciative thanks go to Martin Lester, who has kept the faith, provided advice, eaten cake and supplied maps without hesitation.

Collecting the data, and completing this thesis, involved the help and support of many other people along the way. I am extremely grateful to Lizzie Dale and Maddie Downes, for many days spent out in the field as my recording assistants. Warm thanks to those who gave of their time proof-reading and editing; Peter Green, Hugh Laidlaw, Julie Zac, but most especially Gerrard Smallwood. I thank Dr. Peter Carey, Owen Mountford, and Dr. Stuart Warrington for guidance and information on species lists, habitat maps and the flora associated with the fen. Thanks also to those provided information on their grazing herds and systems; Adrian Barnett, Vicki Breakell, Gjis Kirsjens, Henri Kerkdijk-Otten, Kate Lemon, Esther Linnartz, Richard Mason, Andy Needle, Pete Short, and David Tallentire. Thanks go to John Hughes and Luke Underwood for providing cheerful support and inspirational quotes.

Lastly, a tip of the hat to the cattle and horses; conservation grazers, ecosystem engineers, escape artists, research subjects and awkward hairy articles. Life, and the completion of this research, would not have been quite as interesting without them.

This research was funded by the National Trust and Waste Recycling Environmental (Grant name and number; Wicken Fen Vision Habitat Creation, 08719-BAF10).

ANGLIA RUSKIN UNIVERSITY

ABSTRACT

FACULTY OF SCIENCE AND TECHNOLOGY

MASTER OF PHILOSOPHY

THE BEHAVIOUR OF FREE-ROAMING HERDS OF HIGHLAND CATTLE AND KONIK POLSKI AT WICKEN FEN NATURE RESERVE.

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Semi-feral or domestic livestock are often utilised by nature reserve managers in order to maintain or increase the biodiversity of a particular habitat; a technique known as conservation grazing management. This study investigated the maintenance behaviour, space use and social organisation of free-roaming Highland cattle and Konik polski (horses) introduced to Wicken Fen Nature Reserve in 2003 as part of the 'Wicken Fen Vision': a landscape scale habitat creation project in the East Anglian Fens. It provides the first description of the behaviour of large herbivores at this important site and was conducted to improve understanding of grazing animals in conservation management.

Data were collected by scan sampling at 15 minute intervals over a total period of 162 non-consecutive hours in 2011. Scan sampling of individuals was used to record activity, nearest neighbour and sub-area location of three study groups (mixed sex cattle, female cattle and horses). Null hypothesis significance tests (NHSTs) and the generalized linear model were used on activity and location data to assess variation across individuals, time and space. Social network analysis and NHSTs were used on the nearest neighbour data to assess social structure and relationships.

Variation in the proportion of scans spent in different activities was evident between sexes for cattle but not horses and between age categories for horses but not cattle, although data constraints may explain the latter. Variation in the proportion of scans spent in different activities varied within day and between seasons for all groups. The relative use of sub-areas also differed by season for all groups but there was only an association between sub-area and activity for the mixed cattle group. The variation in activity and space use between individuals and across seasons indicates that the outcome of conservation grazing is likely to be dependent on herd composition and timing. The cattle had a uniform, stable social network with strong ties between kin. The horse herds contained sub-groups centred on adult individuals with long term stable associations, with strong ties between mother and recent offspring and unrelated adults.

This study demonstrates that behavioural data on free-roaming grazers can be effectively collected and analysed, using traditional and emerging statistical techniques, to describe patterns of variation relevant to the ethical use of large herbivores in conservation management. It has also generated questions, and provided insights for protocols, for future research exploring causal factors in variation and linking behaviour to specific ecological outcomes. **Keywords:** landscape scale; free-roaming; Highland cattle; Konik polski; social network analysis.

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THE BEHAVIOUR OF FREE-ROAMING HERDS OF HIGHLAND CATTLE AND KONIK POLSKI AT WICKEN FEN NATURE RESERVE.

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Chapter One

Introduction

1.1 Introduction

Habitat management involves influencing or disturbing the process of succession for the benefit of one or more species (Ausden, 2007). Succession is the gradual process by which populations of plants and animals change over time in the absence of disturbance, and was described in the early twentieth century by scientists studying Wicken Fen (Ausden, 2007; Godwin, 1929). Disturbance can be introduced to habitats through management techniques such as mowing, burning or grazing.

Grazing can positively influence species diversity of plant communities, and may be less damaging than cutting or burning on a large scale. The effects of grazing will depend upon a number of factors, such as the species of large herbivore introduced, the duration of the grazing and the numbers of animals used (Ausden and Treweek, 1995; Sutherland, 1995). Different types of herbivores, such as cattle and horses, graze in different ways and this impacts upon their suitability for grazing certain habitats. Conservation grazing tailors the type, number and timing of grazing to be of greatest benefit to the target species and environment (English Nature, 2005).

In 2003 the National Trust introduced free-roaming cattle and horses to its ‘Wicken Fen Vision’ (WFV) project to act as one of the main drivers for habitat diversification in a progressive landscape level approach to management. The aim was to create a shifting mosaic of vegetation that was influenced across time by the animals’ grazing patterns and movements. Research regarding the effects of the grazing upon the Fen’s ecosystem has been published (Stroh, 2012), but prior to this research the animals themselves have not been the focus of investigation. This thesis addresses this gap by exploring their behaviour and social relationships through the analyses of data from an observational study conducted over the course of a year. This work was facilitated, and its potential impact on management enhanced, by my long-term experience of working with these animals and by the availability of unpublished records kept by the National Trust.

This Chapter provides the background of the study by outlining the different approaches to conservation grazing, with a reference to current literature and focus on the novel grazing system as employed by the National Trust as part of the Wicken Fen Vision. It puts the study in the context of modern approaches to addressing challenges facing the natural environment, particularly fens and wet grassland. It also provides some additional background on the study system (the Wicken Fen Vision) and the study species (Highland cattle and Konik horses). The Chapter closes by stating the main aims and objectives of this study and describing the structure of the rest of the thesis.

1.2 Conservation context

1.2.1 Challenges

Challenges to the natural environment have been recognised for a number of years; agricultural intensification, population increases, flood defence and climate change have all led to habitat fragmentation and a loss of biodiversity (Colston, 1997, 2003; Harrison and Bruna, 1999; Lawton, 2019; Sutherland and Hill, 1995). Lowland and wetland habitats are especially vulnerable to loss; as inundation of the land is usually seasonal, such sites are readily drained. Underlying soils are often extremely productive, leading to rapid implementation of highly intensive farming focussed on high yielding crops (Colston, 2003; Stroh, 2012). For example, the Fens of East Anglia have been the focus of drainage and intensification of farming since the 1500's, and now less than 0.1% of the original undrained fens survive (Colston, 2003; Moore, 1997). Similar losses have also occurred across Europe, with fen and wet grassland areas disappearing or becoming highly fragmented (Stroh, 2012). Colston (2003) reported that the average size of SSSIs and Wildlife Trust reserves in Cambridgeshire was only 89.5 ha and 16.4 ha respectively.

Legislation is in place to protect and preserve such areas; for example, the European Habitats Directive ensures the conservation of 200 rare and characteristic habitat types through the designation of Special Areas of Conservation and Special Protected Areas (European Commission Environmental, 1992). In the United Kingdom (UK), National Nature Reserve (NNR) and Site of Special Scientific Interest (SSSI) designations award protection to areas of rare or considerable wildlife interest (DEFRA, 2018; Stroh, 2012). However, habitat fragmentation and geographical isolation continue to threaten these areas and in Cambridgeshire the average size of a protected area remains small.

1.2.2 Landscape-scale conservation

Towards the end of the twentieth century, a shift in conservation thinking to address these challenges became apparent. Conservation management had traditionally been focussed on small reserves preserved through intensive management aimed at a particular species, or range of species. This form of conservation had been partially successful in stalling habitat and species decline, but it is a highly limited conservation strategy; it is expensive, highly intensive and, no matter how well managed, is still likely to suffer from local extinctions due to the small and isolated nature of sites (an effect identified through the theory of island biogeography conceived by MacArthur and Wilson, 1967). A shift in conservation strategies started to focus on habitat restoration and recreation on a larger scale, often with a more 'open-ended' approach (Harvey, 1995; Colston, 2003; Hughes et al., 2011). This is often referred to as landscape-scale conservation (Eigenbrod et al., 2016; Taylor, 2005) and this shift to 'thinking bigger' was a step-change in conservation philosophy within Britain (Taylor, 2005).

A succinct definition of landscape scale conservation is provided by Stroh (2012, p.56); "this approach promotes the linkage of existing nature reserves and/or expansion of the reserve boundaries to create more space and appropriate habitat for species dispersal and establishment". As early as the 1960's, European conservationists had led the way with large scale habitat recreation projects such as Lauwersmeer in the Netherlands (Colston, 2003; Staatsbosbeheer, 2018). Reserves like these proved it was possible to maintain a wide diversity of habitats over a large area. During the late 1990's and early 2000's, British conservation organisations like the National Trust (NT Wicken Fen Vision), The Wildlife Trusts (WT Living Landscapes) and the Royal Society for the Protection of Birds (RSPB Futurescapes) started to implement their own landscape scale projects (Colston, 1997, 2003; National Trust, 2011; RSPB, 2018; The Wildlife Trusts, 2018).

1.2.3 Grazing as a conservation tool

Studies by Vulink and Drost (1991, 2000) as well as Duncan (1983) have given useful insights into the costs and benefits of using cattle and horses in wetlands both new and old. At low stocking densities, grazing is a gradual form of vegetation removal and is more apt to produce a mosaic of different vegetation types and height than cutting or burning (Ausden and Treweek, 1995). It is therefore a potentially useful tool in conservation management: approaches range from 'traditional' to 'naturalistic'.

Traditional conservation grazing utilises large herbivores under domestic-type management, with controlled densities of animals (Ausden and Treweek, 1995). It is typically used to produce the most suitable conditions for specific target species on small blocks of land. It is usually in place for a short defined period, often seasonal, and generally uses herds of similar age and/or sex. In contrast, with naturalistic conservation grazing, there is little to no human intervention after the animals are introduced. Furthermore, there are generally few to no specific targets and grazing is over a larger area. In addition, herds are mixed in age and sex, becoming integrated into the landscape over time and animals are rarely removed. Typically more than one species is used, as mixed species grazing is believed to maintain heterogeneity in sward height and diversity, thus increasing landscape value (Putfarken et al., 2008).

The conservation grazing system introduced as part of the WFV is towards the naturalistic end of this spectrum but is not fully naturalistic because the National Trust is legally and morally obliged to comply with current welfare legislation such as the Abandonment of Animals Act (1960) and the Animal Welfare Act (2006). Where applicable, unnecessary suffering is prevented, utilising veterinary support. In common with domestic systems, legal requirements regarding tuberculosis testing, movements and identification of cattle are adhered to, as is the identification of horses through micro-chipping and passporting. However, the cattle and horses at Wicken Fen are not supplementary fed nor are they treated with prophylactics such as ivermectin wormers or antibiotics (National Trust, 2011). They are not regularly rounded up or hoof trimmed. Animals form their own social groups and sexually functional males and females, along with their young, are kept together. Intervention with population control is kept to a minimum. Young born at Wicken Fen are permitted to stay with their parental groups; young are only removed from the breeding herds if they are physically, temperamentally or genetically unsuitable for breeding (National Trust, 2011). Stroh (2012) describes this form of grazing as ‘free-roaming’, and defines it as an approach which allows naturally fluctuating numbers of animals to graze over large areas, unrestricted (in the main) by fences.

1.2.4 Re-wilding

Re-wilding is a term that has multiple meanings, but has been used to describe projects that aim to recreate or return land to a lost historical state by using guilds of large herbivores as replicants for now extinct megafauna (Lorimer et al., 2015; Donlan et al., 2006). Even with the re-establishment of ecological processes and the use of naturalistic grazing, returning to a previous historical baseline is often unobtainable due to irreversible damage to soils, vegetation and hydrology (Lorimer et al., 2015; Stroh, 2012).

A British example of re-wilding is the Knepp Wildland, a 3,500 acre project based in West Sussex (Tree, 2018). Re-wilding can be an innovative way to create vibrant landscapes that are rich in wildlife and it has been very successful at the privately owned Knepp estate (Tree, 2018). However, re-wilding can create controversy if it ignores cultural norms and current legislation; the starvation of animals in the Oostvardersplassen, a re-wilding project using naturalistic grazers in the Netherlands, has resulted in a governmental and public backlash against the project (Lorimer et al., 2015; Lorimer and Driessen, 2013). Re-wilding is sometimes linked to practices such as de-domestication, back-breeding and de-extinction of animals, as exemplified through the creation of the Heck cattle, or Tauros, used at the Oostvardersplassen (Goderie et al., 2013; van Vuure, 2005; Vermeulen, 2015).

As a result of the mixed species grazing using tough hardy breeds of animals in a dynamic ecosystem, the WFV currently has a loose fit as a re-wilding project. However, if it is accepted that one of the key aims of a re-wilding project is to return the landscape to a historic baseline, then the re-wilding tag does not fit, as this is not one of the key aims of the WFV (National Trust, 2011).

1.3 The Wicken Fen Vision

At the end of the twentieth century, the National Trust-owned Wicken Fen National Nature Reserve (NNR) faced the problems of species loss and habitat fragmentation common to many small, isolated reserves (National Trust, 2011; Colston, 2003; Stroh, 2012). In order to buffer the NNR from these effects and provide broader ecosystem services, in 1999 the National Trust began the Wicken Fen Vision (National Trust, 2011).

Over the next 100 years, the National Trust aims to create a 53 square kilometre nature reserve adjacent to, and including, the NNR (Figure 1.1). The National Trust plans to use open-ended ecological restoration techniques to create and restore wildlife habitats on previously intensively farmed arable land (National Trust, 2011; Hughes et al., 2011; Colston, 2004).

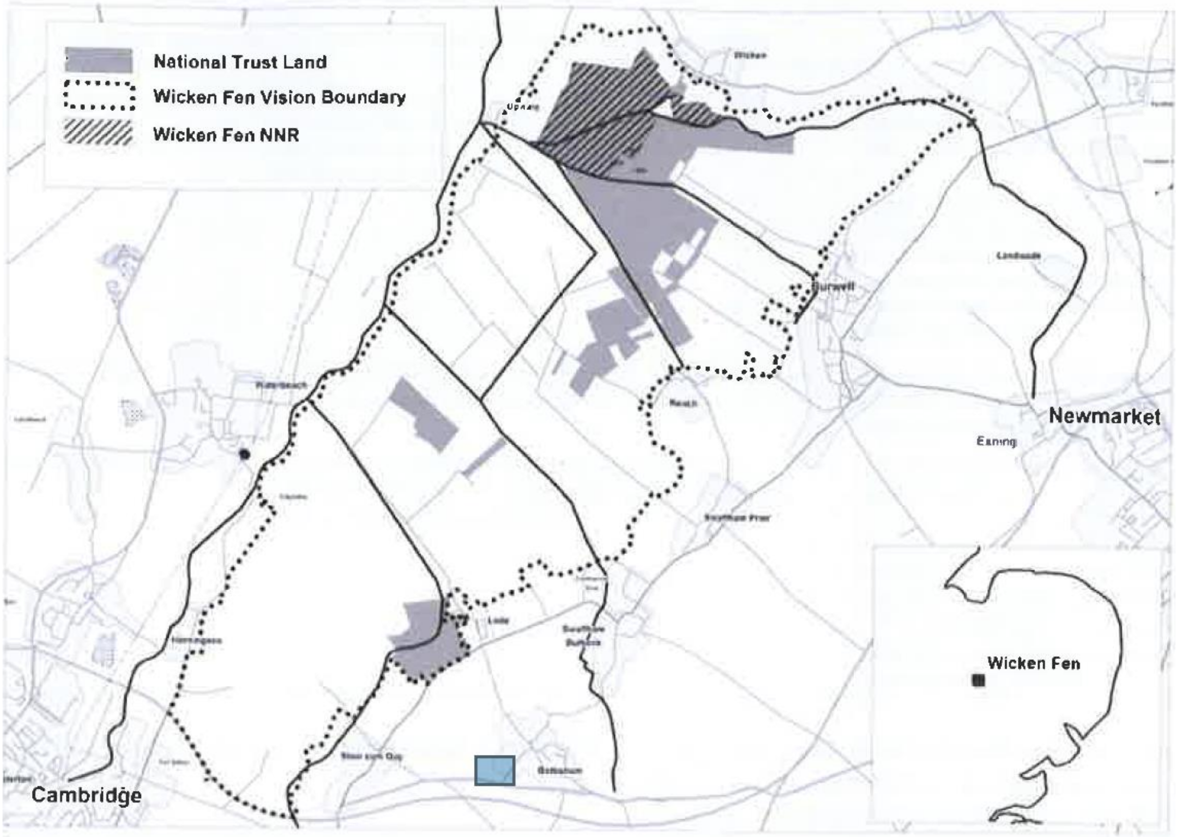

Figure 1.1 Aspirational area of the Wicken Fen Vision, denoted by the dotted line. Land already owned by the National Trust is shaded in grey.

Management of the Wicken Fen Vision has a non-prescriptive, non-targeted approach; id est, the National Trust has not chosen a range of defined species or vegetation communities to outline as targets for remedial action (Stroh, 2012). Instead, the NT is aiming to establish shifting vegetation mosaics through the use of factors such as hydrology and low intensity grazing provided by large herbivores; in this case, cattle *Bos taurus* and horses *Equus caballus* (National Trust, 2011).

1.4 The study species

Animals introduced into a minimal husbandry system such as at Wicken Fen are required to be tough and hardy in order to thrive in a wetland environment year round. After extensive consultation, the National Trust identified and introduced to the fen two breeds (Highland cattle and Konik polski) that already had a history of being successfully used in Europe as robust conservation grazers of wetlands and floodplain (E. Linnartz, pers.com).

1.4.1 Highland cattle

Highland cattle are used extensively across Britain in wetland nature reserves (D. Tallentire; K. Lemon; P. Short; A. Needle; R. Mason, personal communications). Highlands are an extremely hardy breed with extensive ranging behaviours particularly suited to grazing large sites (Tolhurst and Oates, 2001). They are one of the smaller breeds of native cattle, with an average weight of 400 kg for females (Tolhurst and Oates, 2001). As a genetically very diverse breed, sourcing unrelated members to forestall genetic drift through inbreeding should be relatively easy (S.J.G. Hall, unpublished communication to the National Trust).

There is local historical precedent for introducing Highland cattle to the fens. During the 17th century, Highland cattle were often driven down from Scotland to fatten on southern pastures before being sold on as meat or breeding stock (Koufopoulos, 2004). Farmers local to Wicken Fen have themselves run Highland cattle on their land within living memory (A. Barnett, pers.com).

The cattle introduced to the WFV had previously been kept under a domestic system, where one male remains with the females for a set time each summer for breeding purposes. Young born to the herd are removed for weaning at eight to ten weeks old. There is no information available as to what happens when a previously domestic herd is given social freedom. The closest models available within the UK are those provided by the feral cattle of Swona or the wild white cattle of Chillingham (Hall, 1986, 1988, 1989).

1.4.2 Konik polski

The Konik is an Eastern European breed of hardy pony. There are claims that this pony can trace its lineage back to the extinct wild horse, the Tarpan *Equus ferus ferus* (Pasicka, 2013). However, these claims have been disproved by recent research (van Vuure, 2015). Genetic research has shown that the Konik is more closely clustered with domestic horses than any form of wild or feral horse known to have existed in Europe (Kerkdijk-Otten, pers.com).

The Konik of today is a created breed. The process was started in the 1900's by Professor Vetulani, a polish scientist who saw feral and domestic horses in Poland that he believed looked like the extinct Tarpan (Pasicka, 2013). Concurrently, the Heck brothers in Germany started their own back-breeding programme (van Vuure, 2015). Both Vetulani and the Heck brothers crossed feral and domestic horses, such as Highland ponies, in order to try and recreate the Tarpan. After Vetulani's death in 1952, the Polish state took over the breeding of the Konik, which continues to this day (van Vuure, 2015).

The Konik is a robust and hardy grazer that is used extensively in conservation grazing programmes in the UK; for example, the Royal Society for the Protection of Birds (RSPB) have herds grazing Minsmere, the Norfolk Broads, the Loch of Strathbeg and Blacktoft Sands (P. Short; A. Needle; R. Mason; pers.com). The Norfolk Wildlife Trust and the Wildwood Trust also use Koniks to graze a range of sites across southern England (D. Tallentire; V. Breakell; pers.com). Despite the occurrence of Koniks throughout the UK, the WFV manages one of the few long-term breeding herds of Koniks in this country. This provides a unique opportunity to conduct novel research into Konik grazing and social behaviour.

1.5 Thesis aims, objectives and structure

The main aim of this thesis is to investigate the grazing and social behaviours of free-roaming horses and cattle permitted to live 'as wild' in the context of the WFV; a novel open-ended, landscape scale wetland creation project (see chapter two for a detailed account of the study areas and animals). This investigation is carried out by addressing the following objectives;

I. To determine if the behaviours and land use of the cattle and horses differ across sex, age category, time of day or season (Chapter 3).
II. To describe the social structure of the horses at Wicken Fen using Social Network Analysis and to assess for differences in individual metrics by sex, age category, and season (Chapter 4).
III. To summarise the key findings from Chapters 3 and 4 in order to suggest future directions for research and management of the cattle and horses at Wicken Fen (Chapter 5).

The next chapter (Chapter 2) presents general information on the study site, study animals and data collection relevant to both subsequent data chapters. Chapter 3 considers the behaviour of the animals in terms of basic maintenance behaviour states, including an assessment of individual variation by sex and age and variation over time, within and between days. Chapter 3 also looks at use of space in relation to behaviour and season.

Chapter 4 focusses on social structures and individual differences in sociality by sex. The final chapter (Chapter 5) summarises the findings from chapters three and four, and provides future directions for research. It also suggests some applications for this research in future management of the herds.

Chapter Two

Description of the study site and grazing herds at Wicken Fen

2.1 Introduction

This chapter describes the study site, grazing herds and methods used during the research. Section 2.2 looks at the overall nature reserve, including a brief illustration of the study site's history. The areas specific to the research are described in section 2.3, while section 2.4 takes an overview of the study animals. Section 2.5 details the methods used during the course of this research.

2.2 The research site

Wicken Fen Nature Reserve is a wetland conservation area owned and managed by the National Trust. It is situated on the edge of the Fens of eastern England, 25 kilometres north of Cambridge. The Fens were an area of mostly submerged peat subject to extensive, irregular flooding from both the North Sea and local freshwater rivers such as the Nene and the Ouse (Moore, 1997). Until the mid-17th century, the Fens covered approximately 3,850 square kilometres between the Lincolnshire wolds, Cambridgeshire, Suffolk and Norfolk (Figure 2.1, Yapp, 1908). Drainage of the Fens started in the 17th century and has continued since. Wealthy landowners such as the Honourable N.C Rothschild and other groups concerned about the loss of wetland habitat were able protect small areas of remaining fen from this wholesale change through purchasing the land or gifting already purchased land to charitable or government organisations (Great Fen, 2018).

Wicken Fen is one of these remaining areas of fen, others being Woodwalton and Holme Fens near Peterborough and Chippenham Fen near Newmarket (Figure 2.1, Yapp, 1908). All of these fens are nature reserves, with Wicken Fen being the first (Moore, 1997).

Figure 2.1 Location of Wicken Fen Nature Reserve in East Anglia, denoted by a black square situated under Ely. Other fen reserves are also indicated with black squares (Yapp, 1908).

The National Trust bought the first 0.8 hectares from entomologist J. C. Moberly in 1899, and another 89 hectares were bequeathed to the Trust after scientist G. H. Verrall's death in 1910 (Rowell, 1997). The reserve (Figure 2.2) has continued to increase in size since then. The most recent purchase in 2017 added a further 11.77 hectares to the landholding (Appendix I).

Wicken Fen's current landholding covers 805.72 hectares (Lester, pers.com). Two hundred and fifty five hectares of that are recognised as requiring special protection under national and internationally recognised designations (Table 2.1). The designations relate to land purchased in a period from 1899 – 1924, lying mostly on undrained and uncultivated deep peat soils. Unlike the other remaining Fens (such as Holme Fen) which lie on acidic peat soils, Wicken Fen's soil chemistry is recorded as being neutral to alkaline (Friday, 1997).

Table 2.1 List of designations awarded to Wicken Fen, along with the date of the award. The list is accurate as of 31st December 2017 (Natural England, 2018).

Designation	Year awarded
Site of Special Scientific Interest (SSSI)	1951, re-notified 1983
National Nature Reserve (NNR)	1993
Ramsar site (Wetland of International Importance)	1995
Fenland Special Area of Conservation (SAC)	2005

The designations have been awarded due to the assemblage of inland wetland habitats and species, particularly plants and invertebrates. Updated in 2017, the recorded number of species is 8,954 (Warrington, 2017), with Coleoptera (beetles) and Diptera (flies) being the greatest proportion of this (Appendix II). Many of these species are rare or threatened and are covered under the United Kingdom's Biodiversity Action Plan (Appendix III).

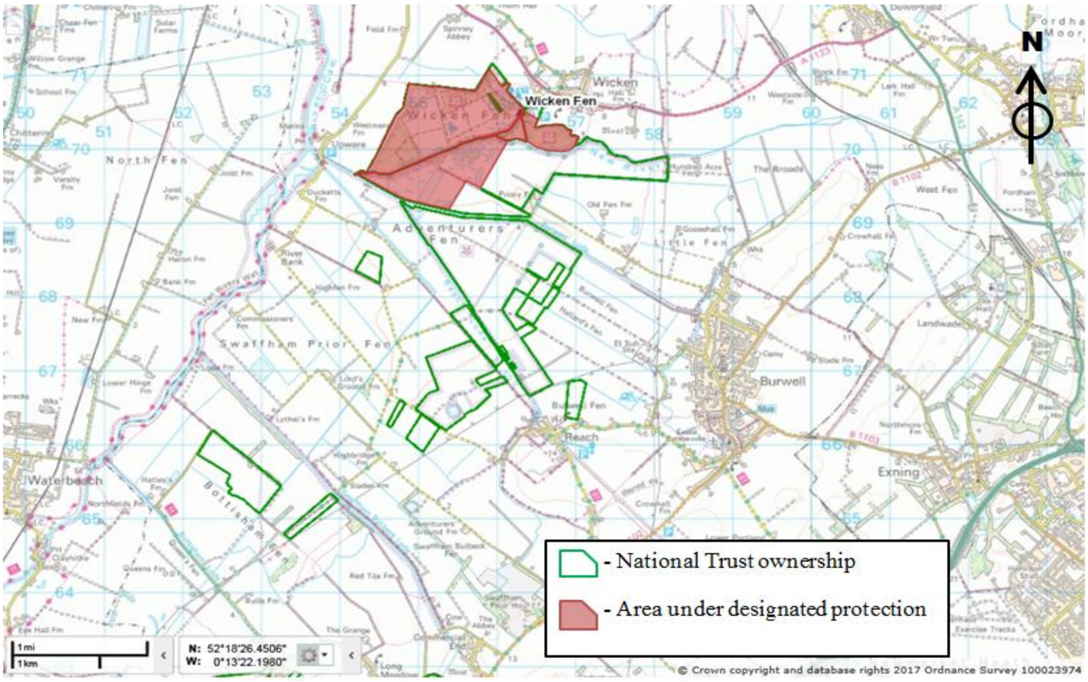

Figure 2.2 Current reserve boundaries, as of 31st December 2017. Wicken Fen has two parts; Wicken Fen NNR (shaded red) and Wicken Fen Vision (outlined green).

As discussed in Chapter I, section 1.2.1, there are challenges on a global and local scale facing these specialist Fen species and communities. It is hoped that these challenges will be mediated through a long-term plan to increase the size of the reserve. Work on this plan started in 1999 (The National Trust, 2011).

Since 1999, the National Trust has added 447.67 hectares to the established reserve (358.05 hectares). Much of this additional land (the unshaded outlined area in Figure 2.2) has been intensively farmed and drained prior to National Trust purchase. As a result, the deep peat soils have been depleted and this land now lies 2 – 5 metres below the level of the original, undrained reserve (National Trust, 2011). The colonising plant communities are currently less diverse than those found on the undrained areas of the reserve. Surveys in 2017 on one of the new land parcels found mostly species-poor neutral grassland dominated by plants such as oatgrass *Arrhenatherum*, creeping bent *Agrostis stolonifera* and creeping thistle *Cirsium arvense*, with stands of elder *Sambucus nigra* and hawthorn *Crataegus monogyna* (Carey, 2017).

2.3 The research areas

These areas were chosen as they mirror the extent of the land available to the grazing herds over the course of 2011 (Figure 2.3). Both areas cover reclaimed arable land with no designations attached, and both areas include land with SSSI, NNR, Ramsar and SAC designations.

For historical and conservation management reasons, the nature reserve is divided into named areas and smaller, numbered compartments. This system of naming and numbering has been implemented by the National Trust (National Trust Management Plan, 2011 – 2015). This research utilises this naming/numbering convention. Five named sub-areas and 24 numbered compartments are identified within the two areas that are part of this research (Table 2.2).

The sub-areas have been all been drained and cultivated for variable periods in their history. Drainage and cultivation of peat leads to oxidation, peat wastage and shrinkage (Friday and Rowell, 1997). As a result, some of the areas now show much reduced levels of peat. The hydrological profile of each compartment differs, with some compartments experiencing winter inundation. The soil chemistry, hydrology and management of the compartments before and after purchase has resulted in different vegetation profiles between each named sub-area, but not necessarily each compartment (Stroh, 2012).

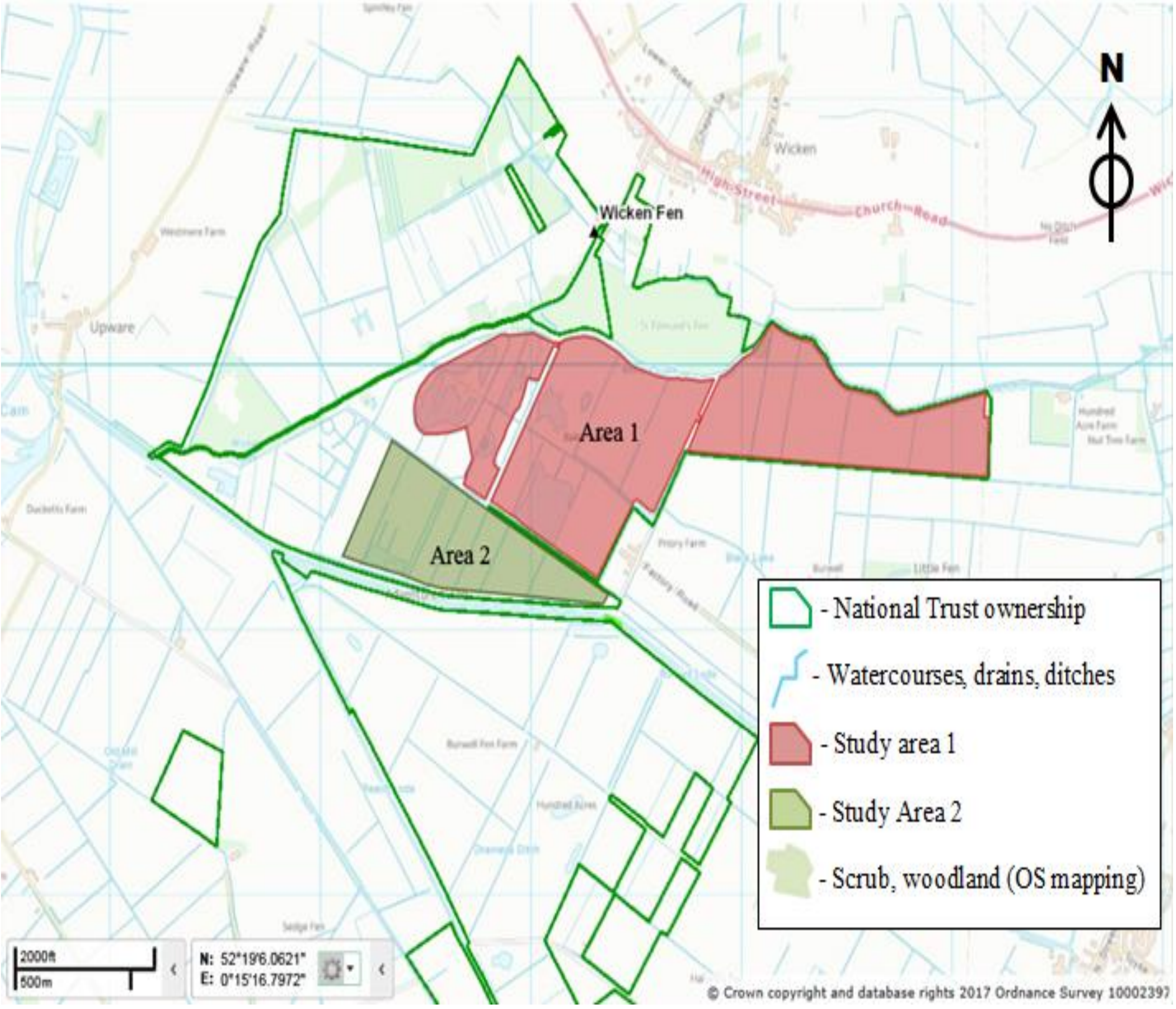

Figure 2.3 Wicken Fen reserve with study areas highlighted

Table 2.2 Details of study areas, including associated sub-areas and compartments. The purchase date of each sub-area, compartment size in hectares and management prior to National Trust ownership is included. Areas with SSSI, NNR, Ramsar and SAC designations are highlighted red.

Study Area	Sub-area name	Associated compartment numbers	Hectares per compartment	Year(s) of purchase	Land use prior to National Trust management
Area 1	Brett's	44	1.60	1907 - 1924	Used during World War II for arable crops. Returned to the Trust in 1953.
		45	5.20		
		46	4.87		
		47	1.99		
		49	9.60		
	Baker's Fen (hereafter – "Baker's")	101	11.38	1993	Arable crops
		102	9.46		
		103	9.69		
		104	8.25		
		105	3.95	1901	Used in World War II for arable crops - Returned 1953.
		106	3.80		
		107	3.86		
	Guinea Hall	108	9.82	2000	An orchard until the 1940's, then arable crops
		109	6.89		
		110	10.67		
		111	8.30		
		112	9.72		
Area 2	Rothschild's	41	4.43	1907 - 1924	Used during World War II for arable crops - Returned 1953.
		42	9.98		
	Harrison's	60	4.18	1930 - 1990	Arable crops
		61	4.06		
		62	3.81		
		63	5.09		
		64	4.72		

2.3.1 Descriptions of Areas 1 and 2

Area 1 consists of three named sub-areas and 17 numbered compartments (Figure 2.4a). Area 2 consists of two named sub-areas and 7 numbered compartments (Figure 2.5b). The areas are 119.05 hectares and 36.27 hectares in size respectively (Table 2.3).

Table 2.3 Size in hectares of named sub-areas in areas 1 and 2. Areas with SSSI, NNR, Ramsar and SAC designations are highlighted in red.

Research area	**Sub-area name**	**Total hectares within sub-area**
Area 1	Brett's	23.26
	Baker's	50.39
	Guinea Hall	45.40
Area 2	Rothschild's	14.41
	Harrison's	21.86

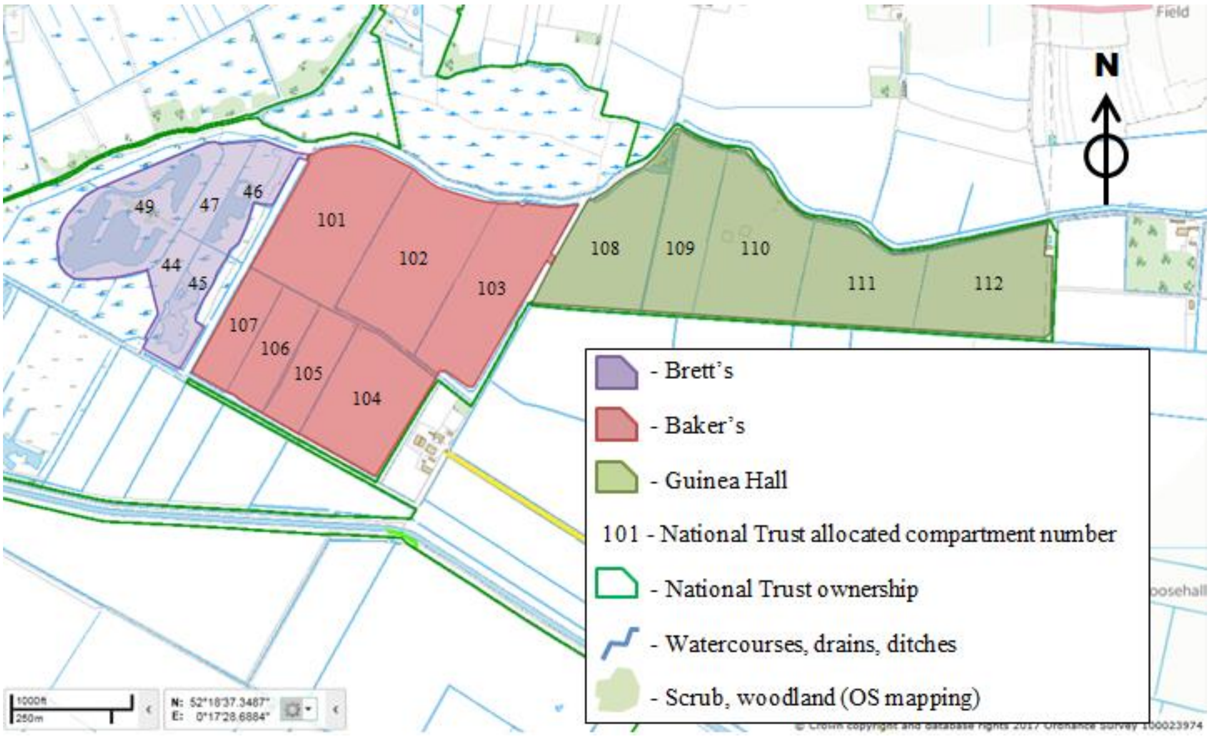

Figure 2.4a Area 1, with sub-areas Brett's, Baker's and Guinea Hall identified and individual compartments numbered.

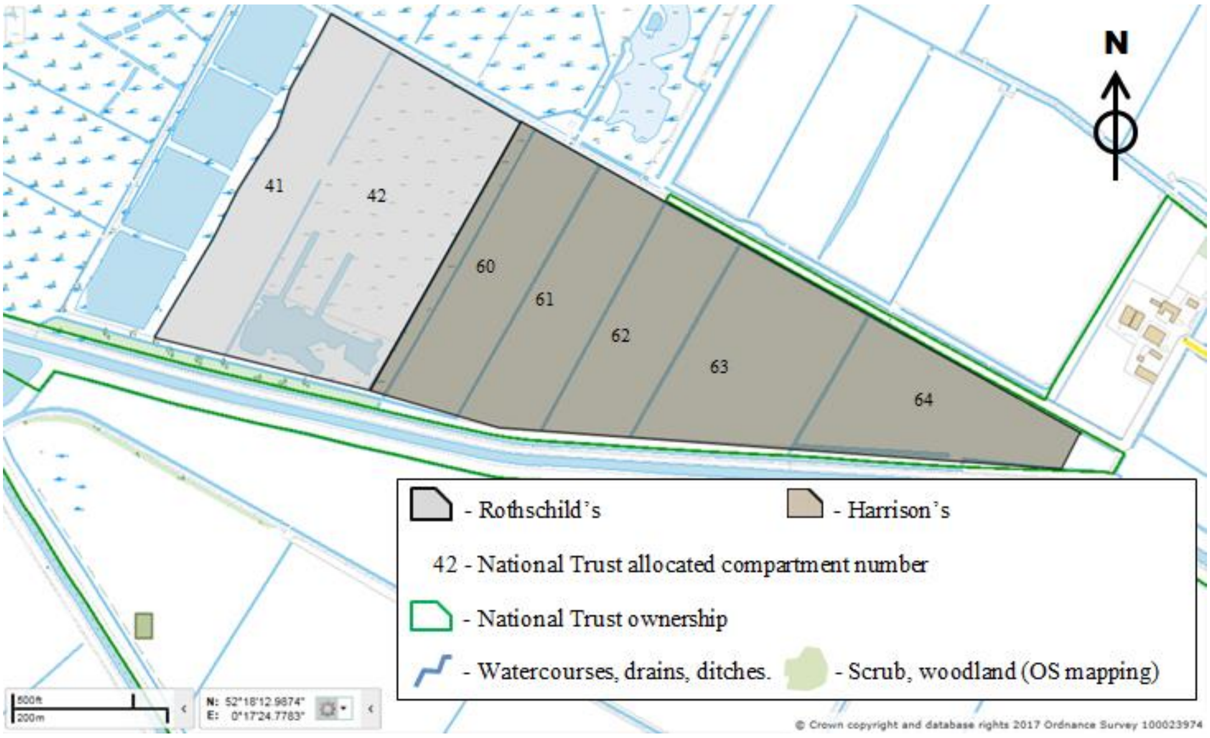

Figure 2.4b Area 2, with sub-areas Rothschild's and Harrison's identified and individual compartments numbered.

2.3.2 Boundaries and access

Brett's perimeter is bounded by ditches, banks and reedbeds. There is one access point to the area, in the north-east corner. There are public footpaths around the perimeter, but they do not follow the boundary closely. Baker's perimeter is bounded by ditches, fences and areas of taller willow scrub, with well used footpaths running closely parallel to all four sides. Guinea Hall perimeter boundary consists of a slow flowing small river and stock fences. There are public footpaths that follow the entire perimeter of this area, with three of the four sides experiencing much less foot traffic.

Harrison's and Rothschild's perimeter boundary is comprised of stock fencing. The northern perimeter of Rothschild's/Harrison's has a single lane, broken concrete highway running parallel to it. This effectively separates area 2 from area 1. The southern boundary has a public footpath running parallel to it. A significant area of conservation reedbed with no public access bounds the north-western edge of Rothschild's.

All internal compartments within the sub-areas are divided by ditches. Every ditch has one or two crossing points (usually an earth bank spanning the width of the ditch) to facilitate access around the compartments.

2.3.3 Hydrology

The water table behaves in a very similar manner between each sub-area, with it dropping below ground level in the late summer and autumn, rising to ground level or higher in the winter and spring (Friday and Rowell, 1997). Table 2.4 records the highest and lowest points for the water table in each sub-area (National Trust, 2018).

Table 2.4 Maximum and minimum water table levels recorded from 1st January to 31st December 2011 across three sub-areas (not including Rothschild's and Harrison's. No separate data exists for these as they are under the same hydrological control as Brett's and Baker's respectively). Levels are given in metres above (+) or below (-) ground level. 0.00m indicates ground level. SSSI/NNR/Ramsar/SAC designations are indicated in red.

Sub-area	**Maximum**	**Month of occurrence**	**Minimum**	**Month of occurrence**
Brett's	+0.25m	January	-0.75m	June
Baker's	0.00m	January	-1.45m	October
Guinea Hall	0.00m	March	-1.25m	May

The physical boundaries of the sub-areas do not reflect the hydrological boundaries (Figure 2.5). The areas of water visible in Brett’s are permanent, although the levels fluctuate with season (National Trust, 2018). There is an abstraction point for this sub-area, which is used to maintain a high water level in the perimeter ditches. Brett’s forms one hydrological unit with Rothschild’s.

Baker’s is subject to seasonal inundation. The National Trust has abstraction rights to take water (limited to 120,000 cubic metres, taken from November to March inclusive) from a nearby watercourse. Five of the seven compartments in this sub-area (compartments 101, 104, 105, 106 and 107) are flooded above ground level from November to June for up to 50% of their area (Figure 2.6). From April to October, the water draws down up to 1.5m below ground level (National Trust, 2018). Raising the water levels on Baker’s has the effect of raising the levels on Harrison’s, as these two areas are one hydrological unit. In Harrison’s, the water collects in paleo-channels that cross compartments 60, 61 and 62 (Boreham, 2013). As water levels drop on Baker’s and Harrison’s during the summer, this leaves the previously flooded areas bare, with short vegetation evident in the shallower parts.

Guinea Hall is a separate hydrological unit from all other sub-areas. This sub-area becomes waterlogged on the southern boundary during the winter but generally remains much drier than Brett’s and Baker’s (National Trust, 2018).

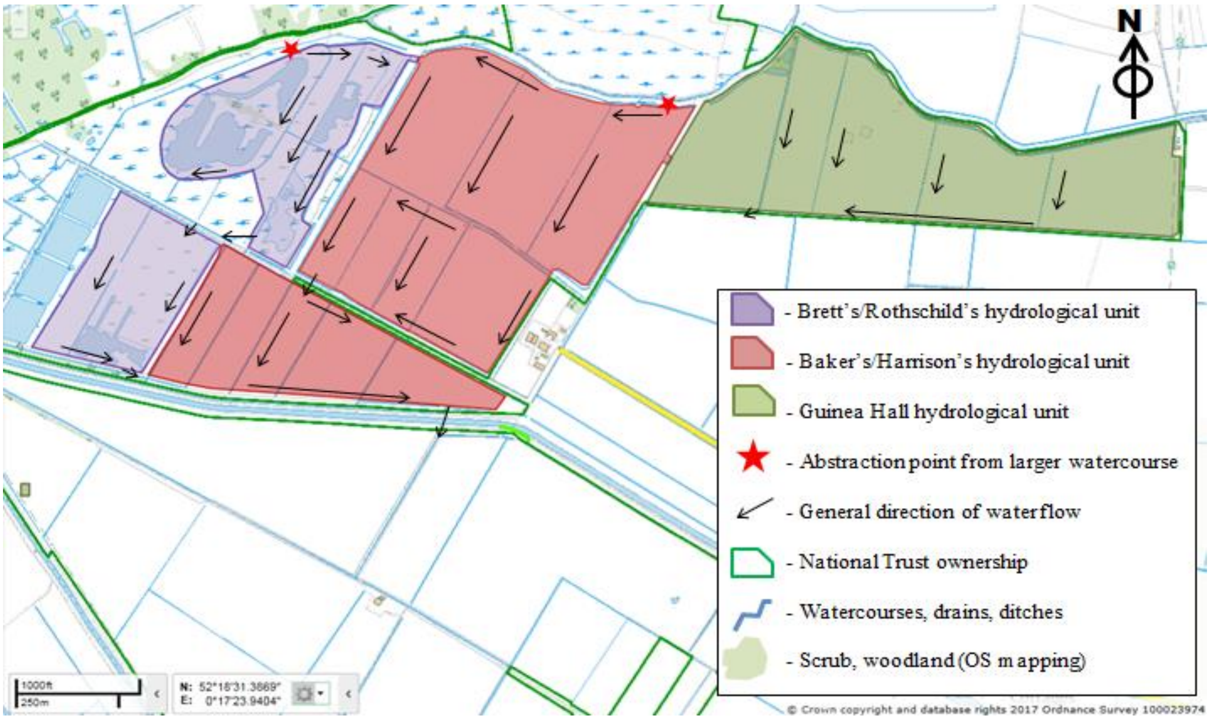

Figure 2.5 Sub-areas, showing individual hydrological units, direction of water flow and abstraction points.

Figure 2.6 Baker's (foreground and left of picture) and Brett's (to the mid-ground and right) showing seasonal inundation of compartments alongside permanent areas of standing water (Brett's). Photograph taken in 2013. Aspect is looking south. © National Trust 2013.

2.3.4 Soils

Brett's, Rothschild's and Baker's compartments lie on medium depth remnant peat soils while Guinea Hall and Harrison's lie on clay soils with very little peat remaining (Stone, 2006). The underlying geology of all the sub-areas consists of silty loams, sand, marl and clay loams which are then overtopped by Holocene peat (Boreham, 2013; Stone, 2006). Table 2.5 shows the peat levels across the sub-areas. The vegetation patterns across Wicken Fen are linked to the peat and water levels, as well as the soil chemistry (Friday and Rowell, 1997), and this pattern can be seen on the sub-areas.

Table 2.5 Depth of remaining peat in sub-areas. Areas of SSSI/NNR/Ramsar/SAC designations are indicated in red.

Sub-area name	**Average peat depth remaining (cm)**
Brett's and Rothschild's	56 - 84
Baker's	31 – 39
Guinea Hall	23 - 25
Harrison's	38

2.3.5 Vegetative profiles

Cultivation of Brett's last occurred in 1947 (Friday, 1997) and it has been in wetland reversion ever since. Vegetation was allowed to regenerate naturally, primarily from the soil seed bank and colonisation of plants which had survived in ditch boundaries (Stroh, 2012). Species typical of wetland plant communities are found in this area in small numbers (e.g. marsh bedstraw *Galium palustre,* Amphibious bistort *Persicaria amphibia*) (Stroh, 2012; Mountford, 2017). The vegetation overall consists of wet grassland largely dominated by reed *Phragmites australis,* large areas of rush *Juncus spp.* alongside various sedges *Carex spp*, and reed canary grass *Phalaris arundinacea*. As well as established mature Crack willows *Salix fragilis*, there are mature areas of scrub, typically comprised of Sallow *Salix spp*., hawthorn and elder (Mountford, 2017). Rothschild's (compartments 41 – 42) has a similar vegetative profile.

Baker's seasonally flooded areas are largely dominated by rush species (for example; hard rush *Juncus inflexus*, blunt flowered rush *Juncus subnodulosus* and, surprisingly, saltmarsh rush *Juncus gerardii*). Shorter sward in these wetter areas is primarily dominated by bent *Agrostis stolonifera* (Mountford, pers com). Plants that can tolerate exposure and grow on moist-wet mud such as watermint *Mentha aquatica*, mare's tail *Hippuris vulgaris,* trifid bur-marigold *Bidens tripartite* and pink water speedwell *Veronica catenata* are also relatively widespread. The higher, drier areas are mixed coarse grassland with couch *Elytrigia* dominant and some localised patches of creeping thistle (Mountford, pers.com). These areas also have small patches of young hawthorn scrub emerging.

Guinea Hall plant communities are as discussed in Section 2.2, with substantial bushes of blackberry *Rubus fruticosus* also interspersed throughout the elder and hawthorn scrub. Flowering plants that prefer dry grasslands, such as ox-eye daisy *Leucanthemum vulgare* and bee orchid *Ophrys apifera*, have also been recorded (Laidlaw, pers.obs.).

Compartments 63 and 64 in Harrison's have a very similar vegetative profile to Guinea Hall, being primarily species poor neutral grassland. The compartments that are seasonally inundated (60 – 62) support plant communities that thrive in wet mud and draw down habitats, similar to those found in Baker's (Mountford, pers. com). There is establishing hawthorn scrub approximately 2 - 6 metres in height.

2.4 The animals, a general overview

The management of areas 1 and 2 is influenced by the herds of Konik horses and Highland cattle that have been introduced to the Fen as part of the National Trust's Vision. The first grazing animals were introduced to the NNR in 2001, but this research focusses on the animals introduced to, and bred on, the research areas over 2003 – 2011. There are three groups of animals identified as part of this research (Table 2.6). In total, 92 individuals were included (Appendix IV).

Table 2.6 Numbers of cattle and horses with their breeding status and distribution at Wicken Fen nature reserve as of 31 December 2011. Three horses (two male, one female) were included in the data collection, but were not recorded in this census as they were moved off site prior to the census date.

Area	**Hectares**	**Species**	**Number**		**Breeding status**
			M	F	
1	119.5	Cattle	0	26	Non-breeding
		Horse	27	19	Breeding
2	36.27	Cattle	13	4	Breeding

2.4.1 Introduction and integration of the cattle and horses to Wicken Fen Nature Reserve

The founder horses were imported from nature reserves in Holland in collaboration with an organisation called Stitching Ark. Founder animals were sourced from sites which had similar management principles and habitats (where possible) to those at Wicken Fen. Groups of animals that were familiar with each other but that were as genetically unrelated as possible were sought. The first breeding animals were introduced in 2003.

This organisation preferred to move entire family groups or entire male groups as intact units, rather than splitting up groups. This was to reduce stress during handling and travelling by providing animals with the comfort of a familiar family unit (Gjis Kirsjens, Stichting Ark, pers.com).

The founder cattle were imported from two separate sites in Scotland. The female group was sourced from an organic farm on the Isle of Mull, while the male was sourced from a farm on the mainland near Oban. A further two female cattle were introduced from Strumpshaw Fen reserve near the Norfolk Broads in the spring of 2008.

The National Trust introduced small numbers of animals in limited areas (Table 2.7). This allowed staff time to become familiar with the animals and their behaviour, and effectively support the animals' welfare as they habituated to the site.

Table 2.7 Species and numbers of animals introduced to the sub-areas area by year.

Year	Sub-Area	Species	Numbers introduced	
			Male	**Female**
2003	Brett's	Horse	2	4
2004	Baker's	Horse	2	0
2004	Guinea Hall	Horse	1	4
2005	Baker's	Cattle	1	8
2008	Rothschild's/Harrison's	Cattle	0	2

Once grazing systems were established, sub-areas were linked (by creating crossing points over perimeter ditches and footpaths) to form one grazing unit, in line with the National Trust's vision to create one large unified nature reserve. In 2006, Brett's and Baker's were linked, creating one grazing unit of 73.65 hectares with ten horses and eight cattle grazing it. In January 2008, Guinea Hall was added, creating one unit of 119.05 hectares with 29 horses and 25 cattle utilising it. Area 1 and area 2 remained as separate grazing areas until March 2016, when the highway separating the two areas was spanned by a 'green' bridge to allow the animals to cross.

Due to breeding, cattle numbers increased from nine in 2006 to 41 in 2008. Based on this rise, it was thought that the cattle population could increase beyond the ability of the land to sustain it too early on in the project. To prevent this, all males with the cattle herd in area 1 were removed over a period from 2008 – 2010 (a total of 13 males). They were re-formed into a separate, smaller mixed herd in area 2 (this included the two females brought in from the Norfolk Broads). From 2010, cattle breeding ceased in area 1, and continued on a very small scale in area 2. No further changes were made to the structure of the cattle herds after this point, other than those applicable to natural population shifts.

Very little was done to alter the structure of the horse herd after its amalgamation in 2008. Apart from three individuals removed from the herd and taken to other areas over the course of 2011, the only changes to the herd structure were those caused by births and deaths.

2.4.2 Welfare and management

The cattle and horses are managed under an extensive, minimal management system. Within current welfare laws and moral obligations, common husbandry practices found in domestic or commercial systems, such as the administering of prophylactics for worm control, hoof trimming or supplementary feeding are rarely undertaken.

Animals live out in their grazing units, year round. They have access to a variety of forage and browse throughout their home range. Drinking water is from natural sources such as ditches and waterways. Shelter is found in the lee of banks, trees and existing scrub. Man-made structures such as corrals and relics of old farm buildings are also available in a few areas.

Within their grazing units, the animals have considerable freedom to determine where they will graze, rest and drink. Occasionally, the animals' range will be restricted for management reasons such as statutory weed control. Animals form their own social groups and the establishment of naturalistic social dynamics is welcomed.

2.4.2.1 Checks, monitoring and veterinary interventions

Without a reliance on prophylactics to prevent or cure welfare issues, members of staff are trained to recognise behavioural and physiological cues to an animal's state early. There is a robust system of daily checks on all animal groups, with an emphasis on breeding animals and animals with known issues. Monthly condition checks monitor and record the hoof and body condition of all individuals. Qualified veterinary surgeons check the animals twice a year, providing a written report on their health. The National Trust is also a signatory to the Royal Society of the Prevention of Cruelty to Animals' Assured scheme, which is underpinned by the RSPCA's welfare standards. The animals at Wicken Fen are checked once a year by RSPCA Assured inspectors.

Animals are not treated for endo- or ecto-parasites. Pooled and individual bi-monthly faecal egg counts monitor the changes in intestinal worm numbers in both horses and cattle. Despite marked seasonal fluctuations, these checks have not shown any correlation between poor condition or ill health and numbers of intestinal worms.

Animals with welfare issues are monitored, to determine how they are coping. If the animal is not coping (id est, cannot keep up with the herd, is not eating and is evidencing distress, discomfort or depression), treatment or euthanasia is given after discussion with the attending veterinary surgeon. Animals that are coping are left to heal without intervention but are closely monitored.

During the course of data collection for this research the veterinary surgeon attended the Fen five times; three times for emergency treatment of two horses and twice to perform pre-arranged non-emergency surgery.

2.4.2.2 Population changes

Cattle and horses are permitted to breed freely. For both species, males accompany females year round. Young of both sexes are permitted to stay with their parental group until they are naturally evicted or migrate away from that group. Individuals that are not fit to breed for reasons of poor physiology or temperament are prevented from breeding; otherwise intervention with population control is kept to a minimum. Animals are left to calve or foal unassisted in the field but are carefully monitored.

The cattle started calving in 2006, and the horses foaling in 2004. Young have been born in every year to both cattle and horses since the start of breeding (Figure 2.7). Calves were born to all females of breeding age (over one year of age and able to conceive) in every year until 2008, when the males were removed and breeding slowed down. Not all female horses of breeding age foaled in every year.

Cattle calving in the years 2006 – 2008 was relatively tightly synchronised, occurring in a two month window from mid-March to mid-May. After 2008, births were more widely scattered, occurring across the year.

Foalings were also tightly synchronised from 2004 – 2008, occurring in a one month window from mid-April to mid – May. After the sub-areas (and horse herds within them) were amalgamated in 2008, foalings became widely scattered across the year, occurring from January to December with a small cluster occurring around April – May.

From 1st January 2003 to 31st December 2011, 18 animals died or were euthanased. The age range of death ran from zero days old to mature adults and the reasons for death ranged from traumatic injury requiring euthanasia to stillbirths. Ten of the 18 deaths were as a result of active intervention and the remainder were deaths out in the field with no veterinary intervention. Eleven of the deaths were horses, seven were cattle. The greatest proportion of losses occurred in 2010 for the horses and 2008 for the cattle (Figure 2.8).

It is a legal requirement in Britain that all domestic or farmed animal carcasses must be removed for disposal by a licensed contractor within 24 hours of death. The same applies to the animals at Wicken Fen, despite their wild-type management.

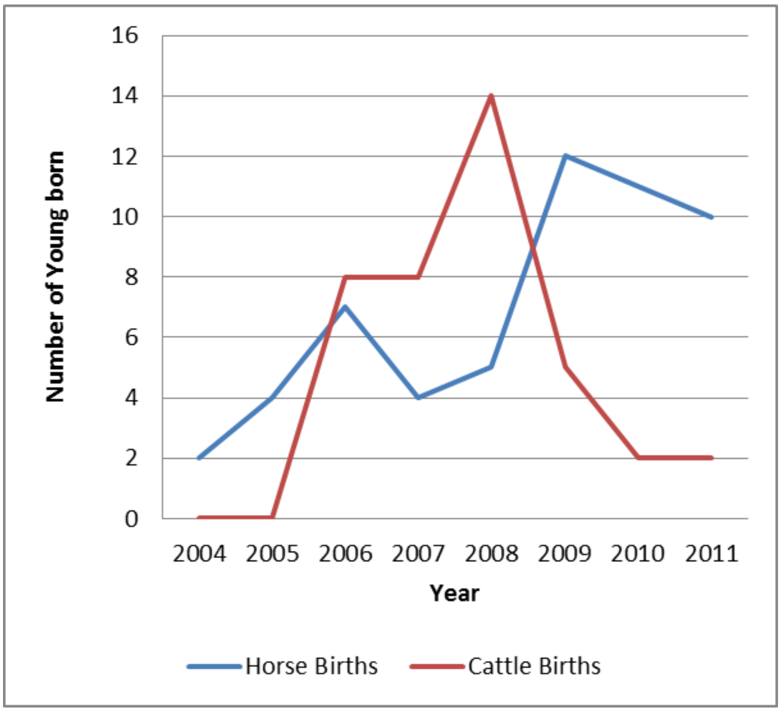

Figure 2.7 Young born to the cattle and horses from 1st January 2004 – 31st December 2011.

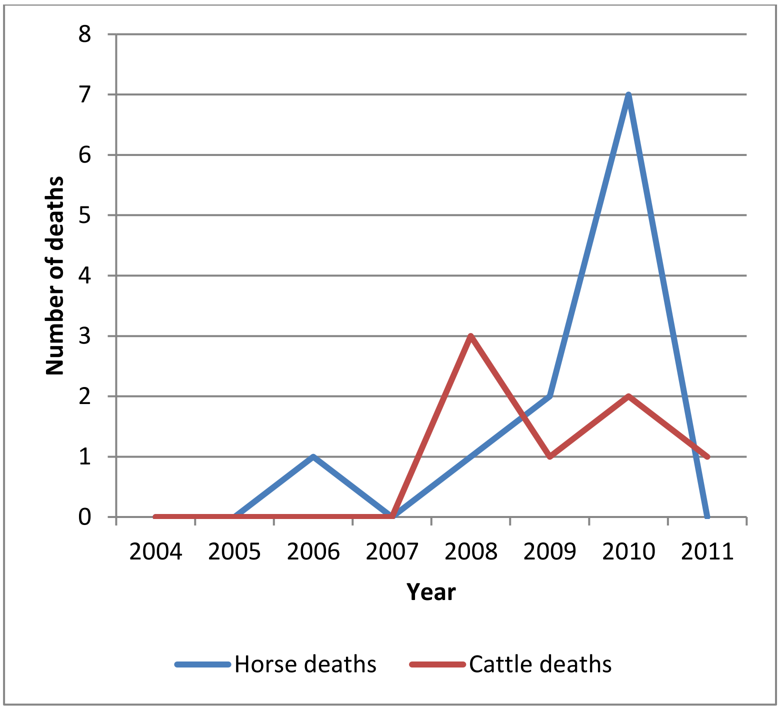

Figure 2.8 Animals deceased from 1st January 2003 to 31st December 2011.

2.5 Methods

2.5.1 Data collection

The methods for the data gathering exercise for the cattle and horses at Wicken Fen were informed by Altmann (1974) and Boy and Duncan (1979). Data for the Konik horses and Highland cattle were collected for one hour per day on selected days over the calendar year 1st January 2011 to 31st December 2011. As the data collection schedule was dictated by work requirements, data were collected on pre-arranged dates and times throughout the year and were set to coincide with a five day working week (Table 2.8).

Table 2.8 Dates when hour long scan samples were performed in 2011. Sessions that were focussed on the horses are coloured green, those for cattle are shaded blue (all-female cattle group days contain a '♀' symbol), no collection = unshaded. The 20th August contained one sampling session on the horses and one on the cattle (split colour cell). The 30th July and 8th October had two cattle sampling sessions at separate times, indicated by the combined symbols '♀ + ♂'. Total days containing sampling sessions for cattle numbered 86, for horses, 79.

Date	Months											
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1st												
2nd			♀			♀						
3rd								♀				
4th			♀		♀							
5th		♀										
6th												
7th												
8th			♀							♀ + ♂	♀	
9th		♀										
10th					♀						♀	
11th		♀										
12th	♀			♀								
13th												
14th	♀			♀								
15th										♀		
16th				♀								♀
17th			♀						♀			
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21st									♀			♀
22nd						♀						
23rd												
24th						♀					♀	
25th					♀							
26th												
27th					♀							
28th										♀		
29th												
30th			♀		♀		♀ + ♂					
31st												

Data were collected in every month of the year. For the purposes of analysis, months were grouped together into seasons. As per Boy and Duncan (1979), this followed the seasonal pattern for temperate areas in the northern hemisphere (winter = December, January, February; spring = March, April, May; summer = June, July, August; autumn = September, October, November).

Days were split into equal 3.5 hour sections corresponding to a ‘time of day’ (early morning = 06:00 – 09.30, morning = 09.30 – 13:00, afternoon = 13:00 – 16:30 and evening = 16:30 – 20:00). Data collection aimed to cover an even spread of time across early morning, morning, afternoon and evening over the course of the year. Tables 2.9a and 2.9b show the accumulated hours spent scan sampling across time of day and through the seasons for both the cattle and horses.

Table 2.9a Accumulated time in hours spent with cattle, conducting periodic scan sampling during study period (1st January to 31st December 2011) by time of day and season.

Cattle	**Time of day**				
Season	**Early Morning**	**Morning**	**Afternoon**	**Evening**	**Total**
Winter	2	10	5	0	17
Spring	8	9.5	8	2	27.5
Summer	5	4	6	5	20
Autumn	5	10	9	1	25
Total	20	33.5	28	8	89.5

Table 2.9b Accumulated time in hours spent with horses, conducting periodic scan sampling during study period (1st January to 31st December 2011) by time of day and season.

Horses	**Time of day**				
Season	**Early Morning**	**Morning**	**Afternoon**	**Evening**	**Total**
Winter	2.5	11	5	0	18.5
Spring	4	8.75	8	3	23.75
Summer	3.5	5	7	2.25	17.75
Autumn	2	6.25	3.5	.25	12
Total	12	31	23.5	5.5	72

Data collection between the two species followed an alternating cycle throughout the year. On cattle data weeks, collection rotated between the female group in grazing area 1 and the mixed sex group in grazing area 2 (Table 2.8). Observations were made within available daylight hours (typically 06:00 – 20:00 in the summer and 08:00 – 16:00 in the winter). Data were collected for an hour each day. Appendix V details data collection dates, hours observed and species followed.

2.5.2 Sampling and recording technique

The study required that multiple data (behaviour, location, nearest neighbour) be recorded on multiple individuals over the course of one year. The daily time allowable to collect this data was limited, due to work commitments.

Scan sampling was chosen in order to fulfil the requirement to record behaviour on multiple individuals. Individuals were identifiable through coat markings such as dorsal or zebra stripes (horses), white patches (cattle), horn shape (cattle) or hair whorls (horses and cattle). The researcher has worked with the animals since their introduction in 2003 - 2005, so identification of individuals was very robust.

Scan sampling means that a whole group of subjects is rapidly scanned at regular intervals and the behaviour of each individual at that instant is recorded. It allows for the collection of data that is evenly representative of all individuals across time of day and season (Martin and Bateson, 2007). Scan sampling has proved to be an effective method of sampling groups of domestic and wild species such as bottlenose dolphins *Tursiops truncatus* (Constantine et al., 2004), capuchin monkeys *Cebus olivaceus* (Ruiter, 1986), chickens *Gallus gallus domesticus* (Weeks et al., 2000), pigs *Sus scrofa domesticus* (Bowden et al., 2008) and northern shoveler *Anas clypeata* (Guillemain at al., 2000).

A scan sample was taken every 15 minutes in each hour (Appendix VI): at 0, 15, 30 and 45 minutes (time sampling). Each sample recorded the behavioural state, location, and the identity of the nearest neighbour for every individual in a herd (instantaneous sampling). Animal behaviours, identities and locations were ascertained by the researcher and were communicated to an assistant, who recorded these on a field sheet. The four samples taken on each day cannot be regarded as being statistically independent measures, but this can be overcome by averaging the data to provide a single score for each day and individual (Martin and Bateson, 2007).

Young were born to the herds over the course of the research, and these were included in the data collection. As the young were born three or four months into the data collection period, there is less data recorded for these individuals. Data were collected for 92 individuals (Appendix IV), within the age and sex classes in Table 2.10. Data regarding the age category an individual belonged to was extracted from records held by the National Trust, and knowledge of the herds provided by the researcher.

Table 2.10 Study animals categorised by age class and sex. In total, 92 animals were observed.

	Adult >4 years old		**Sub-adult 1 – 4 years old**		**Young 0 – 1 year old**		**Total**
	Male	**Female**	**Male**	**Female**	**Male**	**Female**	**All sexes**
Cattle (Area 1)	0	13	0	13	0	0	26
Cattle (Area 2)	3	2	9	2	1	0	17
Horses (Area 1)	8	9	16	6	5	5	49

Due to regular management welfare checks all animals were habituated to being observed from close quarters. All animals were approachable within 10 metres without visible disturbance to their behaviour (i.e., the animals did not approach or move away from the researcher at this distance). During scan sampling sessions, identification and observation were conducted readily without disturbance to the animals' behaviours as researchers did not approach any closer than 10 metres to individuals.

All individual animals are known by name to the researcher, and data were recorded against named individuals. However, to assist with input and analysis, each individual was also given an identification code (ID code). Each ID code consists of five numbers (for example; ID code 51110). The position and sequence of numbers indicate the sex of the animal, species, the year of birth and order of birth in that year. The first digit represents both the sex and species of the individual (5 = male horses, 6 = female horses, 1 = male cattle, 2 = female cattle). The next two digits represent the last two digits of the year of birth (for example; 2010 = 10, 2011 = 11 etcetera), and the final two digits are assigned to each individual depending upon the order of birth in that year. Thus, ID code 51110 indicates that it refers to a male horse born in 2011, and he was the tenth individual born in that year. Appendix IV details all individuals and their associated ID codes.

2.5.3 Management notes

Data were not collected in dusk or dark conditions, due to the difficulty of identifying and approaching the animals then. Test runs during 2010 using night-vision binoculars showed that the animals were difficult to identify as fine detail of coat colour and hair whorl positioning was lost. The animals were more reactive to noises and lights (such as torches), often running from the source of the disturbance (Laidlaw, pers. obs. 2010).

During the course of collecting the data, animal access was occasionally restricted from certain compartments within the study areas due to National Trust management of those areas. Table 2.11 records which areas the animals were excluded from and for how long.

Table 2.11 Compartments temporarily inaccessible to the grazing animals during 2011. Compartments 104 – 107 were excluded for a total of 97 days; compartment 112 was excluded for a total of 57 days.

Compartment(s) inaccessible to animals	**Date exclusion started**	**Date exclusion finished**	**Species excluded**	**Total days excluded**
104 - 107	21/01/2011	16/03/2011	Horses and female cattle	54
	20/07/2011	31/08/2011		43
112	20/07/2011	14/09/2011		57

Occasionally, data collection sessions were cut short or abandoned due to work emergencies (such as veterinary visits for a sick animal) or other work related requirements. Where this occurred, efforts were made to replace the lost time at another equivalent point within the data schedule.

2.5.4 Further sources of data

Data have been collected by the researcher on the status, distribution and behaviour of the herds since the introduction of the first horses in 2001. Costs, veterinary records, records of births and deaths are all included. Daily welfare checks have resulted in detailed records on herd changes and behaviour. These have been made through field observations and recorded in paper form since grazing started. Data are stored in Excel spreadsheets and diaries at Wicken Fen, and these sources have been made available for the purposes of this research.

Chapter 3

Grazing and Maintenance Behaviours of Horses and Cattle at Wicken Fen

3.1 Introduction

To support the ongoing management of the extended nature reserve at Wicken Fen, the National Trust has introduced groups of mixed sex and age cattle and horses (National Trust, 2011). These groups of animals are grazed over an extensive area year round. The aim is to develop a low input management system using self-reliant herds of herbivores to create a mobile mosaic of self-regenerating wildlife habitats (Colston, 2003; National Trust, 2009).

In order to understand the influences of grazing upon a landscape, such as that found at Wicken Fen, comparative data can be obtained from European and worldwide sites. It is known that conservation grazing can bring a wide range of benefits to the species diversity of the area being managed (Gibson and Brown, 1991; Smith et al., 2000; Stroh, 2012). Research on the foraging and maintenance behaviours of free-ranging cattle and horses found that grazing of wetland or grassland sites benefitted the overall diversity of the site (Marty, 2005) although this effect can be dependent on the numbers, age classes or sexes of each species grazed (Menard et al., 2002).

Different species, sexes and ages exhibit varied forage preferences, which in turn influences habitat choice (Cornelissen and Vulink, 2015). Similarly, Hall (1988) and Rook et al., (2004) have suggested that the introduction of groups of mixed sex and age grazers could benefit diversity by spreading grazing intensity across different vegetation communities.

While maximising intake of high quality forage is an important driver shaping ungulate habitat choice and behaviour (Duncan, 1983; Vulink and Drost 1991), there are many other influences upon ungulate behaviour. For example, external environmental factors can cause cattle and horses to cease foraging in the push to seek relief from insect harassment or high temperatures (Boyd et al., 1988; Duncan, 1983; Keiper and Berger, 1982). In addition, a review of cattle behaviour at pasture by Kilgour et al. (2012) and research by Linnane et al. (2001) demonstrated that variables such as time of day and season impacted on grazing animal behaviour, with cattle and horses demonstrating differing patterns of circadian activity (Arnold, 1984).

Equally, intrinsic factors, such sex and age, can influence ungulate behaviour and habitat choice. Côté et al. (1997) and Duncan (1980) demonstrated that variance in behaviour is influenced by the age class of the individual (young animals were likely to be found resting more often than adults, for example) while research by Boyd (1988) showed that gender affected the levels of foraging behaviours in male and female horses. However, counter to this, Ruckstuhl and Neuhaus (2009) found no differences in behaviour between the sexes for the monomorphic ungulate, the African oryx *Oryx gazelle.*

However, while the studies and research introduced above are valuable in aiding understanding in how the behaviours of grazing animals may shape the landscape at Wicken Fen, the grazing system implemented there is innovative within the United Kingdom (Stroh, 2012) and little exists in literature relating directly to this. In addition, conservation grazing management in the UK has often been experience led, and not evidence led, partially due to a paucity of relevant evidence (Pullin and Knight, 2000). With these factors in mind, this study aims to add to the understanding of novel conservation grazing practice by evaluating the behaviour and area use of the grazing animals at Wicken Fen. In order to do this, the following three questions were addressed for the cattle and horses:

1. Are there differences in maintenance behaviours between individuals across sex and age?

2. Are there differences in maintenance behaviours across time of day and season?

3. Are there associations in sub-area use with season or maintenance behaviours?

3.2 Methods

The methods for this study are described in detail in Chapter 2, including details of the study area and sub-areas (Section 2.3), study animals (Section 2.4) and sampling regime and data collection protocols (Section 2.5). This section only gives additional key information relevant to the questions and analyses for this chapter.

Behavioural definitions for the cattle and horses were constructed during 2010 (Appendix VII) using in field observations with reference to McDonnell (2003) and Boy and Duncan (1979). Maintenance behaviour states were recorded during data collection sessions (if event states such as fighting and playing occurred at the point of sampling they were recorded under a catch-all category called ‘other’). McDonnell (2003) defines maintenance behaviours as those commonly associated with basic survival activities such as feeding and resting.

3.2.1 Statistical analysis

Data were analysed using IBM SPSS Statistics Data Version 20. A critical significance level of 0.05 was used throughout. Where variables were judged to be normally distributed, parametric alternatives were used to assess differences between individuals by sex and age (Sections 3.3.2 and 3.3.3).

In order to compare variability of the different groups in relation to each other, errorplots were used (Hawkins, 2009). The mean for each sample is represented by a point and the variability of the sample is indicated by two ‘T’ shaped bars extending above and/or below the point.

Boxplots are used to show the shape of the distribution of the data, its central value and its variability. The box indicates the interquartile range, containing 50% of the values. The top of the box represents the 75^{th} percentile; the bottom, the 25^{th} (Hawkins, 2009). The thick line within the box indicates the median, and the two ‘T’ shaped bars extending from the ends of the box indicate the range.

3.2.1.1 Overview

In order to assess the relative occurrence of behaviours and whether it could be assumed that parametric criteria could be met for t-tests and Anovas, descriptive statistics and histograms were generated for all behavioural variables. Data were first aggregated by day and then individual, with individuals being used as the unit of analyses (n= 43 for cattle and n = 49 for horses) to generate medians, means, standard deviations and histograms.

3.2.1.2 Individual differences across sex and age category

Differences in behaviour by sex (male, female) and age (young, sub-adult, mature adult) were analysed separately for horses and cattle using tests of differences (Hawkins, 2014). In order to deal with lack of independence, data were first aggregated by day and then by individual. This produced a mean percentage of scans of each behaviour performed by each animal. T-tests (parametric) or Mann-Whitney U tests (non-parametric) were then used to compare males and females. One-way Anova (parametric) or Kruskal-Wallis tests (non-parametric) were used to compare age-categories. The decision to use parametric or non-parametric tests was based upon inspection of histograms (Figure 3.1a and b). If a behaviour variable looked approximately normally distributed, a parametric test was used; otherwise the non-parametric alternative was used (Table 3.1a and b).

Throughout analysis, sex was defined as either male or female for both species. Age for the cattle and horses are split into three categories (Table 2.10) and are the same for both species. The category "Young" was not included in analysis of difference across age for the cattle, as there was only one late-born individual in this category in 2011.

3.2.1.3 Behavioural differences across time of day and season

Differences in behaviour over time (within days and between seasons) were analysed separately for the horses and cattle using a Generalised Linear Mixed Model through the Generalised Estimating Equations function on SPSS (Grafen and Hails, 2002; Hawkins, 2014; IBM SPSS Statistics Data Version 20 on-line help). As time of day and season were measured in categories, these analyses were effectively tests of difference that utilised the GLZM framework as an alternative to a traditional analysis of variance. Only the four most frequent behaviours for each species (Tables 3.2a and b) were considered due to low frequencies in other categories making it unlikely that the model assumption would be met.

In order to deal with lack of independence within individual samples, individual ID was added to the model as a random variable. The following word equation summarises the analyses:

Behaviour = Season (or Time of Day) + Animal ID

With a logit link function, Time of Day or Season was entered as a fixed factor, and Animal ID as a random factor. A link function transforms the response variable (in this case behaviour) so that it equates to the explanatory variables in a linear fashion. The logit function is the natural log of the odds that the response variable equals the explanatory variable and is recommended for use with binary data, in this case behaviour occurred/didn't occur (Hawkins, 2014).

Time of day was categorized as early morning, morning, afternoon and evening and season as spring, summer, autumn and winter for both cattle and horses (Section 2.5.1).

3.2.1.4 Differences in area use across season and behaviours

Analyses looking at associations of use of space (grazing sub-area, Section 2.3.1) with season (spring, summer, autumn, winter; Section 2.5.1) and with behaviour were analysed using two-way chi-square tests (Hawkins, 2014). Since different groups had access to different sub-areas the analyses were done separately for the three different groups (female cattle, horses and mixed sex cattle). Only the four most frequent behaviours for each species (Tables 3.1a and b) were considered due to paucity of data in other categories leading to low expected frequencies which cause lack of reliability in chi-square analyses. In order to deal with lack of independence within a day and within groups, data were sub-sampled so that only the location of the group on the first scan each day was used.

3.3 Results

3.3.1 Overview

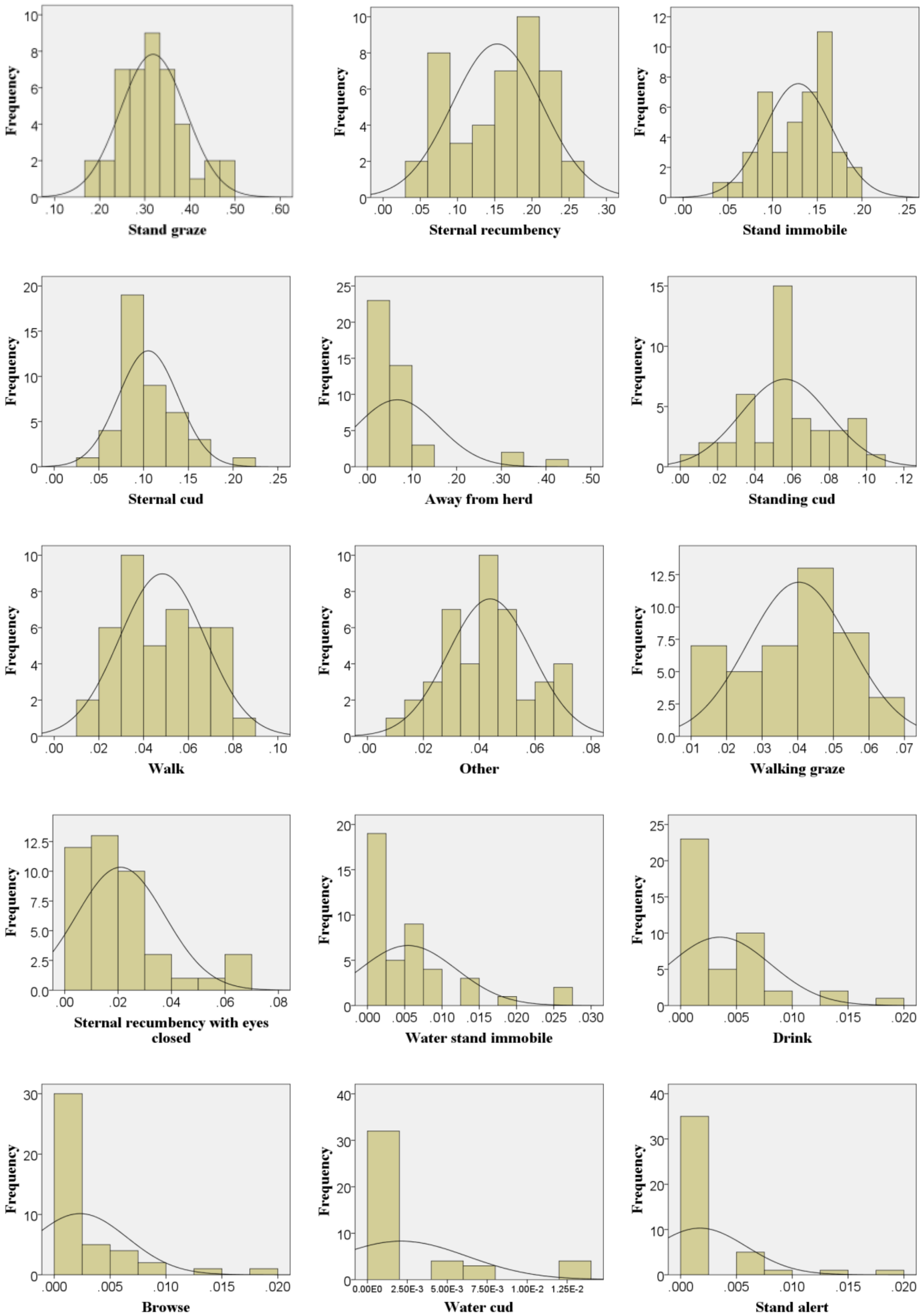
Data were collected on 19 behaviours for cattle and 16 behaviours for horses (cudding behaviours were not performed by horses, otherwise, data were collected for the same suite of behaviours as the cattle). The median, mean and standard deviations for all behaviours are presented in Table 3.1a for the cattle and 3.1b for the horses. The tables also indicate which variables were judged to be normally distributed, based upon examination of the histograms, presented in Figures 3.1a (cattle) and 3.1b (horses).

Table 3.1a Descriptive statistics for 19 maintenance behaviours of cattle. Individuals were used as a unit of analysis as described in Section 3.2.1.1. Behaviours listed in descending order of mean. Unshaded cells indicate that data were judged to be normally distributed. Grey shaded cells indicate that data were not judged to be normally distributed, based upon inspection of Figure 3.1a. (n = 43).

Behaviour	Median	Mean	Std. Deviation	Distribution
Standing Graze	0.316	0.318	0.073	
Sternal Recumbency	0.163	0.153	0.061	
Stand Immobile	0.136	0.129	0.038	
Sternal Cud	0.096	0.105	0.033	
Away from herd	0.046	0.067	0.093	
Standing Cud	0.056	0.056	0.024	
Walk	0.046	0.048	0.019	
Other	0.045	0.044	0.015	
Walking Graze	0.045	0.040	0.014	
Sternal Recumbency with eyes closed	0.019	0.021	0.017	
Water Stand Immobile	0.005	0.005	0.006	
Drink	0.000	0.004	0.005	
Browse	0.000	0.002	0.004	
Water Cud	0.000	0.002	0.004	
Stand Alert	0.000	0.002	0.004	
Lateral Recumbency	0.000	0.002	0.004	
Lateral Recumbency with eyes closed	0.000	0.001	0.002	
Run	0.000	0.001	0.002	
Standing Doze	0.000	0.000	0.001	

Table 3.1b Descriptive statistics for 16 maintenance behaviours of horses. Individuals were used as a unit of analysis as described in Section 3.2.1.1. Behaviours listed in descending order of mean. Unshaded cells indicate that data were judged to be normally distributed. Grey shaded cells indicate that data were not judged to be normally distributed, based upon inspection of Figure 3.1b. (n = 49).

Behaviour	**Median**	**Mean**	**Std. Deviation**	**Distribution**
Standing Graze	0.488	0.445	0.129	
Stand Immobile	0.201	0.208	0.043	
Walk	0.093	0.097	0.029	
Standing Doze	0.052	0.057	0.034	
Other	0.042	0.044	0.029	
Walking Graze	0.035	0.038	0.021	
Sternal Recumbency	0.018	0.033	0.036	
Browse	0.011	0.020	0.019	
Lateral Recumbency with eyes closed	0.004	0.019	0.032	
Sternal Recumbency with eyes closed	0.005	0.013	0.022	
Stand Alert	0.010	0.012	0.012	
Lateral Recumbency	0.000	0.006	0.012	
Run	0.003	0.005	0.005	
Drink	0.000	0.002	0.003	
Away from herd	0.000	0.001	0.003	
Water Stand Immobile	0.000	0.001	0.002	


Frequency
Stand graze
Sternal recumbency
Stand immobile
Sternal cud
Away from herd
Standing cud
Walk
Other
Walking graze
Sternal recumbency with eyes closed
Water stand immobile
Drink
Browse
Water cud
Stand alert

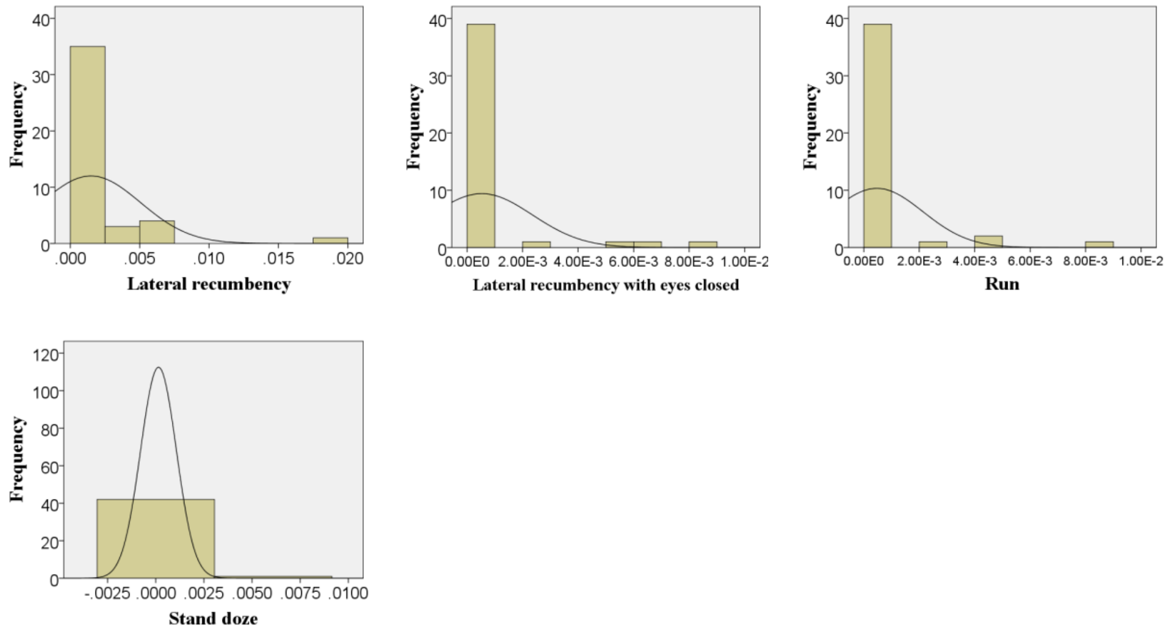
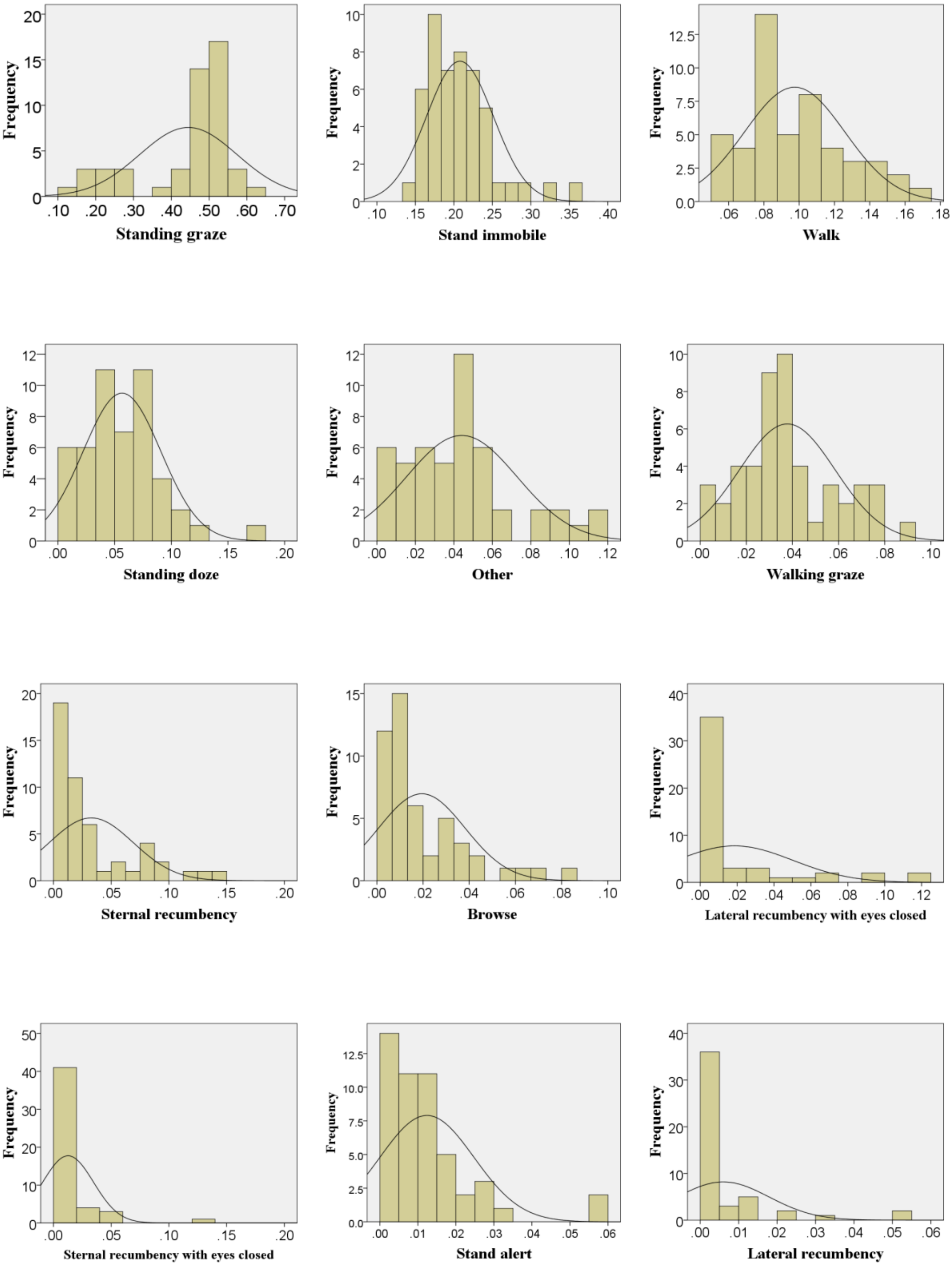


Figure 3.1a Histograms for 19 maintenance behaviours of cattle with distribution curve generated by SPSS. Individuals used as a unit of analysis as described in Section 3.2.1.1. (n = 43). Behaviours ranked in descending order of mean as stated in the legend to Table 3.1a.


Frequency
Standing graze
Stand immobile
Walk
Standing doze
Other
Walking graze
Sternal recumbency
Browse
Lateral recumbency with eyes closed
Sternal recumbency with eyes closed
Stand alert
Lateral recumbency

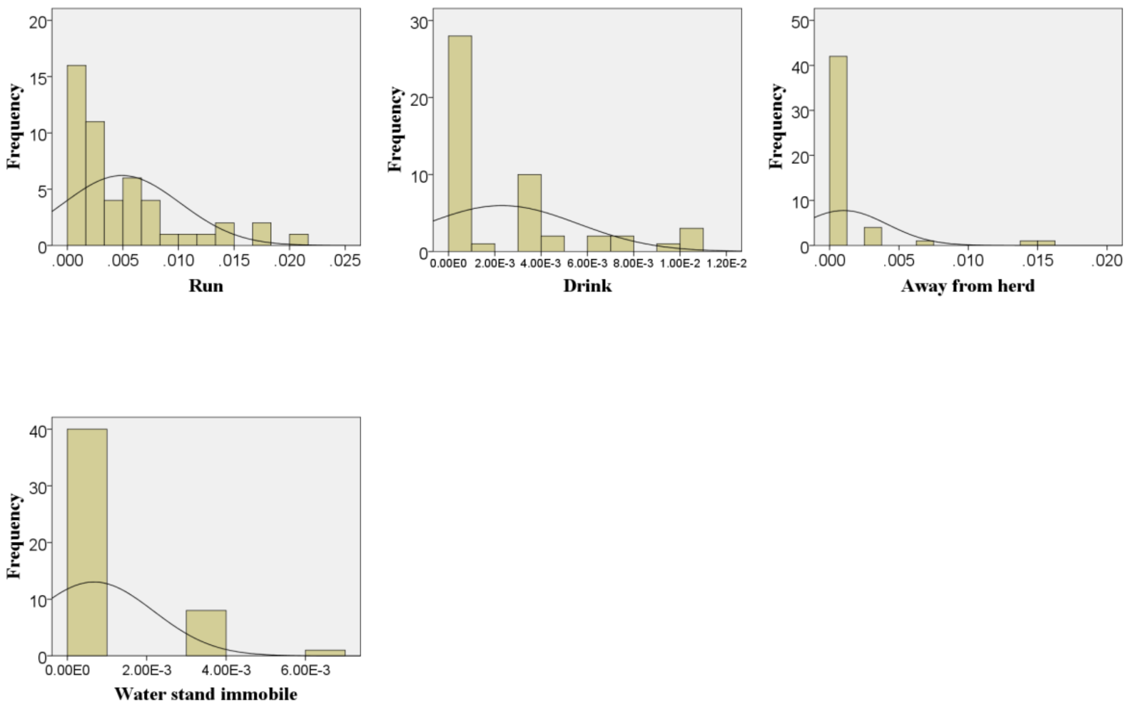


Figure 3.1b Histograms for 16 maintenance behaviours of horses with a distribution curve generated by SPSS. Individuals used as a unit of analysis as described in Section 3.2.1.1. (n = 49). Behaviours ranked in descending order of mean as stated in the legend to Table 3.1b.

Please note; to reduce prolixity during presentation of the results and discussion, terms such as 'performed more' and 'spent more time' were used rather than 'were more likely to be observed'.

3.3.2 Differences in behaviour by sex

Female cattle spent more time in sternal recumbency, standing immobile, walking and drinking than male cattle (Table 3.2a, Figure 3.2a). Male cattle spent more time away from the herd and standing grazing than the female cattle (Tables 3.2a, Figure 3.2a) Two out of 16 tests produced significant results for the horses, with male horses having performed the behaviours other and stand alert more than female horses (Table 3.2b, Figure 3.2b).

Table 3.2a Statistical results for differences in maintenance behaviours between the sexes in cattle (**$P \leq 0.05$ indicated by bold type**). For both tests n_1 (male) = 13, n_2 (female) = 30.

Behaviour	**T-test Statistic (t_{41})**	**Mann-Whitney U Statistic (U)**	**P**
Standing Graze	2.085	-	**0.043**
Sternal Recumbency	-6.344	-	**0.000**
Stand Immobile	-2.865	-	**0.007**
Sternal Cud	-0.778	-	0.441
Away from herd	-	35.0	**0.000**
Standing Cud	0.370	-	0.713
Walk	-3.819	-	**0.000**
Other	-0.535	-	0.569
Walking Graze	0.169	-	0.867
Sternal Recumbency with eyes closed	-	265.5	0.062
Water Stand Immobile	-	162.5	0.377
Drink	-	269.0	**0.032**
Browse	-	200.0	0.871
Water Cud	-	194.5	0.986
Stand Alert	-	224.0	0.258
Lateral Recumbency	-	206.0	0.694
Lateral Recumbency with eyes closed	-	178.0	0.372
Run	-	158.0	0.052
Standing Doze	-	201.5	0.510

Table 3.2b Statistical results for differences in maintenance behaviours between the sexes in horses (**P ≤ 0.05 indicated by bold type**). For both tests n_1 (male) = 29, n_2 (female) = 20.

Behaviour	**T-test Statistic (t)**	**Mann Whitney Statistic (U)**	**P**
Standing Graze	0.225	-	0.823
Stand Immobile	-0.490	-	0.626
Walk	-1.183	-	0.243
Standing Doze	-0.646	-	0.521
Other	2.357	-	**0.023**
Walking Graze	-0.099	-	0.922
Sternal Recumbency	-	281.500	0.863
Browse	-	302.500	0.799
Lateral Recumbency with eyes closed	-	320.000	0.529
Sternal Recumbency with eyes closed	-	316.500	0.587
Stand Alert	-	106.500	**0.000**
Lateral Recumbency	-	300.000	0.824
Run	-	284.500	0.909
Drink	-	288.000	0.964
Away from herd	-	289.000	0.973
Water Stand Immobile	-	303.000	0.964

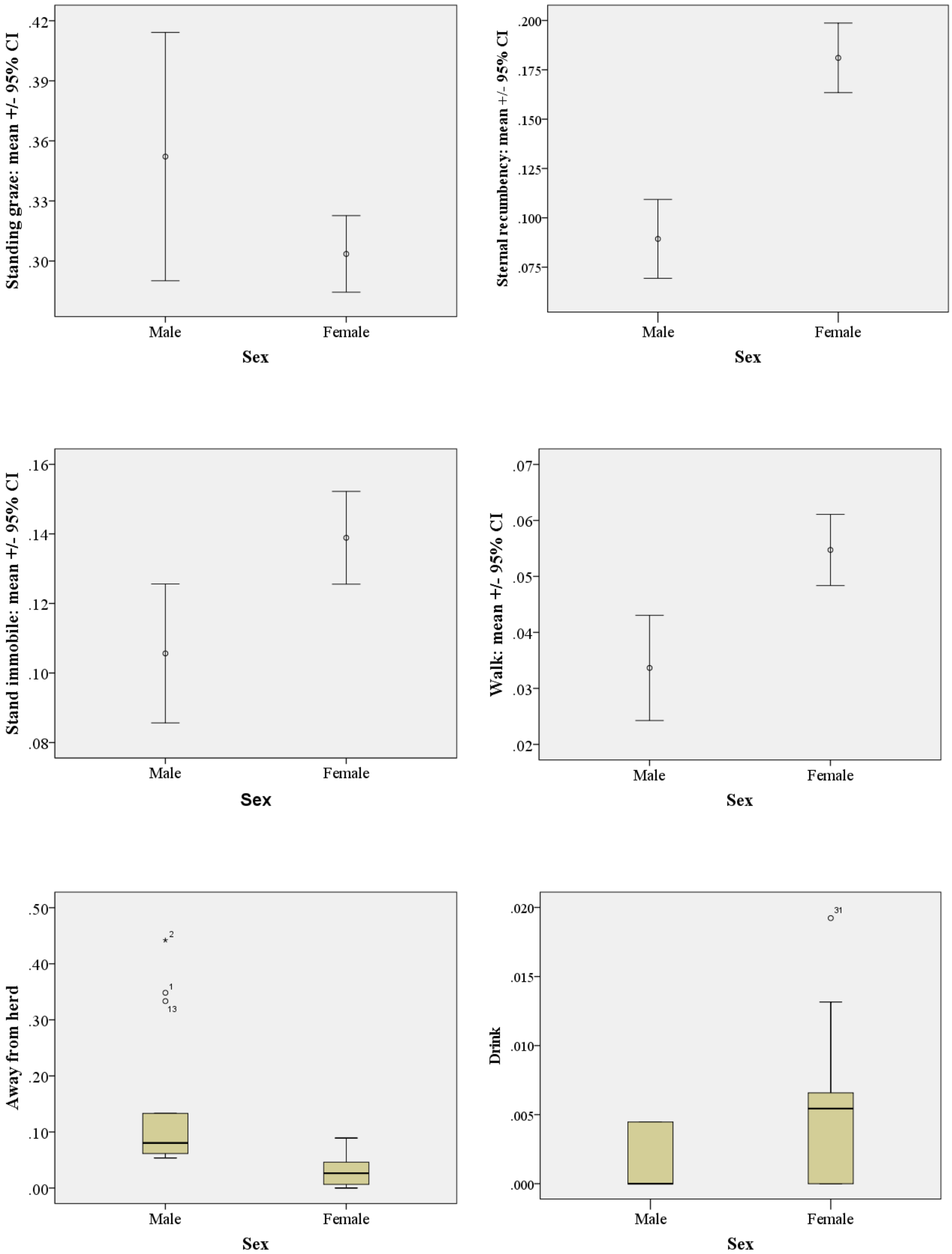


Figure 3.2a Comparison of proportion of scans (Section 2.5.2) between males (n = 13) and females (n = 30) in cattle for six maintenance behaviours with significant results (Table 3.2a). Individuals used as a unit of analysis (Section 3.2.1.2). For general information on errorplots and boxplots, see Section 3.2.1.

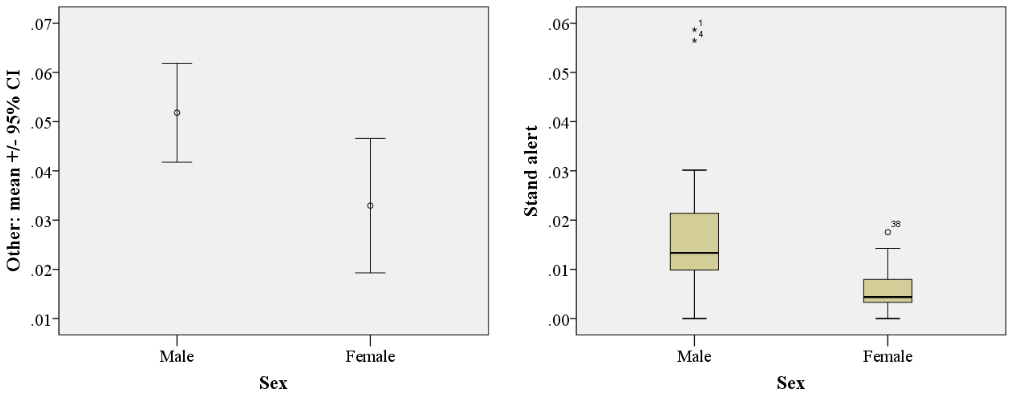


Figure 3.2b Comparison of proportion of scans (Section 2.5.2) between males (n = 29) and females (n = 20) in horses for two maintenance behaviours with significant results (Table 3.2a). Individuals used as a unit of analysis (Section 3.2.1.2). For general information on errorplots and boxplots, see Section 3.2.1.

3.3.3 Differences in behaviour by age

Sub-adult cattle spent more time standing grazing than mature adult cattle (Table 3.3a, Figure 3.3a). There were no other significant differences between sub-adult cattle and mature adult cattle in any other behaviours tested (Table 3.3a).

Young horses performed stand immobile, walk and other more than either sub-adult or mature adults (Table 3.3b, Figure 3.3b). Sub- adults and mature adults stood and grazed more than young horses, while mature adults stood and dozed more than either of the other age categories (Table 3.3b, Figure 3.3b). Mature adults also performed walking graze more than either sub-adults or young (Table 3.3b, Figure 3.3b). Mature adults were observed drinking and standing resting in water more than sub-adults and young, although both of these behaviours were rarely observed (Table 3.3b, Figure 3.3b). The resting behaviours sternal recumbency, sternal recumbency with eyes closed, lateral recumbency and lateral recumbency with eyes closed were all performed more by young horses than adults and sub-adults (Table 3.3b, Figure 3.3b). Young horses also spent more time browsing than sub-adults and mature adults (Table 3.3b, Figure 3.3b).

Table 3.3a Statistical results for differences in maintenance behaviours between ages in cattle **(P ≤0.05 indicated by bold type)**. N_1 (sub-adult) = 24, n_2 (adult) = 18.

Behaviour	**One-Way Anova Statistic ($F_{1,40}$)**	**Kruskal-Wallis Statistic (x^2_1)**	**P**
Standing Graze	7.465	-	**0.009**
Sternal Recumbency	0.718	-	0.402
Stand Immobile	1.952	-	0.170
Sternal Cud	1.466	-	0.233
Away from herd	-	0.508	0.476
Standing Cud	0.004	-	0.952
Walk	0.155	-	0.696
Other	2.388	-	0.130
Walking Graze	0.128	-	0.722
Sternal Recumbency with eyes closed	-	1.196	0.274
Water Stand Immobile	-	2.093	0.148
Drink	-	2.891	0.089
Browse	-	0.117	0.733
Water Cud	-	0.973	0.324
Stand Alert	-	0.111	0.738
Lateral Recumbency	-	0.279	0.598
Lateral Recumbency with eyes closed	-	0.040	0.842
Run	-	0.598	0.439
Standing Doze	-	1.333	0.248

Table 3.3b Statistical results for differences in maintenance behaviours between ages in horses **(P ≤0.05 indicated by bold type)**. N_1 (young) = 10, n_2 (sub-adult) = 22, n_3 (adult) = 17.

Behaviour	**One-Way Anova Statistic ($F_{2,46}$)**	**Kruskal-Wallis Statistic (x^2_2)**	**P**
Standing Graze	127.322	-	**0.000**
Stand Immobile	11.031	-	**0.000**
Walk	14.303	-	**0.000**
Standing Doze	7.370	-	**0.002**
Other	15.973	-	**0.000**
Walking Graze	15.161	-	**0.000**
Sternal Recumbency	-	34.367	**0.000**
Browse	-	12.213	**0.002**
Lateral Recumbency with eyes closed	-	27.882	**0.000**
Sternal Recumbency with eyes closed	-	8.437	**0.015**
Stand Alert	-	5.157	0.076
Lateral Recumbency	-	25.755	**0.000**
Run	-	0.750	0.687
Drink	-	8.717	**0.013**
Away from herd	-	2.113	0.348
Water Stand Immobile	-	14.218	**0.001**

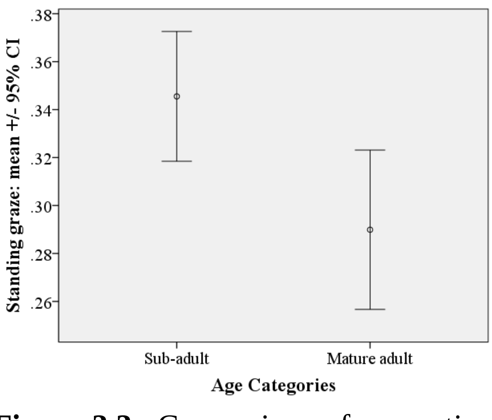
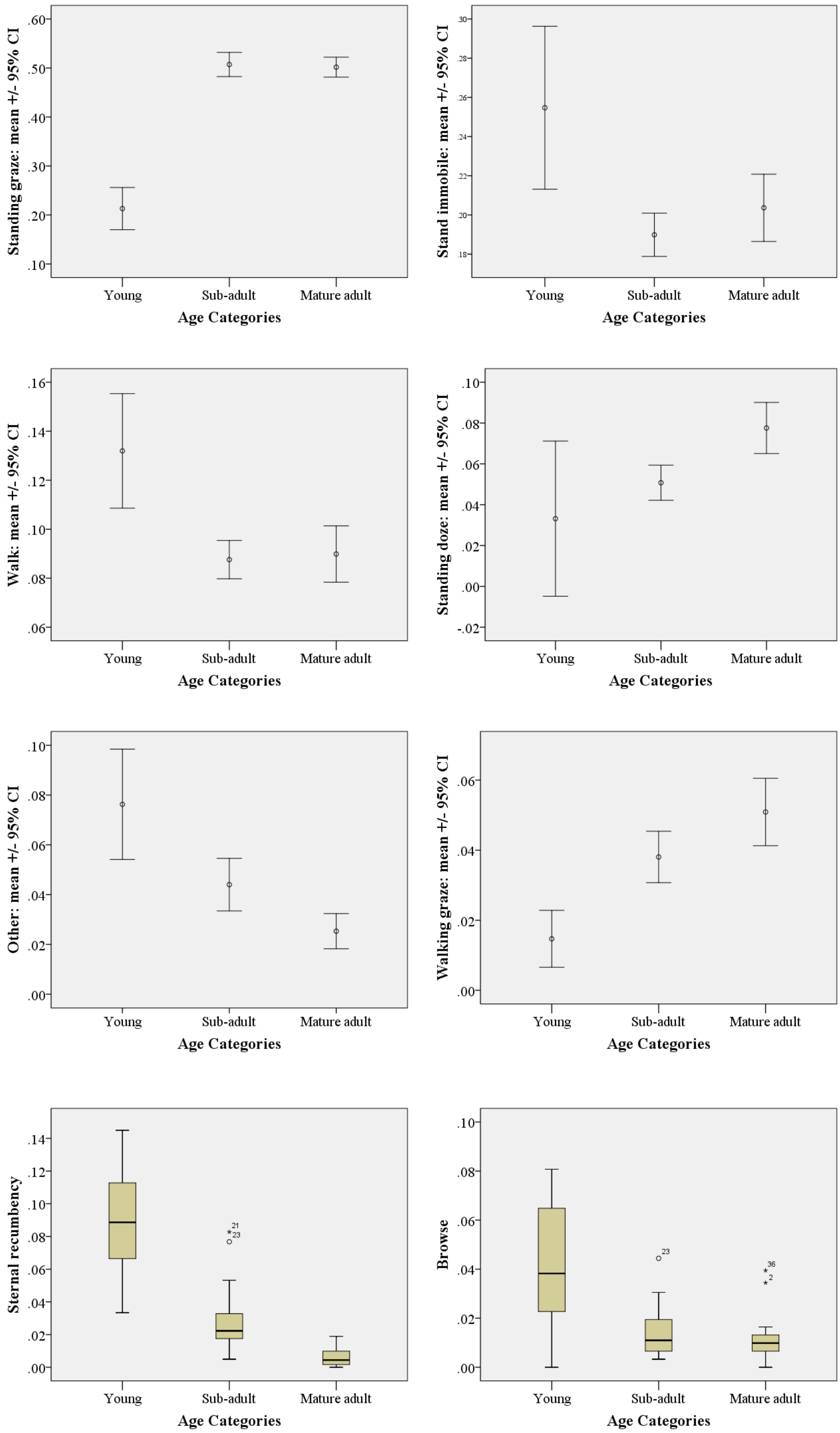


Figure 3.3a Comparison of proportion of scans (Section 2.5.2) between ages; sub-adult (n = 24) and adult (n = 18) in cattle for one maintenance behaviour with significant results (Table 3.3a). Individuals used as a unit of analysis as described in Section 3.2.1.2. For general information about errorplots, see Section 3.2.1.


Standing graze: mean +/- 95% CI
Stand immobile: mean +/- 95% CI
Walk: mean +/- 95% CI
Standing doze: mean +/- 95% CI
Other: mean +/- 95% CI
Walking graze: mean +/- 95% CI
Sternal recumbency
Browse
Young
Sub-adult
Mature adult
Age Categories

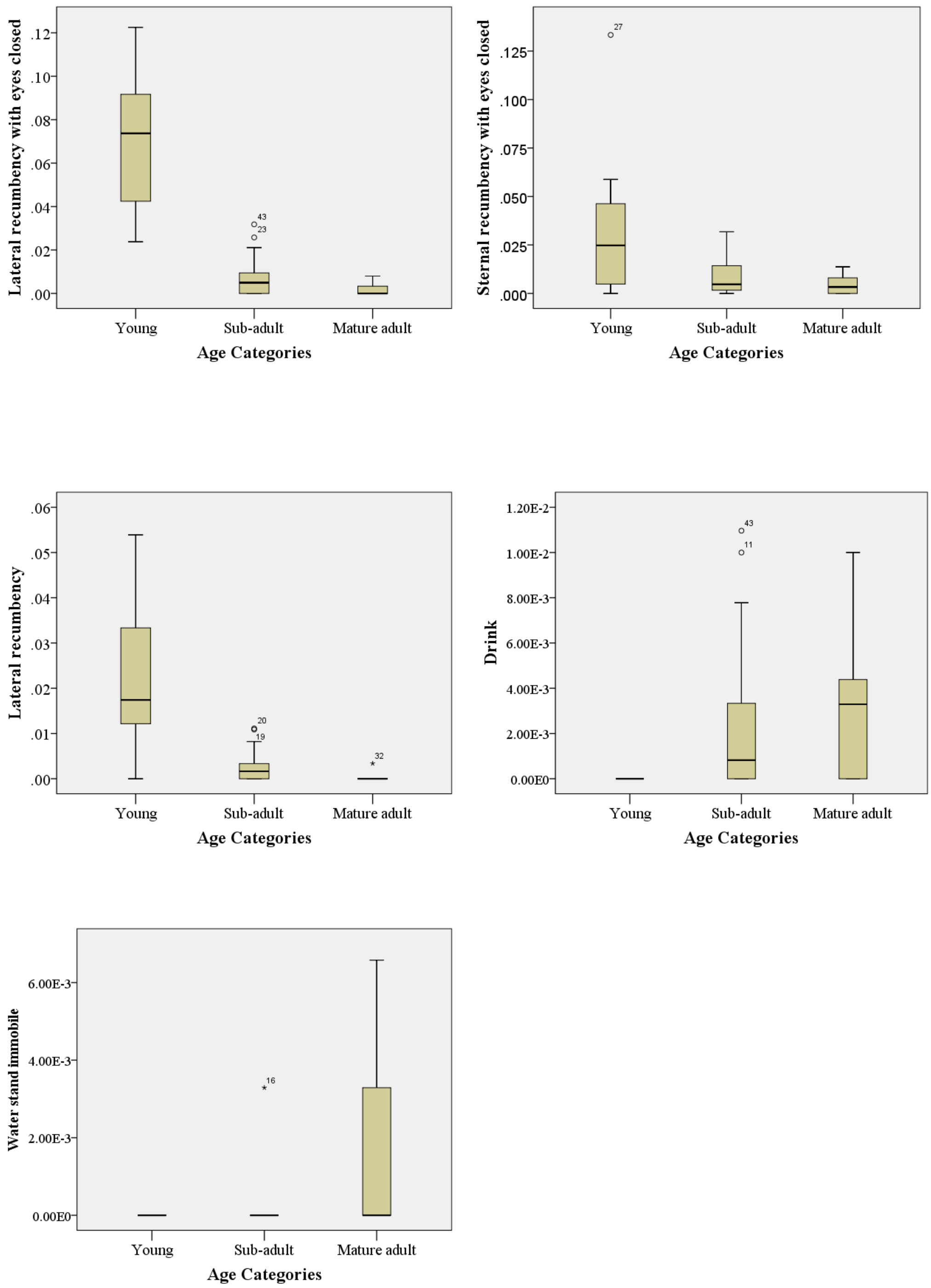


Figure 3.3b Comparison of proportion of scans (Section 2.5.2) between ages; young (n = 10), sub-adult (n = 22) and adult (n = 17) in horses for 13 maintenance behaviours with significant results (Table 3.3b). Individuals used as a unit of analysis (Section 3.2.1.2). For general information on errorplots and boxplots, see Section 3.2.1.

3.3.4 Differences in behaviour by time of day

Overall, the analyses indicate that behaviour varied between time of day categories for both the horses and cattle. Throughout 2011, cattle performed standing graze most during the early morning and evening and least during the mornings and afternoons (Table 3.4a, Figure 3.4a). Cattle performed sternal recumbency most in the early morning and afternoon in summer and autumn respectively, whilst it was seen least in the evenings across both seasons (Table 3.4a, Figure 3.4a). The validity of model fit was uncertain for this behaviour in spring and winter, so these results will not be considered further (Table 3.4a). The behaviour stand immobile was performed most during the mornings and afternoons in the spring and summer and least in the evenings and early mornings (Table 3.4a, Figure 3.4a). During the autumn, cattle stood immobile most during evenings and early mornings and least in the afternoon, while in the winter cattle stood immobile most in the afternoon and least in the morning (Table 3.4a, Figure 4.3a). During the spring and summer, sternal cud was performed by cattle most in the afternoons. This behaviour was seen least in the evenings in spring, and early mornings in summer (Table 3.4a, Figure 3.4a). The validity of model fit for sternal cud in autumn and winter was uncertain, so these results will not be discussed further (Table 3.4a).

Horses performed standing graze through three seasons most in the early morning, with the exception of evenings in the autumn, where standing graze was performed most (Table 3.4b, Figure 3.4b). Standing graze was performed least during mornings in spring, autumn and winter and also afternoons in the summer (Table 3.4b, Figure 3.4b). Stand immobile was performed most by the horses during the morning in spring, autumn and winter and afternoons in the summer. Stand immobile was performed least in the evenings during spring, summer and autumn and also during the afternoon in the winter (Table 3.4b, Figure 3.4b).

Horses walked most during the afternoons, evenings and mornings during spring, summer and autumn respectively, while this behaviour was performed least in the early mornings, mornings and afternoons through the same seasons (Table 3.4b, Figure 3.4b). The model fit was uncertain for horses performing walk during the autumn, so this result will not be considered further. Standing doze was performed most by the horses in the mornings and least in the early mornings during spring and summer (Table 3.4b, Figure 3.4b). The validity of model fit was uncertain for this behaviour during autumn and winter, so this result shall not be considered further (Table 3.4b).

Table 3.4a General estimated equations results for comparison of four maintenance behaviours across time of day in cattle **(P ≤ 0.05 indicated by bold type)**. Observation was used as the unit of analysis, with animal identity included as a random variable in the model as described in Section 3.2.1.3. Only the four most frequent behaviours were selected for analysis (Section 3.2.1.3), based on highest mean values in Table 3.1a. Results highlighted in red indicate results where the validity of the model fit is uncertain. (n = 43).

					Parameter estimates			
Behaviour	**Season**	**Wald Chi-Square**	**Degrees of Freedom**	**P**	**Early Morning**	**Morning**	**Afternoon**	**Eve**
Standing Graze	Spr.	56.515	3	**0.000**	0.186	-0.373	-0.910	/
	Sum.	212.815	3	**0.000**	-1.039	-1.088	-1.206	/
	Aut.	105.988	3	**0.000**	0.247	-0.663	-0.029	/
	Win.	275.949	2	**0.000**	1.163	0.566	/	/
Sternal Recumbency	Spr.	68679.402	2	**0.000**	25.708	25.950	26.192	/
	Sum.	12.367	3	**0.006**	1.216	0.682	1.252	/
	Aut.	29.727	3	**0.000**	1.370	3.366	3.434	/
	Win.	0.388	1	0.533	-30.793	-0.114	/	/
Stand Immobile	Spr.	8.069	3	**0.045**	0.594	0.633	0.250	/
	Sum.	42.777	3	**0.000**	0.130	0.987	0.673	/
	Aut.	5.730	3	0.125	0.495	0.203	-0.021	/
	Win.	2.027	2	0.363	-0.099	-0.303	/	/
Sternal Cud	Spr.	14.908	3	**0.002**	2.473	2.712	2.361	/
	Sum.	40.984	3	**0.000**	-0.526	1.036	1.668	/
	Aut.	20040.495	2	**0.000**	24.159	27.247	26.757	/
	Win.	1.652	1	0.199	-30.372	0.208	/	/

Table 3.4b General estimated equations results for comparison of four maintenance behaviours across time of day in horses **(P ≤ 0.05 indicated by bold type)**. Observation was used as the unit of analysis, with animal identity included as a random variable in the model as described in Section 3.2.1.3. Only the four most frequent behaviours were selected for analysis (Section 3.2.1.3), based on highest mean values in Table 3.1a. Results highlighted in red indicate results where the validity of the model fit is uncertain. (n = 49).

					Parameter estimates			
Behaviour	**Season**	**Wald Chi-Square**	**Degrees of Freedom**	**P**	**Early Morning**	**Morning**	**Afternoon**	**Eve**
Standing Graze	Spr.	246.430	3	**0.000**	0.128	-0.348	-0.422	/
	Sum.	294.064	3	**0.000**	-0.222	-0.854	-0.980	/
	Aut.	661.918	3	**0.000**	0.036	-1.064	-0.817	/
	Win.	615.307	2	**0.000**	-0.447	-1.213	/	/
Stand Immobile	Spr.	53.916	3	**0.000**	0.269	0.046	-0.436	/
	Sum.	271.650	3	**0.000**	-0.724	-0.469	0.332	/
	Aut.	6.129	3	0.105	0.498	0.222	0.401	/
	Win.	21.742	2	**0.000**	-1.609	0.135	/	/
Walk	Spr.	6.331	3	0.097	-0.128	-0.253	-0.373	/
	Sum.	90.518	3	**0.000**	-0.917	-1.580	-1.049	/
	Aut.	34516.163	2	**0.000**	26.146	24.804	25.111	/
	Win.	1.204	2	0.584	0.220	0.050	/	/
Stand doze	Spr.	28.380	3	**0.000**	-1.319	-0.120	-0.987	/
	Sum.	49.573	3	**0.000**	-0.643	0.417	0.605	/
	Aut.	20357.109	2	**0.000**	25.603	25.799	25.493	/
	Win.	6.332	1	**0.012**	-31.089	0.545	/	/

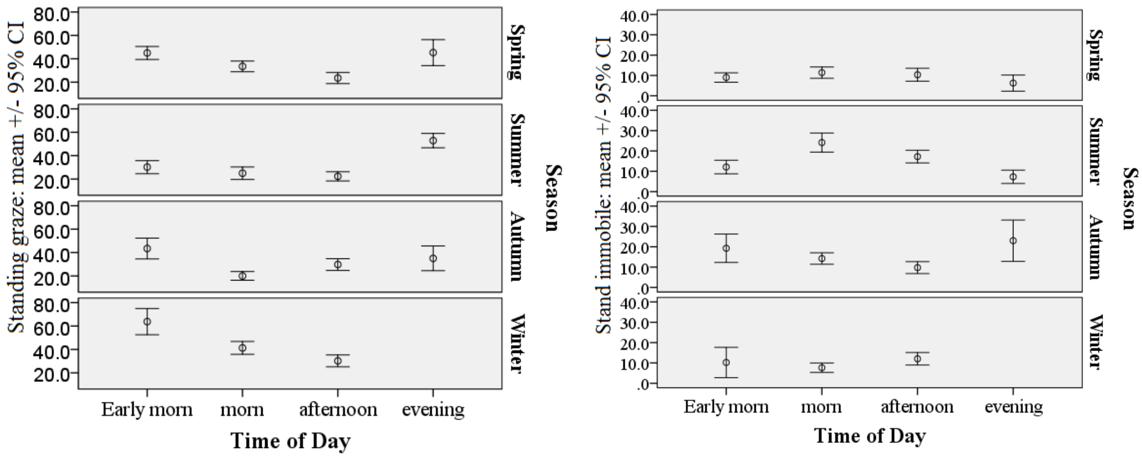


Figure 3.4a Comparison of proportion of scans (Section 2.5.2) across time of day in cattle (n = 43) for two maintenance behaviours. Unit of analysis as described in legend of Table 3.4a. Only behaviours with significant results and valid model fit were chosen for illustration (Table 3.4a). For general information on errorplots, see Section 3.2.1.

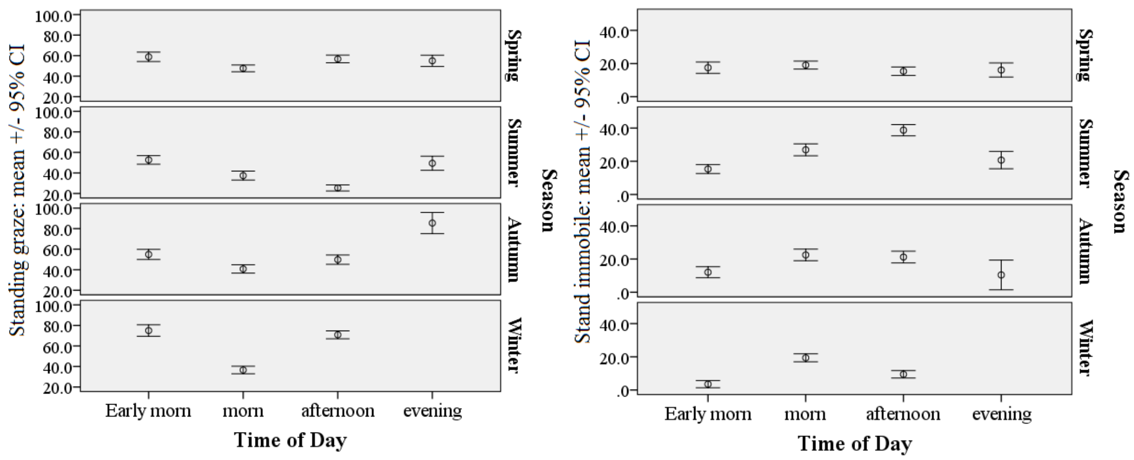


Figure 3.4b Comparison of proportion of scans (Section 2.5.2) across time of day in horses (n = 49) for two maintenance behaviours. Unit of analysis as described in legend of Table 3.4b. Only behaviours with significant results and valid model fit were chosen for illustration (Table 3.4b). For general information on errorplots, see Section 3.2.1.

3.3.5 Differences in behaviour by season

For both the cattle and the horses, the analyses indicate that there were differences in behaviours across the seasons during certain times of day. Standing graze was performed most by the cattle during winter in the morning and afternoon, but it was performed least during autumn mornings and spring afternoons (Table 3.5a, Figures 3.5a and 3.6a). Cattle performed sternal recumbency most in the autumn and spring in the mornings and afternoons respectively. The same behaviour was performed least during the summer in both the morning and afternoon (Table 3.5a, Figures 3.5a and 3.6a). Cattle stood immobile most in the summer during the morning and afternoon while this behaviour was performed least during winter mornings and autumn afternoons (Table 3.5a, Figures 3.5a and 3.6a). The cattle behaviour sternal cud was performed most during autumn mornings and summer afternoons and the same behaviour was performed least in summer mornings and autumn afternoons (Table 3.5a, Figures 3.5a and 3.6a).

Horses stood and grazed most in the spring mornings and winter afternoons, while this behaviour was performed least in winter mornings and summer afternoons (Table 3.5b, Figures 3.5b and 3.6b). The horse behaviour stand immobile was performed most during summer across both morning and afternoon, and least over spring mornings and winter afternoons (Table 3.5b, Figures 3.5b and 3.6b). Across all seasons in the afternoons, there was no significant difference in horses' performance of the behaviour walk, but this behaviour was performed most during winter and least during summer in the morning (Table 3.5b, Figure 3.5b and 3.6b). Horses performed the behaviour stand doze least in the spring across both mornings and afternoons. Stand doze was performed by the horses most during winter mornings and summer afternoons (Table 3.5b, Figures 3.5b and 3.6b).

Table 3.5a General estimated equations statistical results for comparison of four maintenance behaviours across season in cattle **(P ≤ 0.05 is indicated by bold type)**. Observation was used as the unit of analysis, with animal identity included as a random variable in the model (Section 3.2.1.3). Selection of behaviours was based upon highest mean values as seen in Table 3.1a. For all seasons, only data collected during the mornings and afternoons were included in the analyses due to a paucity of data in the early mornings and evenings. (n = 43).

					Parameter estimates			
Behaviour	**Time of Day**	**Wald Chi-Square**	**Degrees of Freedom**	**P**	**Spring**	**Summer**	**Autumn**	**Winter**
Standing Graze	Morn	180.906	3	**0.000**	-0.471	-0.995	-1.166	/
	A'noon	68.781	3	**0.000**	-0.451	-0.556	0.024	/
Sternal Recumbency	Morn	20.614	3	**0.000**	0.252	-0.834	0.036	/
	A'noon	45.555	3	**0.000**	0.380	-0.378	-0.010	/
Stand Immobile	Morn	21.369	3	**0.000**	0.275	0.727	0.217	/
	A'noon	16.960	3	**0.001**	-0.411	0.110	-0.310	/
Sternal Cud	Morn	7.816	3	**0.050**	-0.080	-0.549	0.129	/
	A'noon	10.988	3	**0.012**	-0.222	0.292	-0.153	/

Table 3.5b General estimated equations statistical results for comparison of four maintenance behaviours across season in horses (**P ≤ 0.05 is indicated by bold type**). Observation was used as the unit of analysis, with animal identity included as a random variable in the model (Section 3.2.1.3). Selection of behaviours was based upon highest mean values as seen in Table 3.1b. For all seasons, only data collected during the mornings and afternoons were included in the analyses due to a paucity of data in the early mornings and evenings. (n = 49).

					Parameter estimates			
Behaviour	**Time of Day**	**Wald Chi-Square**	**Degrees of Freedom**	**P**	**Spring**	**Summer**	**Autumn**	**Winter**
Standing Graze	Morn	93.811	3	**0.000**	0.356	-0.141	-0.040	/
	A'noon	733.982	3	**0.000**	-0.931	-1.480	-1.006	/
Stand Immobile	Morn	25.941	3	**0.000**	0.068	0.020	-0.311	/
	A'noon	256.658	3	**0.000**	-0.279	0.957	0.003	/
Walk	Morn	18.380	3	**0.000**	-0.019	-0.546	-0.408	/
	A'noon	0.921	3	0.820	-0.088	0.035	-0.051	/
Stand Doze	Morn	68.181	3	**0.000**	-1.122	-0.488	-0.780	/
	A'noon	72.735	3	**0.000**	-1.443	0.245	-0.541	/

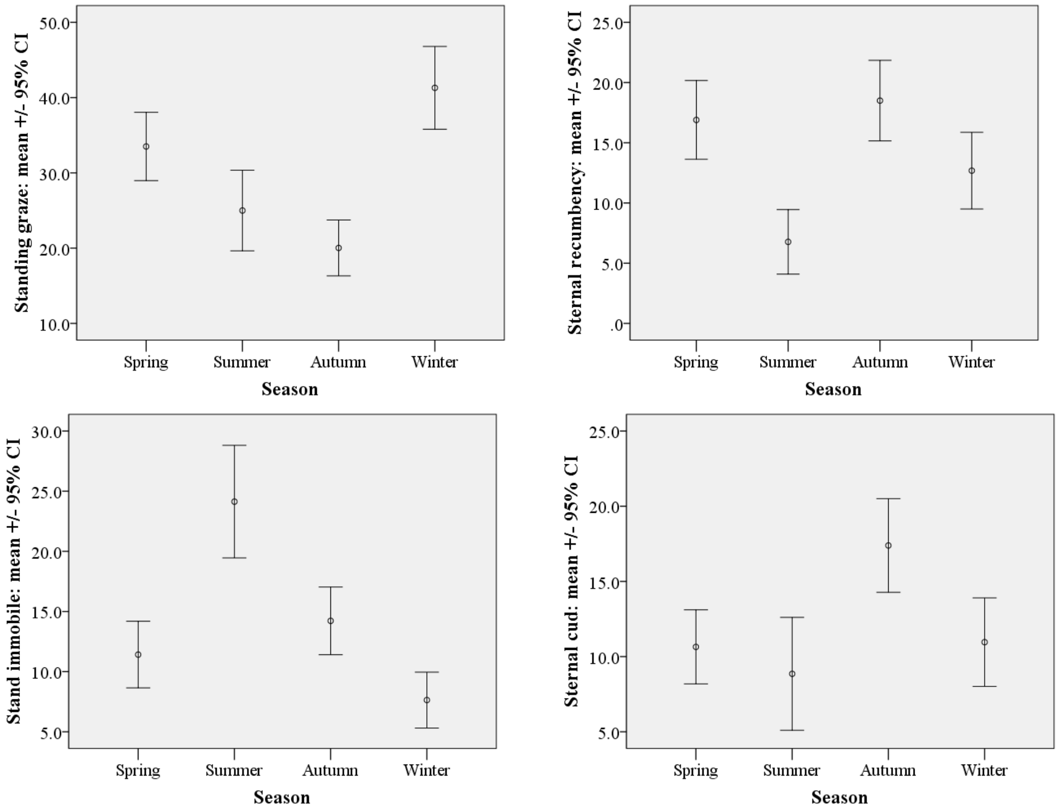


Figure 3.5a Comparison of proportion of scans (Section 2.5.2) across season for four maintenance behaviours of cattle (n = 43), morning only. For details see legend to Table 3.5a. For general information on errorplots, see Section 3.2.1.

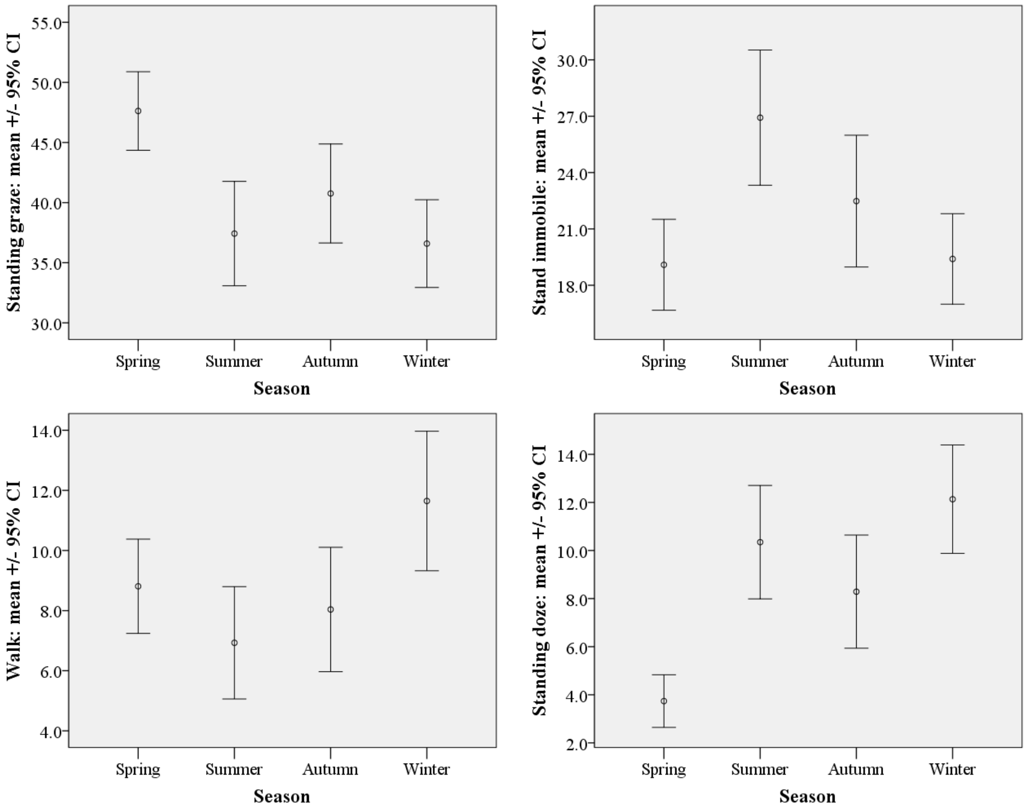


Figure 3.5b Comparison of proportion of scans (Section 2.5.2) across season for four maintenance behaviours of horses (n = 49), morning only. For details see legend to Table 3.5b. For general information on errorplots, see Section 3.2.1.

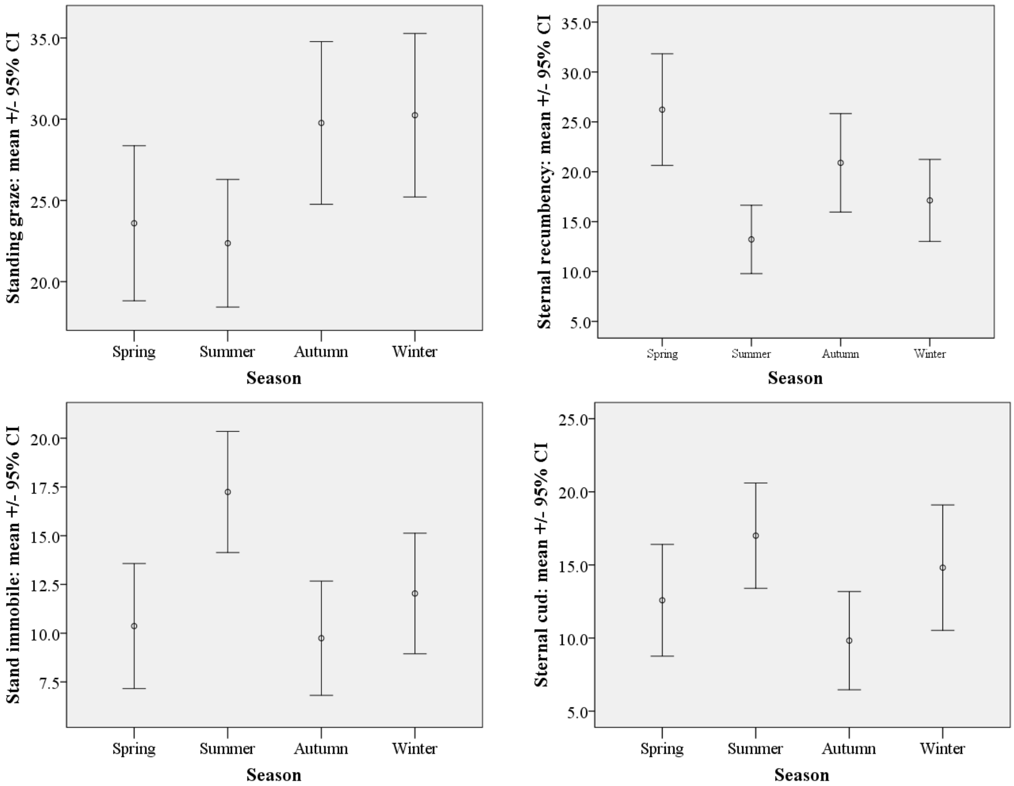


Figure 3.6a Comparison of proportion of scans (Section 2.5.2) across season for four maintenance behaviours of cattle (n = 43), afternoon only. For details see legend to Table 3.5a. For general information on errorplots, see Section 3.2.1.

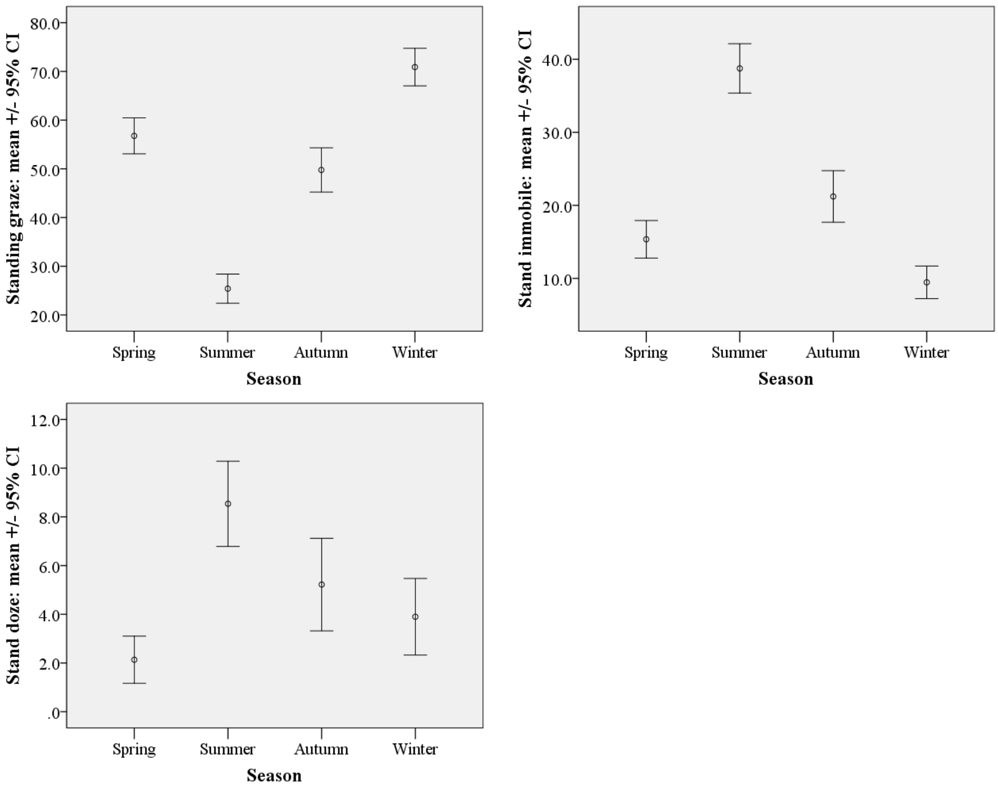


Figure 3.6b Comparison of proportion of scans (Section 2.5.2) across season for three maintenance behaviours of horses (n = 49), afternoon only. For details see legend to Table 3.5b. For general information on errorplots, see Section 3.2.1. The behaviour 'Walk' returned a non-significant result, so was omitted from this figure.

3.3.6 Associations between sub-area and season

Despite having access to sub-area Brett's, the female cattle did not go into this area during the course of data collection in 2011. Their use of Baker's and Guinea Hall occurred in approximately the same relative proportions across the seasons (Table 3.6a). The use of Baker's and Guinea Hall by the horses across the year was largely consistent, but Brett's was not accessed at all during the summer and very little at other times of the year (Table 3.6a).

The mixed sex cattle use of area was very similar across spring, summer and autumn, but Rothschild's was used proportionally less during the winter (Table 3.6b).

Table 3.6a Results of chi-square statistical tests for association between sub-area and season in female cattle (n = 26) and mixed sex horses (n = 49) **(P ≤ 0.05 indicated in bold type)**. Data were sub-sampled so that only the location of the group on the first scan of each data collection day were used, providing a count of the occasions the animals were observed in each area (Section 3.2.1.4). Brett's was not used by the female cattle so counts for this sub-area for female cattle (in red) were not included in the chi-square analysis.

Group	**Grazing sub-area**	**Count**				**Degrees of Freedom**	**P**
		Spring	**Summer**	**Autumn**	**Winter**		
Female Cattle	Brett's	0	0	0	0	3	0.378
	Bakers	7	7	5	7		
	G Hall	8	3	5	2		
Horses	Brett's	2	0	4	5	6	**0.024**
	Bakers	12	14	9	12		
	G Hall	12	9	7	1		

Table 3.6b Results of chi-square statistical tests for association between sub-area and season in mixed sex cattle (n = 17) **(P ≤ 0.05 indicated in bold type)**. Data were sub-sampled so that only the location of the group on the first scan of each data collection day were used, providing a count of the occasions the animals were observed in each area (Section 3.2.1.4).

Group	**Grazing sub-area**	**Count**				**Degrees of Freedom**	**P**
		Spring	**Summer**	**Autumn**	**Winter**		
Mixed sex cattle	Rothschild's	7	11	13	1	3	**0.021**
	Harrison's	10	7	10	11		

3.3.7 Associations between sub-area and behaviour

As in Section 3.3.6, despite having access to the sub-area Brett's, the female cattle did not enter it during data collection sessions, so these data were not included in the chi-squared test. The four behaviours were performed in relatively similar proportions across two sub-areas for the female cattle (Table 3.7a). The horses' four behaviours were performed in relatively equal proportions across three sub-areas (Table 3.7b). The mixed sex cattle, however, performed standing graze and stand immobile more in Harrison's while sternal cud was performed less (Table 3.7c).

Table 3.7a Results of chi-square statistical tests for association between sub-area and behaviour in female cattle (n = 26). **(P ≤ 0.05 indicated in bold type)**. Data were sub-sampled so that only the location of the group on the first scan of each data collection day were used, providing a count of the occasions the animals were observed in each area (Section 3.2.1.4). Brett's was not used by the female cattle so counts for this sub-area (in red) were not included in the chi-square analysis. Only the four most frequent behaviours were selected for analysis (Section 3.2.1.3), based on highest mean values in Table 3.1a.

Group	**Grazing sub-area**	**Count**				**Degrees of Freedom**	**P**
		Stand graze	**Stand immobile**	**Sternal Recumbency**	**Sternal cud**		
Female cattle	Brett's	0	0	0	0	3	0.461
	Baker's	10	3	6	1		
	G Hall	2	2	5	1		

Table 3.7b Results of chi-square statistical tests for association between sub-area and behaviour in horses (n = 49). **(P ≤ 0.05 indicated in bold type)**. For details of data sub-sampling and allocation of behaviours for analysis, see legend to Table 3.7a.

Group	**Grazing sub-area**	**Count**				**Degrees of Freedom**	**P**
		Stand graze	**Stand immobile**	**Stand doze**	**Walk**		
Horses	Brett's	6	1	1	1	6	0.835
	Baker's	22	9	2	4		
	G Hall	15	3	3	4		

Table 3.7c Results of chi-square statistical tests for association between sub-area and behaviour in mixed sex cattle (n = 17). **(P ≤ 0.05 indicated in bold type)**. For details of data sub-sampling and allocation of behaviours for analysis see the legend to Table 3.7a.

Group	**Grazing sub-area**	**Count**				**Degrees of Freedom**	**P**
		Stand graze	**Stand immobile**	**Sternal Recumbency**	**Sternal cud**		
Mixed sex cattle	Rothschild’s	5	2	6	6	3	**0.003**
	Harrison’s	13	4	1	0		

3.4 Discussion

3.4.1 Are there differences in maintenance behaviours between individuals across sex and age?

Results from the analysis investigating if there were differences in behaviours between individuals across sex and age found that the cattle appeared to evidence some difference in named behaviours across sex but not age, while the horses appeared to show an overall lack of difference across sex but showed differences across age.

There are six key behaviours evidencing differences between the sexes for cattle. The foraging behaviour standing graze was performed more by male cattle in this study, while the resting and ruminating behaviours stand immobile and sternal recumbency were performed more by females. This is surprising, as research has shown that females should forage for longer than adult males in order to satisfy increased demands for energy as a result of pregnancy or lactation and higher metabolic rates due to smaller body mass (Demment and VanSoest, 1985; Ruckstuhl, 1998; Phillips, 1993).

The differing results in this analysis for the cattle may be accounted for by the breeding status and herd structure of the two groups. Ninety three percent of the female cattle at Wicken Fen were not pregnant or lactating during 2011, so it is possible that their forage requirement was reduced as a consequence. In addition, 69% of the male cattle were between one to five years of age (Appendix IV) which is a time of high growth and development for young male cattle, potentially requiring more forage input (AHDB, 2018).

Many ungulate species preferentially associate into similar sex and/or age groups in order to optimise their nutritional intake (Ruckstuhl, 1998). In such groups, foraging and resting behaviours are often synchronised (Côté et al., 1997). The management of the Wicken Fen herds of cattle in 2011 had divided the animals into two largely same sex groups with similar age gradients. It is possible that this division of the cattle herds promoted synchronisation of behaviours within the two groups, leading to fewer differences across the sexes than was found in current literature.

As indicated, the analysis of behaviours across sexes for the horses returned significant results for two behaviours out of 16. Previous research has found differences between the behaviours of male and female horses; research on Przewalski horses *Equus ferus przewalskii* found that male Przewalski are more active than females (Boyd, 1988), while Duncan (1980) found sex differences in the time budgets of Camargue horses *Equus caballus*, with males being more active and females resting more. Male horses in breeding herds spend time guarding, tending, defending their females and being vigilant (Duncan, 1980; Boyd, 1988).

The research by Duncan (1980) and Boyd (1988) included event behaviours such as grooming or aggression and rolling. Both of these studies also summed the number of records obtained for each activity recorded, constructing a time budget of behaviours performed for each study individual.

In the current study examining differences in behaviour across the sexes, two significant results were returned, these for the behaviours other and stand alert. Whilst Type 1 error must be considered in interpreting these results, it should be noted that the behaviour 'other' covered a wide suite of behaviours from herding, to defence and play. Males performed this behaviour more than females. The vigilance behaviour stand alert was also performed more by males than females. These results suggest that should a time budget be constructed for the horses and include event as well as maintenance behaviours, differences between the sexes for the Wicken equines, as per Duncan (1980) and Boyd (1988), may become evident.

However, counter to this, research by Ruckstuhl and Neuhaus (2009) indicates that hindgut fermenters, such as horses, should demonstrate less pronounced differences between the sexes than ruminants, as horses are not constrained in their activities by the requirement to ruminate. The results in this research appear to support this, as the horses have evidenced little difference in maintenance behaviours across the sexes.

Behavioural synchronisation may contribute to the lack of difference across age categories for the cattle, but the biggest factor is likely to be the absence of young (individuals <1 year old) from the analysis (section 3.2.1.2).

Analysis on the Wicken horses included 49 individuals from ranging three months of age to 18 years (Appendix IV) covering three age categories (Table 2.10). Overall, young horses under one year of age performed foraging behaviours such as standing graze and walking graze less than adults and sub-adults. Other research has shown that developing young of cattle and horses spend less time foraging than adults as their energy needs are initially met by their mother's milk (Boy and Duncan, 1979; Phillips, 1993).

3.4.2 Are there differences in maintenance behaviours across time of day and season?

Cattle and horses exhibited differences in four main behaviours (Section 3.2.1.3) across time of day and season, showing seasonal variations in daily rhythms. Cattle are crepuscular, showing peaks of activity associated with early morning and evening (Kilgour, 2012; Kilgour et al., 2012, Linnane et al., 2001; Heising and Smid, 2013, Phillips, 1993). The cattle at Wicken appeared to follow this pattern, as grazing activity occurred primarily during the early morning and evening throughout the year, while resting or ruminating behaviours tended to occur during the morning and afternoon. The horses appeared to evidence a similar behavioural structure, with grazing activities occurring just after dawn and just before dusk across most of the year. Other research has found such diurnal rhythms in Przewalski horses and Camargue horses (Boyd et al., 1988; Berger et al., 1999; Duncan, 1985, Waring, 2003).

Daily and seasonal rhythms are primarily shaped by nutritional needs, but are also influenced by environmental factors such as temperature or insect harassment (Berger et al., 1999; Duncan, 1985; Boyd et al., 1988; Waring, 2003). For example, the cattle at Wicken performed the behaviour sternal recumbency least during the morning and afternoon in the summer, while the behaviour stand immobile was performed the most during this same time period (Section 3.3.4. and 3.3.5). It is likely that this pattern may be a possible response to increasing temperatures during the warmer season; cattle are thought to stand more rather than lie when it is hot, as the air can circulate around the whole body, thereby cooling the animal more effectively (Tucker et al., 2008; Heising and Smid, 2013).

The horses at Wicken may have demonstrated changes in behaviour as a result of environmental influences. The behaviour stand immobile was performed the most during summer, primarily during the hours of 09:30 – 16:30. During this time, individuals clustered closely together in tight knit groups, often nose to tail, on areas without vegetation cover or extremely short vegetation; grazing activities occurred rarely during this time (Laidlaw, pers.obs). This clustering and resting behaviour is likely to be a response to increasing summer temperatures and avoidance of insect harassment (Berger et al., 1999; Duncan 1985; Keiper and Berger, 1982).

3.4.3 Are there associations in sub-area use with season or maintenance behaviours?

Upon analysis, there appeared to be no associations in sub-area use and season, or sub-area use and behaviour for the all-female cattle group; although this group were not recorded at all in Brett's, one of the three sub-areas available to them. The horses appeared to show an association between sub-area use and season (but no association between sub-area use and behaviour was found) while the mixed-sex cattle showed associations in sub-area use with both season and behaviours. These mixed results are surprising, as other studies indicate that there could be associations expected between area use and season or area use and behaviour in both horses and cattle (Gander et al, 2003; Duncan, 1983; Linklater et al., 2000; Menard et al., 2002; Putfarken et al., 2007). However, interpretation of non-significant results must take into account that subsampling, to deal with lack of independence of data points within days, led to sample sizes below those recommended for adequate power by Cohen (1992).

The all-female cattle group appeared to utilise the sub-areas Baker's and Guinea Hall relatively equally throughout the year but were not recorded at all in Brett's during the course of the study. This is a notable observation. Cattle prefer swards dominated by grasses, only shifting to less preferred vegetation types as the availability and nutritional value of grasses decline though the seasons (Cornelissen and Vulink, 2015; Menard et al., 2002). Where not out-competed by horses, cattle will preferentially utilise grasslands year round for forage (Menard et al., 2002). As discussed in Section 2.3.5, each sub-area in this study possesses differing vegetative profiles, with Guinea Hall and Baker's overall having a more grass dominated sward than Brett's. It is possible that the vegetative profiles of Baker's and Guinea Hall provided enough forage for the all-female group of cattle year round to graze; thereby not requiring them forage in Brett's at all.

Hall (1988) suggests that to maintain grazing pressure in areas that are less attractive to cattle, mature bulls of over 4 years of age should be included in the herd. Observations of cattle sub-area use and this study may support this. The all-female cattle group were not recorded using Brett's during 2011. Records kept at Wicken Fen show that the all-female cattle group overall have not used this area since 2008 (National Trust data 2005 - 2011, Laidlaw, pers. obs). Over 2008, all of the adult males were removed from this group and by 2010 all remaining juvenile males under one year old were removed (Section 2.4.1). Prior to 2008, the sub-area Brett's was used by the mixed sex, breeding cattle group during the autumn and winter months for foraging, and during the spring for calving. It appears that the removal of the adult males from the group may have influenced how the remaining all-female cattle moved around their grazing areas.

Although the primary driver for both horses and cattle in using an area is the availability of preferred forage, other factors such as pest avoidance, predator awareness, availability of water and comfortable resting areas also play a part (Duncan, 1983; Duncan, 1985; Keiper and Berger, 1982; Putfarken et al., 2007). On average, cattle ruminate for 31% of their time (Kilgour, 2011) and during the warmer months, open yet shaded areas are sought for both resting and ruminating (Putfarken et al., 2007; Heising and Smid, 2013; Albright and Arave, 1997). As Brett's was wet year round (Table 2.4), with dense stands of vegetation and scrub, it is possible that the needs of the cattle for dry, shaded yet open areas to rest and ruminate in were not met, causing them not to use it.

Horses prefer grazing areas where grasses dominate the sward and where the sward height is shorter than five centimetres (Cornelissen and Vulink, 2015, Menard et al., 2002). As the availability of grasses decreases from autumn to winter and into the early spring, horses will shift to other less preferred vegetation types such as sedges, reed and assorted *Juncus* species (Cornelissen and Vulink, 2015). The fact that Brett's vegetative profile consisted mostly of reed, rush and reed canary grass (Section 2.3.5) potentially made this area marginally more attractive to the horses during the autumn and winter months in order to increase green matter uptake (Duncan, 1983), although the primary foraging areas were Baker's and Guinea Hall with their more grass dominated swards.

Brett's sub- area was enclosed on four sides with dense reed and banks (Section 2.3.2), so it is possible that the horses used this sub-area during the colder months to shelter from the prevailing winds (Duncan, 1985). Although Guinea Hall was drier overall than Brett's and Baker's sub-areas (Section 2.3.3), it was relatively exposed to the prevailing weather, with little natural shelter available. It is possible these factors may have caused the horses to use Guinea Hall sub-area less during the colder winter months.

Conversely, during the warmer months, in order to avoid insect harassment, horses tend to seek out bare ground and avoid flooded areas for non-feeding activities such as resting (Duncan, 1983). The relative exposure of Guinea Hall sub-area to the prevailing winds and openness of both it and Baker's may have made these areas more attractive to the horses during the summer months. The hydrological profile of Brett's (Table 2.4) and the fact that it lacked short swards and areas of bare ground (Section 2.3.3) may have made this sub-area less attractive to the horses during the summer.

As expected, and as evidenced in similar research detailed above, the mixed sex cattle group grazing sub-areas Rothschild's and Harrison's showed associations both between use of sub-area and season, and sub-area with behaviour. Whilst use of both sub-areas over the seasons was relatively even, Rothschild's was used much less than Harrison's during the winter. The sub-area known as Rothschild's was inundated with water during the winter months (Section 2.3.3., Table 2.4). This reduced available grazing and resting areas to the mixed sex cattle, which may have reduced their use of the area. However, during the summer, the water was drawn down below ground level, making access and use of the area possible.

Rothschild's possessed a significant linear stand of mature willow which provided a cool area of shade during the summer. The cattle have been observed (Laidlaw, pers.obs) using this shaded area almost exclusively during the summer since grazing was introduced to Rothschild's and Harrison's in 2007. As indicated in Section 3.4.2, during the warmer months, cattle seek out open shaded areas to ruminate or rest in, in order to thermo-regulate and avoid insect harassment. This may explain the association of sub-area Rothschild's with resting and cudding behaviours. Harrison's possessed large areas of palatable grasses while Rothschild's evidenced a vegetative profile similar to Brett's (Section 2.3.5), which may have been unpalatable to the cattle for much of the year. This may possibly explain why Harrison's was associated more with grazing behaviours.

Horse and cattle use of habitat is influenced by many factors, as discussed above. The analysis of habitat use with behaviour has been done on a sub-area level in this study, as opposed to compartment level. The vegetative profile did not differ sufficiently enough between compartments to provide a statistically sound basis for testing. However, as horse and cattle use of habitat is influenced by more factors than availability and variety of forage, it may be more appropriate to assess associations between behaviours and area use at a compartment level. For example, compartment 101 is flooded extensively during the winter and early spring (Chapter 2, Figure 2.6). By the summer, this water has 'drawn down' to below ground level, leaving areas of open, bare ground. During the summer, compartment 101 is used more than any other compartment in sub-area Baker's by horses performing resting behaviours (Laidlaw, pers. obs).

3.4.4 Summary

This study provides evidence of differences in behaviours across sex but not age in cattle, and age but not sex in horses in Wicken Fen during 2011. Previous research on ungulates, including cattle and horses, suggest that there are differences in behaviours across sex and age category, potentially as a result of diverging nutritional requirements influenced by body size, physiology (whether the species is a ruminant or hind gut fermenter) or breeding status (Berger et al., 2014; Brouček et al., 2013; Ruckstuhl, 1998; Neuhaus and Ruckstuhl, 2002; Ruckstuhl and Neuhaus, 2009; Boyd, 1998; Boy and Duncan, 1979; Duncan, 1980; Côté et al., 1997). Although as hindgut fermenters, horses can show fewer differences in behaviours across sex (Ruckstuhl and Neuhaus, 2009). The lack of evidence for differences between age categories in cattle in this study could be due to limited age range of the individuals used in the analyses (i.e., sub-adults and males only as there was only one young individual) or to the breeding status or herd structure of the study animals.

There was also strong evidence of variation in behaviours across time, within days and between seasons. This is consistent with previous research showing that the daily and seasonal patterns in horses and cattle are determined by nutritional needs and environmental factors such as temperature or insect harassment (Berger et al., 1999; Duncan, 1985; Boyd et al., 1988; Waring, 2003).

There was evidence of association in use of different sub areas by season for mixed sex cattle and horses and by behaviours just for the mixed sex cattle group. The findings of previous research suggest that associations would be expected in between area use and season or area use and behaviour in both horses and cattle (Gander et al, 2003; Duncan, 1983; Linklater et al., 2000; Menard et al., 2002; Putfarken et al., 2007). However, lack of statistical power must be considered when interpreting the non-significant results in these analyses in this study.

It was notable that the female cattle group only used two of the three sub-areas to which they had access throughout the study. This is likely to be because Brett's offered less favourable habitat with less good grazing and lack of dry shady places for rumination and rest. Historical records indicate that the female group has not used Brett's since the removal of adult males in 2008. This combines to support Hall’s (1988) suggestion that bulls are important for maintaining cattle grazing in less favourable habitat.

Chapter 4

Wicken Fen cattle and horse group structures

4.1 Introduction

Chapter three of this study described the maintenance behaviours and area use of the horses and cattle at Wicken Fen. Chapter four focusses on the social behaviour and group structures of the Wicken Fen herds. Much is already understood about horse and cattle social structure, as it is well documented for both domestic and free-living animals (for example; Albright and Arave, 1997; Waring, 2003; Melletti and Burton, 2014; Berger, 1986; Boyd and Houpt, 1994; Phillips, 1993). However, an analytical tool known as social network analysis (SNA) has added to available understanding by providing the ability to quantitatively evaluate relationships, individuals and groups within animal communities (Farine and Whitehead, 2015; Wey et al., 2008; Croft et al., 2016).

Social network analysis is applied through the use of metrics such as degree, modularity and connectance. These tools make it possible to describe social structure across different scales of organisation, from individual to population (Croft et al., 2008). Within populations, individuals can form ties or relationships. Degree is a simple count of these ties and can be useful in determining how well connected an individual is (Croft et al., 2008). Modularity is the level to which sets of individuals operate as communities or groups within a population and can be used to explore levels of social organisation (Croft et al., 2008; Whitehead, 2008) while connectance is a measure of the actual connections within a population divided by the total number of possible connections (Croft et al., 2008; Wasserman and Faust, 1994). Connectance can determine how complex or simple a network is.

Social network analysis has been used in sociology to examine the patterns of human relationships and interactions since the 1930's (Wasserman and Faust, 1994; Farine and Whitehead, 2015). It has only relatively recently been applied to animal populations, wildlife conservation and management (Croft et al., 2016; Snijders et al., 2017). Within the last twenty years, the social behaviour of species as diverse as Asian elephants *Elephus maximus* (de Silva et al., 2011) to Great tits *Parus major* (Firth et al., 2017) have been studied using SNA. This technique has also been utilised in tracing disease transmission and spread in wild, captive and domesticated animals (Cross et al., 2004; Firestone et al., 2012; Mittelman, 2011; Noopataya et al., 2015; Spence et al., 2017).

Of more relevance to this study on the horses and cattle at Wicken Fen, SNA has been used to analyse the social behaviour and structure of free-roaming horses in Iceland (VanDierendonck et al., 2009) and Spain (Krueger et al., 2014). The social structure of dairy cattle in the United Kingdom (Boyland et al., 2016) and the Czech Republic (Gutmann et al., 2015) have also been studied using this analytic process. These studies have all added to the available knowledge regarding equine and bovine social behaviour. However, barring research on free-living horses and free-living goats in Wales and the Isle of Rum (Stanley et. al, 2018; Stanley and Dunbar, 2013; Stanley and Shultz, 2012), there is very little in literature detailing the use of SNA in studying the social networks of free-roaming animals in the United Kingdom.

Furthermore, this may be the first study documenting the social structures of free-roaming equids and bovids kept in a novel management system such as at Wicken Fen. With this in mind, this study aims to 1) provide a description of the social structure of the herds at Wicken Fen and 2) analyse some of the factors such as sex, age or season which may affect an individual's social position. In order to do this, this study will utilise basic SNA techniques to answer the following questions;

1) What are the social structures of the three herds at Wicken Fen?
2) What is the modularity and connectance of the herds between the seasons?
3) Are there differences in degree across sex or age category in either summer or winter?
4) Are there differences in degree across the seasons?

4.2 Methods

The methods for this study are described in detail in Chapter 2, including details of the study area and sub-areas (Section 2.3), study animals (Section 2.4) and sampling regime and data collection protocols (Section 2.5). This section only gives additional key information relevant to the questions and analyses for this chapter.

In order to conduct a basic social network analysis on the horses and cattle at Wicken Fen, data on the nearest neighbour of each individual animal were collected over the course of 2011. To investigate potential variation between seasons, the year was divided into two six month sections, summer and winter. Summer (1st March to 31st August, 2011) approximates to a breeding season, while winter (1st January to 28th February, then 1st September to 31st December, 2011) approximates to a non-breeding season.

4.2.1 Study groups

The study groups consisted of a herd of 17 mixed sex cattle, a herd of 26 female cattle and a herd of 49 mixed sex horses. The compositions of the herds are detailed in Section 2.4, Table 2.6. The herd divisions reflect the areas the animals had access to. It was not possible to collect data on any two of the three groups simultaneously as they never occupied the same compartment at the same time.

All study individuals were known to the researcher by sight and by name. For the purposes of this study, each individual was given a unique five digit identification code (ID code). An explanation of how the ID code was constructed is provided in Chapter 2, section 2.5.2. Individuals shall be referred to by their ID code throughout. Appendix IV contains a full list of all the study animals, including their names, sex and ID code. Age category was determined using the categories given in Section 2.5.2, table 2.10.

4.2.2 Definition and recording of the nearest neighbour

The nearest neighbour was an individual identified as being within two cow or horse body lengths (approximately four metres) of the focal individual. Only the identity of the closest neighbour was recorded. If there were several individuals that appeared equally close to the focal animal, priority was given to the neighbour with its head orientated towards or closest to the focal animal. A zero score was recorded for each nearest neighbour slot unoccupied by an individual. The data were used to generate social network metrics at the group (sociograms, modularity and connectance) and individual (degree) level.

4.2.3 Group metrics; definitions of sociograms, modularity and connectance

Sociograms are formal visual representations of data that illustrate interconnections and relations between individuals, groups or organisations. The data are presented in the form of a graph, where individuals are represented as nodes, and each pair-wise relationship within that is represented as an edge or line between the nodes (Croft et al., 2008). The shape, colour and position of the nodes within a sociogram can indicate attributes such as sex, group membership or the connectedness of the individual. The thickness of the lines between nodes (weighting) can indicate stronger or more frequent interactions between individuals (Croft et al., 2008).

Modularity falls on a scale between +1 to -1, with positive values indicating the possible presence of a community (or modular) structure; if modularity equals one, that indicates there is no association between members of different communities within a network (Whitehead, 2008). Networks with a high modularity tend to be more stable and resistant to perturbation; as the communities within the network are more isolated from each other, environmental fluctuations are apt to only affect a small part of the network rather than the whole (Landi et al., 2018).

Connectance is the term used in ecology for network density (Lau et.al, 2017) and will be the term this study utilises. The density of a network goes from zero, if there are no connections present, to one, if all possible connections are present (Wasserman and Faust, 1994). A high connectance (density) value indicates a complex network, with high connectivity between the individuals, communities or species within that network. There are a number of contradictory hypotheses relating to the link between high connectance and the stability of a network (Landi et al., 2017). May (1972) demonstrated that networks with a high connectance were less stable than those with a lower connectance and this is the generally accepted theory; however, some studies have found otherwise (for example, Dunne et al., 2002a).

4.2.4 Individual metric; definition of degree

Degree equals the number of different social connections that an individual has within a network. It is a direct count of how many lines or edges are connected to a node (Croft et al., 2008). Highly connected individuals tend to sit towards the centre of a network, whereas those with few connections will be on the edges (Wey et. al., 2008). Degree is a useful basic measure of an individual’s sociality and can be an important indicator of the interrelations and topology of a network (Croft et al., 2008), which is why degree has been chosen for analysis in this current study.

4.2.5 Statistical analysis

Asymmetric association matrices for each group during each season were constructed using the pivot table function in Microsoft Excel. These data were exported as a comma delimited file into statistical programme R 3.4.3 (R core team, 2017). R packages igraph (Csardi and Nepusz, 2006) and PCIT (Watson-Haigh et al., 2010) were used to produce group and individual metrics. Connectance (C) was calculated using the following equation; $C = L/S^2$, where L is the number of actual links in the network (L in this case is equal to the sum of every individual's degree in each herd) and S equals the total number of individuals in the network (van Altena et al., 2016; Blüthgen et al., 2008).

Boxplots are used to show the shape of the distribution of the data, its central value and its variability. The box indicates the interquartile range, containing 50% of the values. The top of the box represents the 75^{th} percentile; the bottom, the 25^{th} (Hawkins, 2009). The thick line within the box indicates the median, and the two 'T' shaped bars extending from the ends of the box indicate the range.

4.2.5.1 Group metrics

The sociograms and modularities for the cattle and horses in the summer and winter were produced using R package igraph (Csardi and Nepusz, 2006). R package PCIT (Watson-Haigh et al., 2010) was used to weight the edges between individuals. Connectance was calculated as stated in Section 4.2.5.

4.2.5.2 Individual metric

Degree for individual animals was calculated using igraph package (Csardi and Nepusz, 2006). The outputs (Appendices VIII and IX) were analysed in IBM SPSS Statistics Data Version 20 for differences across sex, age category and season. As sample sizes were small and data tended to non-normal distribution, non-parametric tests were utilised for analysis. Individual metrics tested against sex used Mann-Whitney U, while age category was tested using Kruskal-Wallis. The individual metrics for the group of all-female cattle were not included in any analysis comparing sexes, as they were all one gender. One individual (ID code 11101) in the mixed sex group of cattle was not included in the individual metric analysis for age category. He was the only individual in the 'young' age category for the mixed sex cattle group, and this may have affected the statistical power of the test overall. As the data for tests across season were related, Wilcoxon matched-pair signed-rank was used. A critical significance level of 0.05 was used throughout.

4.3 Results

4.3.1 Mixed sex cattle

4.3.1.1 Group metrics; sociograms, modularity and connectance

The analysis of the mixed sex cattle group placed the cattle into four modules during the summer (Figure 4.1a and Table 4.1a). Module 2 consisted of 13 individuals (Table 4.1a). The remaining modules were single individuals (Table 4.1a). Stronger ties were illustrated within module 2 between one pair of individuals (Figure 4.1a). Cross module ties were also found between one pair across modules 2 - 4 (Figure 4.1a).

During the winter season, the analysis split the mixed group of cattle into six modules (Figure 4.1b and Table 4.1b). The largest module in the winter was module 3 (Table 4.1b). All other modules illustrated contained only single animals (Table 4.1b). There were no stronger connections illustrated in the winter sociogram (Figure 4.1b).

There were some shifts in module membership from summer to winter. Three individuals remained in the same module throughout the year (Tables 4.1a and b). Ten individuals shifted from module 2 to module 3 (Table 4.1a and b). One individual moved from a single module to group module (Tables 4.1a and b). Two individuals moved from group modules in the summer to single modules in the winter (Tables 4.1a and b).

One individual was an outlier with few connections during the summer, while three individuals were outliers during the winter (Figures 4.1a and b). The modularity for the cattle during both the summer and winter is reported as 0.00 (Table 4.1a and b). The result for connectance was 0.67 during the summer and 0.58 in the winter (Tables 4.1a and b).

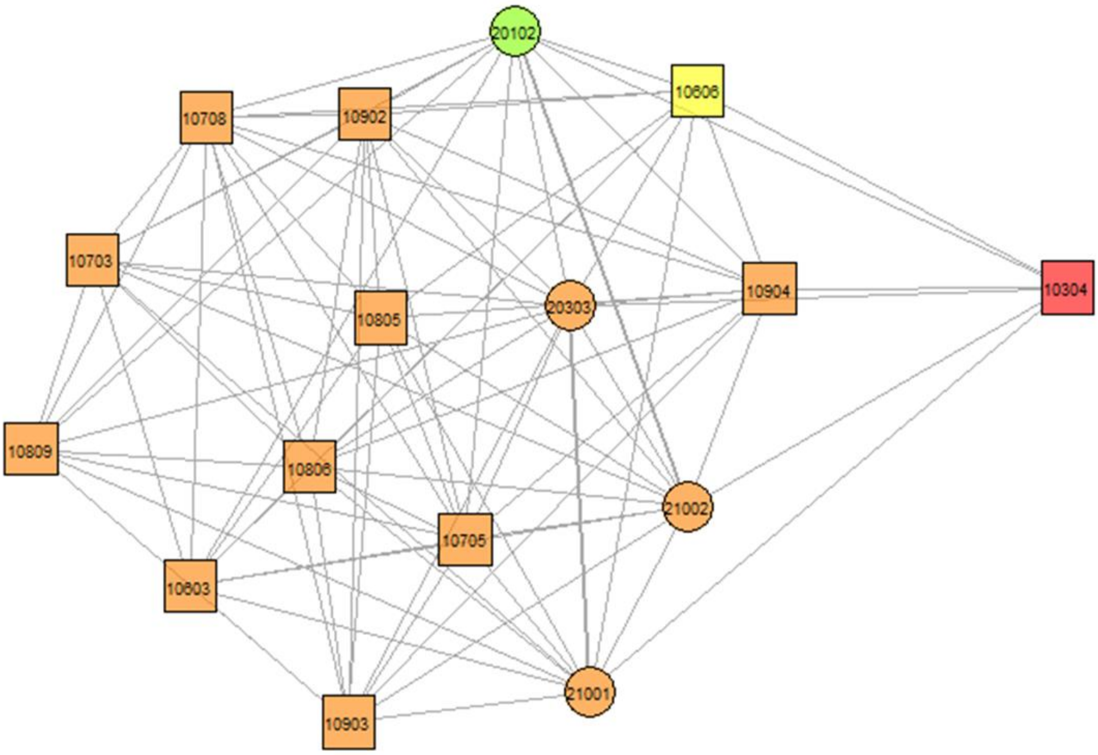


Figure 4.1a Summer sociogram for the mixed sex cattle. Each node represents an individual animal. Individuals with the same colour belong in the same module. Squares represent males and circles females. Numbers within the nodes are individual ID codes. Thicker lines indicate stronger associations between pairs of individuals. Sociograms were produced using R package igraph (Csardi and Nepusz, 2006). One individual was omitted from the summer analysis as it was not born (n = 16).

Table 4.1a Summer (1st March to 31st August) module membership and group metrics for the mixed sex cattle. Metrics were calculated using R packages igraph and PCIT (Section 4.2.5). Connectance was calculated manually using the equation $C = L/S^2$ (Section 4.2.5). One individual was omitted from the analysis as it had not been born (n = 16).

Module colour	**ID number(s)**	**Module number**	**Total module members**	**Modularity**	**Connectance**
Red	10304	1	1	0.00	0.67
Orange	10603, 10703, 10705, 10708, 10805, 10806, 10809, 10902, 10903, 10904, 20303, 21001, 21002	2	13		
Yellow	10606	3	1		
Light green	20102	4	1		

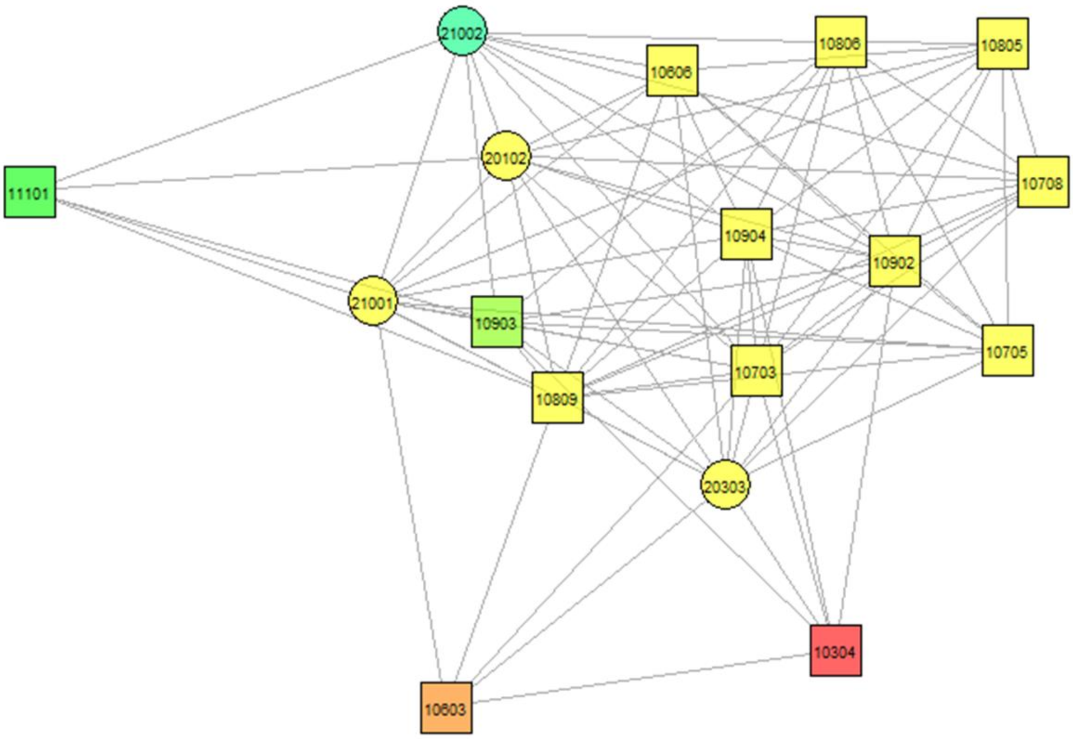


Figure 4.1b Winter (1st January to 28th February, then 1st September to 31st December) sociogram for the mixed sex cattle. Refer to the legend for Figure 4.1a for further detail. One individual was added to the winter analysis as it was born in October (n = 17).

Table 4.1b Winter (see legend to Figure 4.1b) module membership and group metrics for the mixed sex cattle. Metrics were calculated using R packages igraph and PCIT (Section 4.2.5). Connectance was calculated manually using the equation $C = L/S^2$ (Section 4.2.5). One individual was added to the analysis as it was born in October (n = 17).

Module colour	**ID number(s)**	**Module number**	**Total module members**	**Modularity**	**Connectance**
Red	10304	1	1	0.00	0.58
Orange	10603	2	1		
Yellow	10606, 10703, 10705, 10708, 10805, 10806, 10809, 10902, 10904, 20102, 20303, 21001	3	12		
Light green	10903	4	1		
Green	11101	5	1		
Turquoise	21002	6	1		

4.3.1.2 Degree tested across sex, age category and season

There was no significant difference found in degree across sex for the mixed sex cattle in either summer (Mann-Whitney U test: U = 12.000, n_1 = 12, n_2 = 4, P = 0.134) or winter (Mann-Whitney U test: U = 16.500, n_1 = 13, n_2 = 4, P = 0.272). Age category also demonstrated no significant difference in either summer (Kruskal-Wallis: X^2_1 = 0.873, n_1 = 5, n_2 = 11, P = 0.350) or winter (Kruskal-Wallis: X^2_1 = 2.276, n_1 = 5, n_2 = 11, P = 0.350). The mixed sex cattle did not show any difference in degree across season (Wilcoxon matched pairs signed rank: T = 52.500, n = 17, P = 0.667).

4.3.2 Female cattle

4.3.2.1 Group metrics; sociograms, modularity and connectance

Analysis of the data for the female cattle found 12 modules present in the network during the summer of 2011 (Figure 4.2a and Table 4.2a). Modules 1 and 2 contained eight and five individuals respectively (Table 4.2a). With the exception of module 4, which contained 4 members, the remaining modules all consisted of single individuals (Table 4.2a). No within module strong ties were seen, although four cross module ties were illustrated in the sociogram (Figure 4.2a).

The winter sociogram details 13 modules (Figure 4.2b). Modules number 1 and 2 consisted of eight and seven individuals respectively (Table 4.2b). The remaining modules were all formed from single animals (Table 4.2b). There were no stronger ties detailed in the winter sociogram (Figure 4.2b).

With the exception of three individuals, all other individuals were found as members of different modules between summer to winter (Tables 4.2a and b). Four individuals moved into larger modules from single modules, while six individuals moved from group module membership to single module membership and eight individuals moved between group modules (Tables 4.2a and b). Five female cattle remained in single membership modules throughout (Tables 4.2a and b).

Outliers were found in both summer and winter (Figures 4.2a and b). Three outliers were found in the summer and three different individuals in the winter (Figure 4.2a and b and Tables 4.2a and b). Analysis of the data gave a modularity in the summer of 0.10 and in the winter of 0.06 (Tables 4.2a and b). Summer connectance was 0.34 and winter connectance was 0.39 (Tables 4.2a and b).

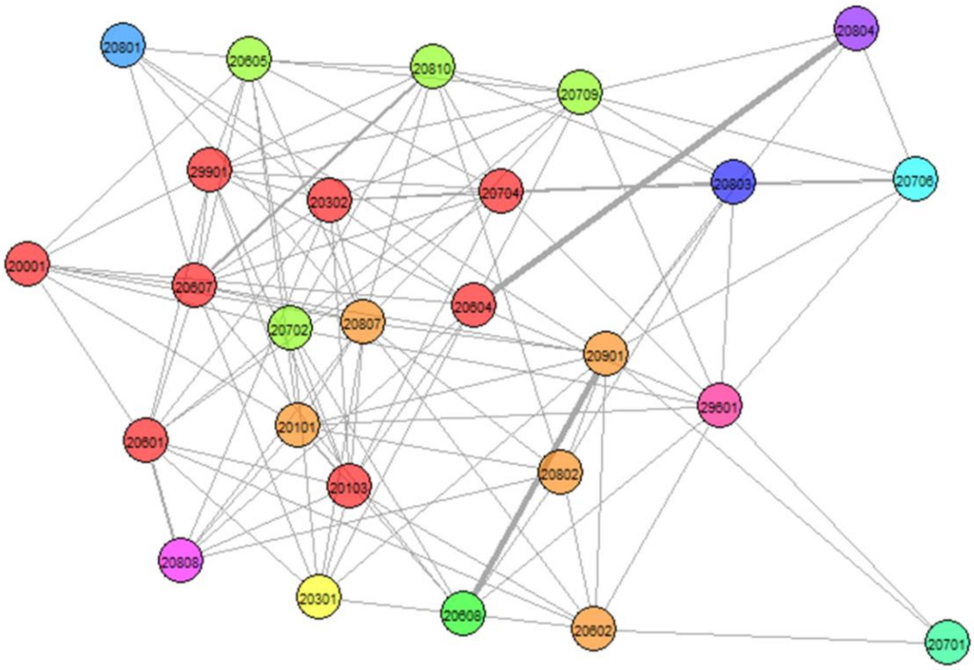


Figure 4.2a Summer (1st March to 31st August) sociogram for the female cattle. See legend to Figure 4.1a for further details. (n = 26).

Table 4.2a Summer module membership and group metrics for female cattle. Metrics were calculated using R packages igraph and PCIT (Section 4.2.5). Connectance was calculated manually using the equation $C = L/S^2$ (Section 4.2.5). (n = 26)

Module colour	ID number(s)	Module number	Total module members	Modularity	Connectance
Red	29901, 20607, 20302, 20604, 20001, 20601, 20704, 20103	1	8	0.10	0.34
Orange	20101, 20602, 20802, 20807, 20901	2	5		
Yellow	20301	3	1		
Light Green	20605, 20810, 20709, 20702	4	4		
Green	20608	5	1		
Turquoise	20701	6	1		
Light blue	20706	7	1		
Blue	20801	8	1		
Dark blue	20803	9	1		
Purple	20804	10	1		
Dark Pink	20808	11	1		
Pink	29601	12	1		

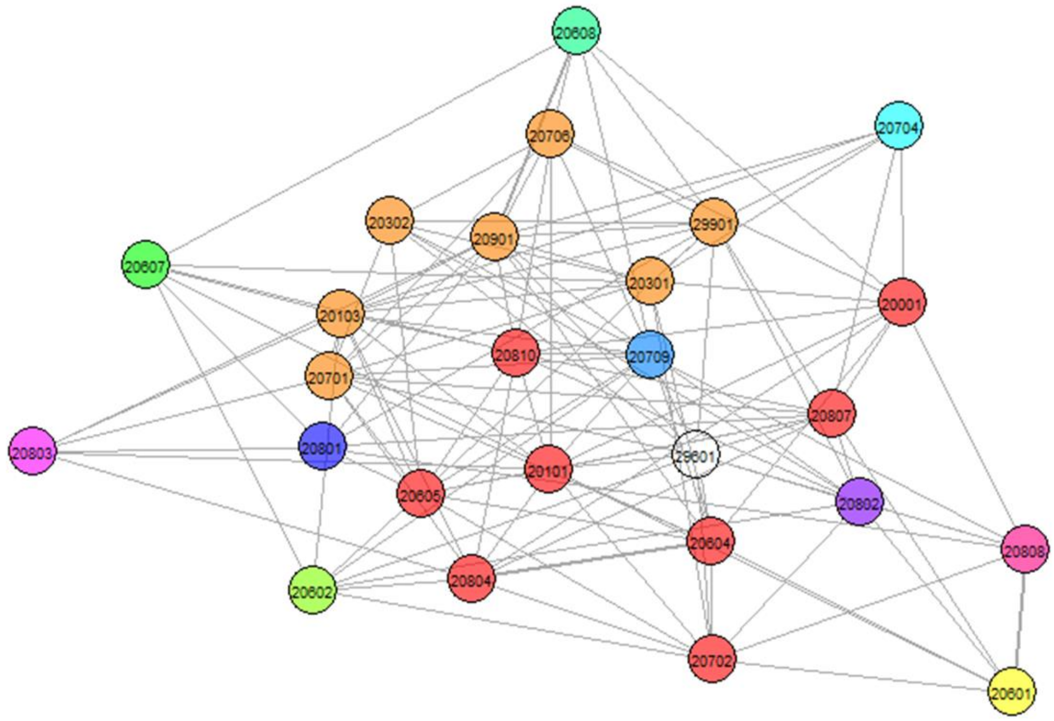


Figure 4.2b Winter (1st January to 28th February, also 1st September to 31st December) sociogram for the female cattle. Refer to the legend for Figure 4.2a for further detail. (n = 26).

Table 4.2b Winter (see legend to Figure 4.2b) module membership and group metrics for the mixed sex cattle. Metrics were calculated using R packages igraph and PCIT (Section 4.2.5). Connectance was calculated using the equation $C = L/S^2$ (Section 4.2.5). (n = 26).

Module colour	ID number(s)	Module number	Total module members	Modularity	Connectance
Red	20001, 20101, 20604, 20605, 20702, 20804, 20807, 20810	1	8	0.06	0.39
Orange	20103, 20301, 20302, 20701, 20706, 20901, 29901	2	7		
Yellow	20601	3	1		
Light Green	20602	4	1		
Green	20607	5	1		
Turquoise	20608	6	1		
Light blue	20704	7	1		
Blue	20709	8	1		
Dark blue	20801	9	1		
Purple	20802	10	1		
Dark pink	20803	11	1		
Pink	20808	12	1		
White	29601	13	1		

4.3.2.2 Degree tested across age category and season

The female cattle did not show any significant difference in degree between age categories in either summer (Kruskal-Wallis: X^2_1 = 1.812, n_1 = 13, n_2 = 13, P = 0.178) or winter (Kruskal-Wallis: X^2_1 = 0.043, n_1 = 13, n_2 = 13, P = 0.836). There was no difference in degree across seasons (Wilcoxon matched pairs signed rank: T = 183.000, n = 26, P = 0.165).

4.3.1 Horses

4.3.1.1 Group metrics; sociograms, modularity and connectance

The summer sociogram for the horses defined 14 modules within the network. Module 1 (red) consisted of 13 individuals (Table 4.1a). Within this module, stronger ties were indicated between 6 pairs (Figure 4.3a). Module 2 (orange) numbered 23 individuals (Table 4.3a). In module 2, stronger ties were shown 2 for four pairs of horses (Figure 4.3a). Stronger connections were also indicated across modules between two pairs of individuals (Figure 4.3a). The remaining 12 modules illustrated in the sociogram each consisted of single animals. The individual modules demonstrated cross module stronger ties across six pairs (Figure 4.3a).

Four modules were illustrated in the winter sociogram for the horses (Figure 4.3b). Module number 1 contained 20 individuals (Figure 4.3b, Table 4.3b). Fewer strong within module ties were evidenced for module 1, with visually thicker links between two pairs only (Figure 4.3b). Module number 2 consisted of 27 individuals (Table 4.3b). There was a small reduction in the number of strong ties within module 2 in the winter, with three strong pairings seen between six individuals (Figure 4.3b). A similar number of cross module stronger connections were seen in the winter, with two pairings showing stronger ties (Figure 4.1b). Two single modules remained in the winter sociogram (Table 4.3b).

Overall, individual membership of the modules 1 and 2 remained relatively similar between summer and winter. Module 1 gained seven individuals from summer to winter, with no losses (Table 4.3a and 4.3b). Three are recorded as having moved from module two and the rest are noted as having moved from the single modules (Table 4.3a and 4.3b). With the exception of these seven additions, the other individuals in module 1 remained the same between the two seasons (Table 4.3a and 4.3b). There were changes within module 2 from summer to winter, with three losses to module 1 and seven gains from modules 3, 4, 6, 7, 9, 10 and 11 (Tables 4.3a and b). Again, the core individuals within module 2 did not change from summer to winter. The individual modules numbered five to 14 did not remain, while modules 3 and 4 remained with different individuals (Table 4.3a and b).

The summer sociogram was densely connected both intra and inter-module (Figure 4.1a). There were 7 individuals indicated as outliers on the edge, these individuals showing fewer connections to the network overall (Figure 4.3a). The modularity of the network for the horses during the summer was 0.19 (Table 4.3a). The summer connectance was 0.38 (Table 4.3a). The winter sociogram was less densely connected, with only 5 outliers visible on the edges of the network (Figure 4.3b). The modularity for the horses during the winter was 0.30, a positive increase from the summer (Table 4.3b). The winter connectance was 0.36, similar to the summer (Table 4.3b).

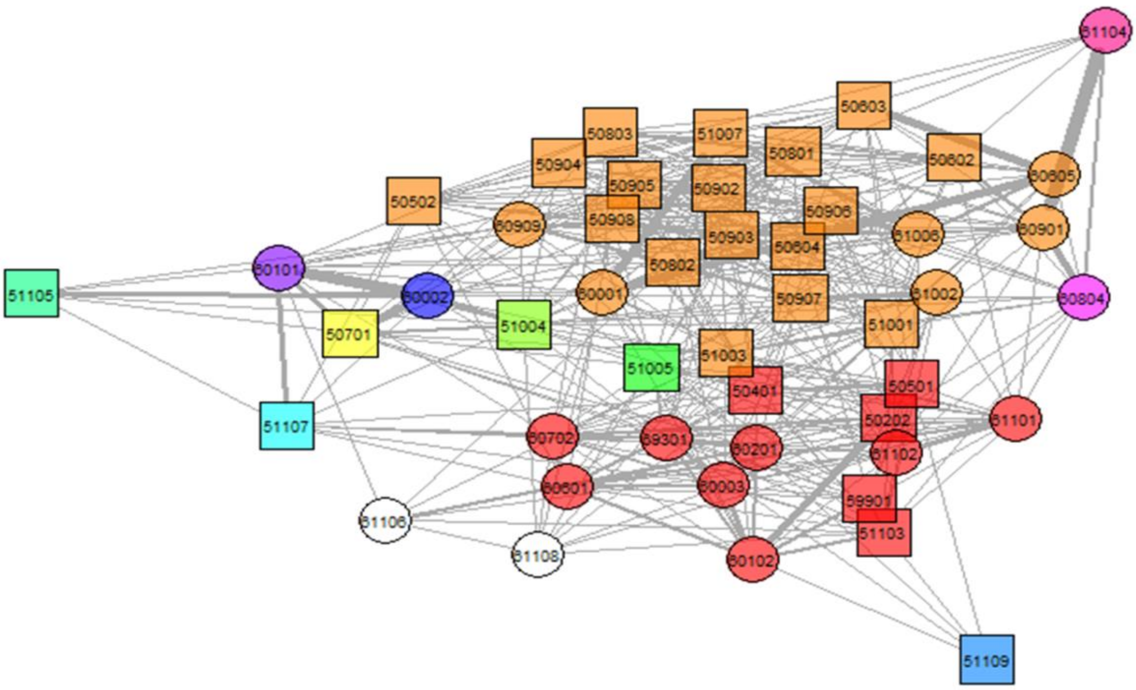


Figure 4.3a Summer (1st March to 31st August) sociogram for the horses. Each node represents an individual animal. Individuals with the same colour belong in the same module. Squares represent males and circles females. Numbers within the nodes are individual ID codes. Thicker lines indicate stronger associations between pairs of individuals. Sociograms were produced using R package igraph (Csardi and Nepusz, 2006). One individual was omitted from the summer analysis as it was not born (n = 48).

Table 4.3a Summer (1st March to 31st August) module membership and group metrics for the horses. Metrics were calculated using R packages igraph and PCIT (Section 4.2.5). Connectance was calculated manually using the equation $C = L/S^2$ (Section 4.2.5). One individual was omitted from the analysis as it had not been born (n = 48).

Module colour	ID number(s)	Module number	Total module members	Modularity	Connectance
Red	50202, 50401, 50501, 51103, 59901, 60003, 60102, 60201, 60601, 60702, 61101, 61102, 69301	1	13	0.19	0.38
Orange	50502, 50602, 50603, 50604, 50801, 50802, 50803, 50902, 50903, 50904, 50905, 50906, 50907, 50908, 51001, 51003, 51007, 60001, 60605, 60901, 60909, 61002, 61006	2	23		
Yellow	50701	3	1		
Light green	51004	4	1		
Green	51005	5	1		
Turquoise	51105	6	1		
Light Blue	51107	7	1		
Blue	51109	8	1		
Dark blue	60002	9	1		
Purple	60101	10	1		
Pink	60804	11	1		
Dark pink	61104	12	1		
White (1)	61106	13	1		
White (2)	61108	14	1		

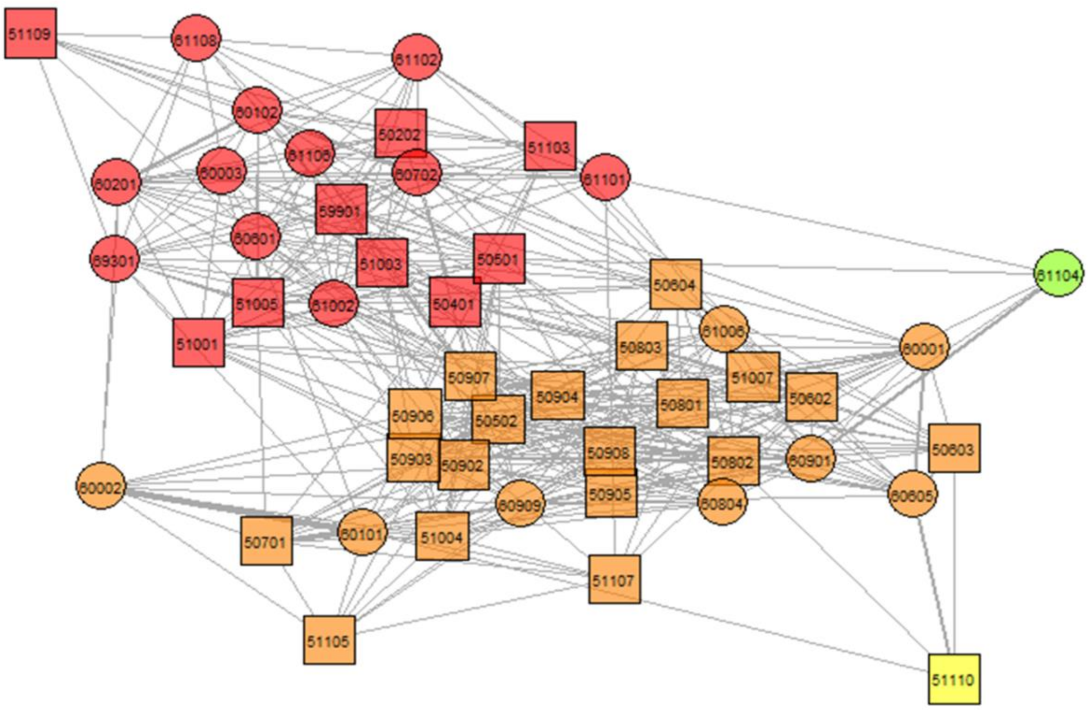


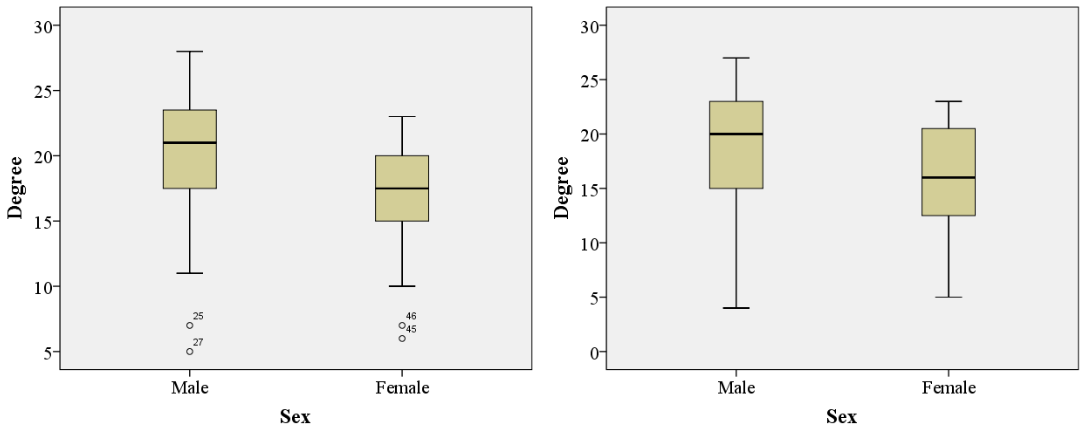
Figure 4.3b Winter (1st January to 28th February, then 1st September to 31st December) sociogram for the horses. Refer to the legend for Figure 4.3a for further detail. One individual was added to the winter analysis as it was born in October (n = 49).

Table 4.3b Winter (see legend to Figure 4.3b) module membership and group metrics for the horses. Metrics were calculated using R packages igraph and PCIT (Section 4.2.5). Connectance was calculated manually using the equation $C = L/S^2$ (Section 4.2.5). One individual was added to the analysis as it was born in October (n = 49).

Module colour	ID number(s)	Module number	Total module members	Modularity	Connectance
Red	50202, 50401, 50501, 51001, 51003, 51005, 51103, 51109, 59901, 60003, 60102, 60201, 60601, 60702, 61002, 61101, 61102, 61106, 61108, 69301	1	20	0.30	0.36
Orange	50502, 50602, 50603, 50604, 50701, 50801, 50802, 50803, 50902, 50903, 50904, 50905, 50906, 50907, 50908, 51004, 51007, 51105, 51107, 60001, 60002, 60101, 60605, 60804, 60901, 60909, 61006	2	27		
Yellow	51110	3	1		
Light green	61104	4	1		

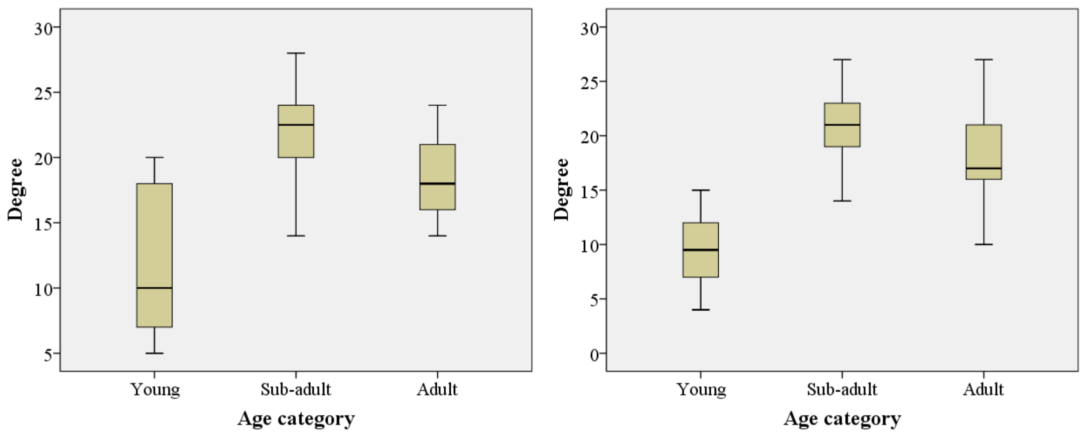
4.3.1.2 Degree tested across sex, age category and season

Horses showed a significant difference in degree between sexes in both summer (Mann-Whitney U test: U = 163.000, n_1 = 28, n_2 = 20, **P = 0.014**) and winter (Mann-Whitney U test: U = 190.500, n_1 = 29, n_2 = 20, **P = 0.042**). Male horses showed a greater degree than females year round (Figure 4.4). A significant difference was also found for degree across age category in summer (Kruskal-Wallis: X^2_2 = 19.204, n_1 = 17, n_2 = 22, n_3 = 9, **P < 0.001**) and winter (Kruskal-Wallis: X^2_2 = 24.116, n_1 = 17, n_2 = 22, n_3 = 10, **P < 0.001**). Sub-adults over both seasons had a higher degree than either adults or young (Figure 4.5). There was no significant difference in degree across the seasons for the horses (Wilcoxon matched pairs signed rank: T = 325.000, n = 49, P = 0.170).



i. Summer ii. Winter

Figure 4.4 Comparison of male (summer; n = 28, winter; n = 29) and female (summer and winter; n = 20) degree in the horses over two seasons. Analysis as described in Section 4.2.5.2. Boxplots; the box indicates the interquartile range, containing 50% of the values. The top of the box represents the 75th percentile; the bottom, the 25th. The thick line within the box indicates the median, and the two 'T' shaped bars extending from the ends of the box indicate the range.



i. Summer ii. Winter

Figure 4.5 Comparison of degree in horses in three age categories (young, sub-adult and adult) across two seasons. [Summer; n = 17 (adult), n = 22 (sub-adult), n = 9 (young)] [Winter n = 17 (adult), n = 22 (sub-adult), n = 10 (young)] For further details, see the legend for Figure 4.4.

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4.4 Discussion

4.4.1 Cattle

4.4.1.1 What are the social structures of the cattle herds?

The mixed sex cattle and female cattle at Wicken Fen showed a social structure that appeared highly uniform. There were no sub-groups identified within the mixed sex herd and while analysis defined some sub-groups in the female cattle herd, the boundaries of these are not readily demarcated. This is consistent with trends observed in dairy cattle, which do not divide into sub-groups, and tend to have individuals belonging to a single cluster (Boyland et al. 2016; Gygax et al. 2009).

Studies on other herds of free-living cattle have detailed matriarchal groups formed of cows, calves and young bulls of up to four years of age (Phillips, 1993; Reinhardt and Reinhardt, 1981; van Vuure, 2005, Lazo, 1994). Older bulls either roam singly or in small groups, possibly staying within identifiable home ranges (Hall, 1988; van Vuure 2005; Lazo, 1995). Within these groups, individuals form long term preferential associations, often across generations (Reinhardt and Reinhardt, 1981; Gutmann et al., 2015; Gygax et al., 2010, Lazo, 1994).

The mixed sex group consisted of 13 sub-adult and adult males and four females. A small matriarchy could be seen, with strong ties evidenced between individuals 20303 and 21001 as well as between individuals 21002 and 20102 (Section 4.3.1.1); herd records showed that these two pairs are mother/daughter pairs (Laidlaw, National Trust data). Despite the ties between the females, this study showed they did not form a separate group away from the males as could be expected. This may be because the majority of the males were sub-adult, not yet of age to leave the matriarchal group.

However, in summer and winter, all three of the adult males in the mixed sex group were found at the edge of the network (Section 4.3.1.1). Analysis has placed individual 10304 on the edge of the network in both seasons; National Trust records show he had lost his status as dominant male to individual 10606 in the winter of 2010 (Laidlaw, National Trust data). Additional observations noted on daily checks during 2011 frequently found male 10304 and male 10603 in different grazing compartments from each other and the rest of the herd (C. Laidlaw, pers. obs). Social network analysis of the data and observational evidence suggests that the mixed sex group social behaviour appeared to partly mirror that of other free-living cattle.

The all-female group showed a profile similar to that found in beef and dairy herds, with little to no sub-division into smaller groups and strong preferential relationships between individuals, often kin (Boyland et al., 2016). Strong ties could be found between three mother/daughter pairs in the female cattle group; these bonds persisted over the summer and winter (Section 4.3.2.1). Otherwise, the sub-groups identified in the analysis showed very little consistency between the summer and winter; research by Boyland et al. (2016) also found that sub-group composition changed across time.

4.4.1.2 What is the modularity and connectance of the cattle herds between the seasons?

The modularity for the mixed sex cattle and female cattle was low for both groups, and tended to show that the two networks did not divide into sub-groups. The Wicken Fen cattle have been maintained as free-living type herds, so it could be expected that some sub-grouping would occur in the herds due to sexual segregation. Cattle are sexually dimorphic ruminants, and in free-living herds it is likely that the different nutritional demands between large males and smaller females may result in sub-grouping, such as that seen in Bighorn sheep, Alpine ibex and cattle (Phillips, 1993; Albright and Arave, 1997; Ruckstuhl, 1998; Neuhaus and Ruckstuhl, 2002).

The low modularity and lack of sub-groups in the Wicken Fen cattle may be an effect of management of the herd; in 2008 the breeding herd was split into two (largely) single sex herds of roughly similar ages. This remained the case until 2013. The enforced division of the sexes during this time mimicked more intensive commercial beef or dairy systems, where sexes and ages are uniformly segregated (Phillips, 1993). Research on cattle in commercial systems describe cattle networks with little to no sub-grouping (Chen at al., 2015; Boyland et al., 2016; Gygax et al., 2009; Gutmann et al., 2015). It may be that, as with the commercial herds, the low modularity of the Wicken Fen herds is influenced by the uniformity of sexes and ages within the herd.

It is interesting to note that selected male and female cattle were united into one breeding herd in 2013. With the exception of the dominant male who stayed with one known adult female, other adult males stayed within recognisable home ranges. Sub-adult males and females often split into three distinct sub-groups that utilised the whole area available. These sub-groups are formed around females who were introduced to the herd at the same time (in 2005, then 2008 and latterly 2017) and their female kin (C. Laidlaw, pers.obs). Conducting social network analysis on this herd could further extend understanding of the social behaviour of free-roaming cattle herds.

Cattle are known to form long term-preferential associations between individuals; if management regimes permit, these associations will be formed from an early age (Raussi et al., 2010; Phillips, 1993, Gygax et al., 2010). Cattle that have grown up together will have closer relationships (Raussi et al., 2010; Gygax et al., 2010). With the exception of three individuals, all of the cattle in the mixed sex group had been born and grown up in the same herd at Wicken Fen, which may explain their relatively high connectance across the year. Additionally, as sub-adults, male cattle also interact more than females and adult males through play and mock-fighting as they develop the social skills needed as a mature adult (Reinhardt and Reinhardt, 1982). As there was a relatively high number of male sub-adults in the mixed-sex group (nine out of 17 individuals), mock play between these individuals may also have raised the connectance for the mixed sex group.

Although the female cattle group had either been born at Wicken Fen (18 individuals) or were imported to Wicken Fen from the same farm (seven individuals), potentially increasing the stability and connectedness of the group, their connectance was lower across both seasons than the mixed sex group. The lower connectance may be a result of the size of the group; Takeda et al., (2000) and Harris et al., (2007) found that larger groups (16 or more) of cattle tended to sub-divide, and individuals would preferentially associate with between three to six others. The slight increase in modularity and suggestion of sub-groups in the female cattle herd (Section 4.3.3.1) may support this idea. The lower connectance for the female group may also reflect that sub-adult and adult females interact less, as play or mock fighting is much reduced in female cattle as they age (Reinhardt and Reinhardt, 1982). It may be that the connectance of the female cattle is affected by them preferentially associating with smaller numbers of individuals within the network and rarely playing.

4.4.1.3 Are there differences between degree between individuals across sex, age category, and season?

Degree was not significantly different across age category or season for the female cattle and analysis found no significant difference across sex, age-category or season for the mixed sex cattle either. Other research has found that individual metrics, such as degree, can be affected by the sex or age of the individuals (Sosa, 2016; Sosa et al., 2018). Higher degree is expected for females than males, as females form longer term stable associations, whereas males can be solitary, or found in small associations of two or three individuals in flexibly sized home ranges (Phillips, 1993; Hall, 1988, 1989). Sub-adult individuals interact with many others in order to gain social skills (Sosa et al., Phillips, 1993; Waring, 2003); the number of associations decreases with age as individuals mature and maintain a position in the hierarchy of the herd (Sosa, 2016; Sosa et al., 2018).

Given this, the lack of significant differences for degree across sex and age category for the cattle at Wicken Fen is surprising, but may be accounted for by considering other factors that may influence individual degree. Associations in social groups are influenced by factors such as age, sex, dominance, kinship or familiarity with conspecifics (Sosa, 2018, Phillips, 1993). Research on the effect of sex and age upon individual sociality and social grouping has primarily focussed on groups in domestic systems (Sosa et al., 2018; Boyland et al., 2016; Takeda et al., 2000; Gygax et al., 2010). Herds in such systems are often not stable, due to management actions such as culling, sale or purchase of animals (Harris, 2007; Phillips, 1993). This type of management results in socially unstable herds formed from largely unrelated individuals (Phillips, 1993). As a consequence, understanding regarding factors affecting the formation of associations in such groups may be limited to sex, age or dominance.

In contrast, the cattle at Wicken Fen are largely kept in long-term stable groups; most of the cattle in both the mixed sex herd and the female herd have grown up together. Individuals in the herds have interacted and formed associations from a very young age; often these associations are between related individuals and are stable over time. Studies have acknowledged that familiarity and being able to grow up together is an important factor in the formation of social relationships in cattle (Sosa et al., 2018; Boyland et al., 2016; Takeda et al., 2000; Gygax et al., 2010; Raussi et al., 2010). The difference in herd stability and composition between the Wicken Fen cattle and cattle herds in other research may be important. It is possible that kinship and familiarity are stronger influences on individual degree than sex and age (Reinhardt and Reinhardt, 1981); for example, kinship has been recognised as a key factor in the formation of associations in Yellow-bellied marmots *Marmota flaviventris* (Wey and Blumstein, 2010). Further research on the re-united breeding herd may help to determine if relatedness and familiarity are stronger factors than sex and age in the formation of associations in cattle herds than has been previously understood.

In other social species, degree has been influenced by seasonal factors such as breeding or access to resources (Deng, 2017; Stanley et al., 2018). Cattle, like Bighorn sheep, wild Yaks and Alpine ibex are a sexually dimorphic species. The sexes in these species segregate for most of the year, possibly in order to optimise acquisition of resources and as a response to predation risk (Bowyer, 2004; Berger et al., 2014; Neuhaus and Ruckstuhl, 2002; Ruckstuhl, 1998). Like many sexually dimorphic ruminants, bighorn sheep, yaks and ibex have a seasonal breeding season, known as a rut, where aggregations of males compete amongst each other in order to secure matings with sexually receptive females (Rubin et al., 2000; Willisch and Neuhaus, 2009; Buzzard et al., 2014). As individuals and groups aggregate during a rut, it is likely that the number of associations for individuals increases as a result.

Unlike those species, cattle do not gather together in a defined breeding season but can breed year round; from 2005 – 2011, Wicken Fen cattle calved in all months of the year except February, June and August (Burthe et al., 2011; Hall and Bunce, 2019; Laidlaw, National Trust data). As the Wicken Fen cattle breed year round, they are unlikely to show seasonal fluctuations in associations as a result of increased contact with other males and females during a rut; analysis of data on degree across season for the Wicken Fen cattle appears to support this idea. However, the cattle tested in this study were a non-breeding group of females and a small breeding group, so understanding of the effects of degree across season in relation to breeding may be limited by small sample sizes and uni-sex groupings. Further exploration of this idea centred on the re-united breeding herd of cattle would be valuable.

Additionally, other research has found that individual social traits, such as degree, remain consistent across time and environmental change (O'Brien et al., 2018, Aplin et al., 2015; Strickland and Frère, 2018). Repeatability of individual social traits can be caused by stability in the social environment; for example, stable social groups of familiar herdmates in an individual's home range (Strickland and Frère, 2018). As already stated, the cattle at Wicken Fen live in stable groups from year to year; with the exception of the calf born in 2011, associations within the herds ran from a minimum of one year to a maximum of six. It is possible that the lack of difference across the seasons in the cattle has been influenced by stability in the social environment.

4.4.2 Horses

4.4.2.1 What is the social structure of the horse herd?

The group metrics for the horses at Wicken Fen indicated that their network had a modular structure; 14 modules were defined during the summer and four in the winter. Brief descriptions of the modules and their composition may show that the horses at Wicken Fen evidence a social structure similar to that found with other free-living horses.

Groups of free-living horses living in the same locality often band together into one population known as a herd (Waring, 2003: Boyd and Keiper, 2005). The horses at Wicken Fen moved around as one herd at all times (C. Laidlaw, pers.obs). Different types of group can be found within a herd; family harems, bachelor bands and mixed sex bands of sub-adults have all been identified (Waring, 2003; Boyd and Keiper, 2005). McCort (1984) also identifies a type of group comprised of multiple adult males and females in long term stable associations.

A family harem usually comprises one or more adult males, one to ten adult females and offspring of the most recent few years (Waring, 2003; Berger, 1986). This is the most common form of grouping in free-living populations (Boyd and Keiper, 2005). In Figures 4.3a and b, as well as tables 4.3a and b, we can see that module 1 was such a family group; as it consisted of adult male and female horses accompanied by related sub-adults and young. Historical records at the Fen show that five of the adult individuals (two males and three females) were imported together in 2004, and that they have remained together since that date (Laidlaw, National Trust data); other research such as Berger (1986) describes such stable long term associations within family harems.

A bachelor band is a group of non-breeding males. These males are often sub-adults leaving their family harem but males of all ages may join a bachelor band (McCort, 1984). The analysis of the herd at Wicken Fen did not appear to identify such an all-male group, despite the large number of sub-adult males in the herd.

Mixed sex peer bands largely consist of male and female sub-adults in short-term unstable associations, as they have yet to join or form stable family harems (Waring, 2003). Multiple adult male and female bands consist of more than one adult male, one or more adult females and their offspring, and this group composition is stable over time (McCort, 1984). Across the year, Module 2 consisted of a mixture of related and unrelated horses of both sexes and all age categories. A minimum of six adults remained in this module throughout the year and these individuals had formed within-pair connections of over five years in duration (Laidlaw, National Trust data); which indicated that this group may have had some stability over time. Offspring of the adult mares were also identified within the module during the winter season. These factors suggest that the group could be identified as a multiple male and female band.

However, there were high numbers of sub-adult horses in module two, and these individuals all had short term associations of two years or less (Laidlaw, National Trust data). The age profile and relatively short term nature of the associations within this module indicate that it may better fit the profile found in other free-living horse groups of being an unstable mixed sex peer band; the instability is demonstrated by some of the sub-adults shifting module during the course of this study.

Modules 3 – 14 are formed of single horses. These individuals are a mix of adult and sub-adult males and females as well as young. As sub-adult males and females are known to disperse from their natal groups between one to four years of age (Berger, 1986) it is possible that the individual sub-adults were dispersing from their natal groups and had not yet settled into a stable band; from 2008 – 2011, sub-adults had been observed leaving their family harems and either joining other harems or forming their own (C. Laidlaw, pers. obs). Young horses are initially dependant on their mothers (Stanley and Shultz, 2012; Stanley et al., 2018), so it is possible that the young individuals had not yet formed associations outside the mother/young bond. This may place them in analysis on the edge of the network. However, it is more likely that the lack of data for these summer-born individuals has affected their placement within the network during analysis of this season (Whitehead, 2008).

The sociogram in Figure 4.1a indicated that two females (60002 and 60101) had a strong association, as illustrated by the thickness of the line between them. National Trust records show they have been an associated pair since their introduction in 2003 (Laidlaw, National Trust data). The two females had a strong association with individuals 50701, 51107 and 51105 (Figure 4.1a) which was maintained into the winter, despite a change of module. Those individuals were respectively a sub-adult male of four years old and the 2011 young of the females. It is possible that these two females were forming a stable family harem with the sub-adult male.

National Trust data collected daily on the herds during welfare checks suggested a herd structure in 2011 that consisted of three family harems, one mixed sex multiple male and female band, one mixed sex peer band and two solitary males unaffiliated to any particular group (Appendix IV, Table 1). The analysis in this study has captured one family harem, but not others recognised in National Trust data. Within both sociograms, however, the positioning of individuals and evidence of strong ties (Figures 4.1a and 4.1b) reflect the groupings identified in long-term National Trust observational data (Laidlaw, National Trust data). The difference between the analysis and observational data may be down to interpretive bias with regards the observational data, or may be the result of the one/zero association sampling of nearest neighbours adopted in this study providing poor resolution of sub-groups. A more accurate technique, as employed by Stanley and Shultz (2012), could be to use inter-individual distances on entire sub-groups, providing more detailed data on social position and group composition.

4.4.2.2 What is the modularity and connectance of the horse herd between the seasons?

Results of the analysis on the horses reported a modularity of 0.19 in the summer and 0.30 in the winter. Modularity is a measure of group structure within a network (Whitehead, 2008). Initially, the relatively low modularity in the summer was surprising; throughout the year, adult male horses in family harems defend the females in the harem from other males (McDonnell, 1986, Linklater et al., 1999, Gray et al., 2012). This behaviour increases the physical distance between each harem, and this is particularly noticeable in the breeding season (Franke Stevens, 1990). This behaviour occurs in the Wicken Fen herd (Figure 4.6). As a result, this behaviour could be reasonably expected to increase the modularity of the Wicken Fen herd in the summer. Inter-group interactions have been shown to decrease in the non-breeding season (Franke Stevens, 1990) which may cause a decrease in modularity in the winter, once breeding has finished and adult males reduce the amount of time herding and defending the females in their family group.

Figure 4.6 Wicken Fen horses demonstrating increased inter-group spacing (i.e. modularity) during the breeding season. The largest family harem is in the centre of the photograph, one further smaller harem to the immediate right and one to the far right. A small mixed sex group of young males and females is seen to the left of the picture. Individual animals standing slightly apart are either sub-dominant males or single males not affiliated to any particular group.

However, analysis of the data for the horses' modularity suggested that the opposite occurred; modularity is lower in the summer than in the winter. This may be explained by environmental effects such as access to shade and avoidance of fly harassment affecting the herd's structure. Other research has shown that family groups of horses cluster together when insect harassment increases in the summer (Feh, 2005; Hughes et al., 1981); such clustering effects could decrease the physical boundaries between the modules in a network (i.e. harems within a herd), thereby lowering modularity. As discussed in Chapter 3, section 3.4.3, it is likely that Wicken Fen horses sought refuge from insect harassment by gathering together in open areas during the summer, which may have affected the modularity of the herd. Modularity may then increase in the winter, when family groups spread out searching for forage (Feh, 2005). This will increase the physical distance between each family group. These factors may have had the effect of increasing the modularity of the Wicken Fen herd during the winter.

The summer and winter connectance for the horses was very similar, being 0.38 and 0.36 respectively. This indicates a network with some complexity and connectivity but with less than half of all possible connections within the network being realised (Section 4.3.1.1, Tables 4.3a and b). Horses are known to form long term, stable family groups (Boyd and Keiper, 2005; Feh, 2005; Feh, 1999) such as seen at Wicken Fen (Section 4.4.2.1). These groups are definable as individual units due to the defence of the group by the adult male(s), who prevent group member interactions outside the family group (McDonnell, 1995; Linklater 2000). It is possible that the horses at Wicken Fen are prevented from interacting outwith their groups by the defence behaviour of the adult males, which resulted in a connectance of under half of those possible in the network.

4.4.2.3 Are there differences between degree between individuals across sex, age category, and season?

Analysis of degree across sex and age category found that, in the horses, males and sub-adults had significantly higher degree in both the summer and winter; however, there was no significant difference in degree across the seasons. Degree captures the number of associates individuals have (Farine and Whitehead, 2015). This result suggests that sub-adult and male horses associated with more individuals than other age groups or sex classes, but that the number of associations realised by individuals varied little across the seasons.

Within free-living or free-roaming horse herds, it may be that males associate with many more individuals than females due to equine social and reproductive requirements. Both male and female horses leave their natal harem between one and four years of age (Waring, 2003). Females usually join, or are co-opted into, other family harems shortly after they leave their natal group (Monard and Duncan, 1996). At this point, they are likely to form long term stable associations with one or two preferred partners within their new family group (Stanley and Shultz, 2012). This behaviour is likely to limit the number of associates a female has contact with; the sociograms for the Wicken Fen horses illustrated a number of females with strong ties to the same individuals in both summer and winter. National Trust data confirmed that some of these associations had been in place for a number of years (Section 4.4.1).

After leaving their natal harem, males initially live in unstable bachelor groups or mixed sex peer groups (Feh, 1999). During this time, they interact extensively with other individuals, especially males, as part of their social development (McDonnell, 1995, Waring, 2003). As the males reach post-puberty, they attempt to form a family group. This is done by either co-opting unaffiliated females or challenging a harem male for 'his' family harem (Berger, 1986). Adult males in family harems form stable long term associations with several females (Boyd and Keiper, 2005; Feh, 2005). The adult male mates with those females and defends them from other males (Boyd and Keiper, 2005, Feh, 1999). This male defensive behaviour has the effect of limiting female access to individuals only in the family harem. Overall, throughout their lifetime, males are required to interact with many more individuals than females (Franke-Stevens, 1990); it may be that individual degree of males at Wicken Fen was higher than females as a result.

Sub-adult horses at Wicken Fen show a higher degree than young or adults throughout the year. As previously discussed, after leaving their natal harem, sub-adults of both sexes are more likely to interact with a wide range of individuals. They have yet to form firm associations within a stable group and such interactions form part of their social development; this is especially true of sub-adult males (Waring, 2003). Adults and young in stable family harems may be prevented from interacting outside the harem by the adult males in that harem; in addition, young are also closely dependant on their mothers for the first weeks in life (Boyd and Keiper, 2005; Stanley and Shultz, 2012). It is likely that these factors increased individual degree for sub-adults, and inhibited degree for young and adult horses. As the Wicken Fen horses showed a social structure (Section 4.4.1) and behavioural patterns (Chapter 3; Laidlaw, National Trust data) similar to other free-living herds it is possible that the factors of intra-harem stability, male defence of harems, female associative preference and emigration of sub-adults all affect degree across sex and age category in the horses.

Analysis showed that degree did not differ across season for the horses; as horses have a defined breeding season, it could be expected that associations would increase during the summer due to horse mating strategy. A study by Stanley et al., in 2018 found an increase in the association of female horses with each other during the breeding season; this was thought to be a social response to avoid male harassment via a dilution effect. Male herding of the females into sub-groups was thought to be an unlikely cause of female grouping, as male herding behaviours were not observed often (Stanley et al., 2018).

However, male herding of females and other intra-harem members was observed often with the Wicken Fen horses, and it occurred during both the breeding and non-breeding season (C. Laidlaw, pers.obs). As the Wicken Fen herd moved around as one unit, it is possible that the frequency of male herding is a consequence of the constant proximity of other (non-harem) males (Linklater et al., 1999). Horses prefer to form long term stable relationships with a small number of individuals and this stability is suggested to increase survival of individuals and their offspring (Berger, 1986, Linklater et al., 1999; Nunez et al., 2015; Stanley et al., 2018). The horses at Wicken Fen showed stability, with core members of the two largest modules remaining in those modules throughout the year (Section 4.3.1.1, Tables 4.3a and 4.3b). It is possible that the lack of difference in degree across the seasons in this study was a reflection of the overall stability of intra-harem associations which were strengthened by the herding behaviours of male horses throughout the year.

4.4.4 Summary

For the first time, using SNA, this study has defined the social structure of the horse and cattle herds at Wicken Fen. Both the horse herd and the cattle herds evidenced social structures similar to that of other free-living herds (Berger, 1986; Waring, 2003; Hall, 1988; Reinhardt and Reinhardt, 1981), although the all-female cattle group showed some evidence of a social structure closer to that of a commercial herd due to the uniformity of age and sex (Boyland et al., 2016; Gygax et al., 2009).

Evidence of sub-groups were expected in the mixed sex cattle herd, due to sexual segregation prompted by differing nutritional requirements (Phillips, 1993; Albright and

Arave, 1997), but these were not found in this herd. This was possibly an artefact of the management of the cattle in 2008, where two effectively single sex herds were created. Some sub-grouping was seen in the all-female herd, possibly as a result of larger herd size prompting sub-division into smaller associative groups (Takeda et al., 2000; Harris et al., 2007). Bonds between kin were maintained across the seasons, and this may be an important factor in maintaining bonds and herd stability across time (Raussi et al., 2010; Gygax et al., 2010).

No significant difference was found for degree across sex, age or season in the cattle. Familiarity and being able to grow up together are important factors in the formation of associations in cattle (Sosa et al., 2018; Boyland et al., 2016; Takeda et al., 2000; Gygax et al., 2010; Raussi et al., 2010). As the Wicken Fen cattle had long prior associations with each other, this may be a factor influencing individual degree. Additionally, research has found that individual social traits can remain consistent over time if individuals are exposed to highly stable social environments, as at Wicken Fen (O'Brien et al., 2018, Aplin et al., 2015; Strickland and Frère, 2018).

Free-living horses associate in different groups, depending upon age and reproductive status (Berger, 1986; Waring, 2003; McCort, 1984). Individuals within these groups form long term preferential associations (McCort, 1984; Boyd and Keiper, 2005; Feh, 1999). Social network analysis has defined a similar social structure for the naturalised horses at Wicken Fen.

Modularity of the horses reduced in the summer, rather than increased, which was unexpected. This effect may be a result of environmental factors (such as avoiding fly harassment) over-riding reproductive urges (Feh, 2005; Hughes et al., 1981). Connectance was very similar across the two seasons. This is likely to be accounted for by the stability of the herd at Wicken Fen, in addition to the herding behaviour of adult males preventing individuals from different harems from interacting (McDonnell, 1995; Linklater, 2000).

Significant results were found for degree across sex and age category for the Wicken Fen horses. Sub-adults and male horses had a higher degree than any other sex or age class. This may be due to the social and reproductive requirements of equines. Females preferentially form a small number of close knit associations, while males interact with many more individuals through herding and defence of associated females (Stanley and Schultz, 2012; Boyd and Keiper, 2005; Feh, 1999). Sub-adults require a period of social development, which involves interacting with many individuals (Waring, 2003). Both historical data and SNA analysis demonstrated that Wicken Fen horses formed preferential, long term associations and sub-adult individuals moved across harems as they matured. No difference was found in degree across seasons, which was thought to be a reflection of the overall stability of the intra-harem associations, combined with the active herding behaviours of the male horses across the year.

It is suggested that due to the small sample sizes and essentially uni-sex nature of the cattle herds at Wicken Fen in 2011 further research using SNA be carried out on the full breeding cattle herd that was re-united in 2013. In addition, long term behavioural observations of the horses illustrated a social structure in finer detail than this current analysis suggests. Further analysis of the horse herd using different data collection techniques may provide quantitative evidence to substantiate, or otherwise, the behavioural observations.

Chapter 5

Discussion and Recommendations

5.1 Introduction

Throughout their life cycle, animals have differing needs, driven by nutritional requirements, reproduction, comfort seeking or predator avoidance. These needs may vary widely, or very little, depending on the species, age, sex, sociality or environmental context of the animal.

Conservation grazing in the UK has traditionally harnessed the needs of large herbivores to produce suitable conditions for specific species in limited spaces. This type of grazing is usually short-term, utilising limited numbers of similarly sexed or aged animals. In contrast, managers of landscape-scale habitat creation projects have often promoted the integration of socially expressive herds of animals back into the landscape, in order to promote a shifting and varied habitat dynamic with no end goal.

The Wicken Fen Vision is one such project. It evolved as a response to large scale habitat challenges to the NNR and local area over the twentieth century. Breeding herds of cattle and horses were introduced in 2003 to add an extra dimension of complexity to the landscape. In 2012, research demonstrated that free roaming grazing had a positive effect on vegetation structure and diversity in the Vision area (Stroh, 2012).

The continued evolution of the minimal management regime and growth of the herds has provided a novel opportunity to investigate the behaviours of cattle and horses in a free-roaming context. This thesis has investigated if the free-roaming herds are expressing any differences in their behaviours across sex, age, time or area. The social structures of the herds and individual associations therein have also been quantified for the first time through the use of social network analysis. Section 5.2 summarises and discusses the key findings from the investigations on differences in behaviours across sex, age, sub-area and season (Objective I). Section 5.3 follows with a summary of the cattle and horses social structures (Objective II). Section 5.4 then suggests some future directions for research on, and management of, the cattle and horses (Objective III).

5.2 Cattle and horse behaviour

In line with wider research, this study found that the cattle and horses exhibited some differences in behaviour across age (horses only) and sex (cattle only). Where these differences were found, they were associated with the nutritional or reproductive requirements related to a particular age or sex category.

Differences were not found across age for the cattle, or sex for the horses. The cessation of large scale breeding and the division of the cattle herd in 2008 promoted synchronisation of behaviours within each group. As a result of the reduction in breeding, the age range of cattle was limited to adults and sub-adults; only one calf was born in 2011 and it was omitted from the analysis of behaviour across age. These two factors can account for the result in this study analysing the difference in cattle behaviours across sex. In line with Neuhaus and Ruckstuhl (2002), the lack of difference across sex for the horses may be accounted for by their morphology. However, this current study used a limited behavioural repertoire to test for differences across the sexes. It may be that further work looking across a wider range of behaviours will identify differences between the sexes, as per Duncan (1980) or Boyd, (1988).

The cattle and horses also showed variation in behaviours across time, within days and between seasons. These circadian and diurnal rhythms were determined in response to nutritional needs and environmental factors. Interpretation of these results may be limited, as data collection was restricted to daylight hours. A fuller understanding of the circadian and diurnal rhythms of the cattle and horses would be facilitated by conducting night-time surveys.

Understanding the daily and seasonal rhythms of animals can be of practical use to individuals working with domestic or free-roaming cattle and horses. Management practices such as veterinary interventions can be scheduled for such times as when animals are restful, potentially making it less stressful for the animal during handling. Equally, events such as statutory tuberculosis testing in cattle could be attempted during periods when cattle are more mobile, making it easier to initiate herding and movement to any on-site handling system (Smith, 1998).

Overall, associations between sub-area use and season for the female cattle and horses were relatively even. The notable exception to this was sub-area Brett’s, which was not used by the female cattle and was rarely used by the horses. For much of the year, the wetter, reed dominated Brett's sub-area provided a sub-optimal environment for both the horses and female cattle. The mixed sex cattle demonstrated associations between sub-area use and season. These associations were driven by environmental factors, such as access to shade in the summer and avoidance of flooded areas in the winter.

Within the context of landscape scale habitat creation, the reduction of grazing impacts in a particular area may not be of concern. However, sub-area Brett's is part of the NNR and so is subject to prescriptions and statutory requirements to improve and/or maintain the habitat.

Habitat data are not provided by this study on a fine enough scale to determine associations with season and compartment (as opposed to larger sub-area) use by the horses and cattle. As the animals' use of habitat is influenced by more factors than the availability and variety of forage, it would be appropriate to assess associations between season, behaviour and compartment.

Closure of certain compartments (Section 2.5.3) as a result of statutory weed control did not appear to impact upon sub-area use at any time, but this could be misleading, as closures were implemented at compartment level, the fine detail of which may have not been captured by the analysis. Interpretation of the results in this study on sub-area use may be hindered by small sample sizes, as a result of sub-sampling to resolve a lack of independence of data.

This study based the analysis of sub-area use on observations of the cattle and horses over an hour, once per day. While this may give an indication of sub-area use and associations with season and behaviour, it is limited in its application and only provides a suggestion of area use by the animals. For example; during testing the viability of conducting data collection during the night-time, a follow of the cattle showed the cattle migrating through the majority of the compartments in their range, returning to the starting compartment by dawn the following day (C. Laidlaw, pers. obs.). The use of GPS collars (as per Putfarken et al., 2007) capturing horse and cattle use of sub-areas over a longer time-frame would be of benefit in providing a more detailed analysis.

As one of the aims of the WFV is to create socially expressive herds of grazers that are an integral part of the ecosystem, careful consideration should be given to management decisions which may create a more homogenous herd type. Although such decisions may be necessary, they may produce unintended effects on the herd or habitat, as with the removal of the bulls from Area 1 in 2008 and apparent lack of use of sub-area Brett's by the female cattle subsequently. However, whether such effects are regarded as negative or not is an important point; in the context of an open-ended, non-targeted habitat creation project, short-term homogeneity in the herd or environment may not matter. On a longer time scale, these changes will blend into the shifting mosaic of the whole; it is the journey that matters, not the destination (Hughes et al., 2011).

5.3 Cattle and horse herd social structures

This study has defined the social structure of the cattle and horse herds for the first time. The cattle herds were shown to be relatively uniform in structure, with little to no sub-grouping. Some long term associations between kin were identified in both cattle groups; and these associations combined with the long term stability of the herds were found to influence individual degree.

The horses showed distinct evidence of sub-grouping, although the herd overall was relatively highly connected. Environmental changes across seasons were shown to influence the social structure of the horse herd, although intra-group loyalty was largely stable across time. Other than mothers to young, stronger associations were only found for unrelated individuals. Factors such as sex and age were found to influence individual associations in the horses; with males and sub-adults having a higher degree that any other age or sex class. The social development of sub-adults and the herding behaviours of males account for the difference in degree across sex and age.

Basing associative relationships on proximity alone may capture a range of behaviours, such as agonistic interactions between males, or individuals simply passing each other, that are not indicative of an affiliation between two individuals. However, if the network is well sampled, it can provide an accurate assessment of associations between individuals (Farine, 2015).

Combining SNA with traditional behavioural observation techniques can provide a fuller picture of the network under observation; SNA is able to define a network on a relatively short timescale and is able to define the fine detail of sub-groups that may not be apparent through traditional techniques (Verdonlin et al., 2014). Future research on the cattle and horses can combine SNA techniques with long-term observational records held by this researcher to provide a high degree of network resolution.

5.4 Future research and management suggestions

Analysis of the data regarding sub-area use and the social structures of the herds captured the fact that the cattle and horses rarely, if ever, occupy the same compartment. This may be significant; are there unseen dominance hierarchies in place between the cattle and horses, and are these affecting how the cattle and horses interact with each other in the landscape? Menard et al., (2002) identified the potential for strong competition between cattle and horses, and it is possible that the combination of SNA and traditional behavioural techniques can demonstrate the interactions between the horses and cattle on a wider spatial scale.

As the cattle and horse herds are breeding, thought must be given to future population control. The use of SNA, perhaps combined with genetic data, to pinpoint family groups suitable for relocation or sterilisation may help to decrease stress and welfare challenges to the animals if affiliated individuals are moved together. Similarly, identifying reproductively successful males that are central to a family group or network could lead to targeted sterilisation, again with the aim of reducing management impact on the free-roaming herds. Monitoring the effects of breeding interventions on the networks may also be useful in determining herd stability both prior to and following any intervention.

This study found that the cattle herds evidenced a very stable social structure across time, and this stability was found to be a product of the long term nature of their associations enhanced by the splitting of the breeding group in 2008. Male and female cattle were re-united to form a breeding group in 2013. Anecdotal evidence appears to show that this group is interacting in a way that mirrors behaviours found in in other feral herds of cattle (Hall, 1986, 1988); use of SNA to illustrate the associations and interactions in this group would add to the understanding regarding free-roaming cattle in a landscape scale habitat creation project.

References

Adams, M.A. (ed.) and Mulligan, M., (ed.) 2003. *Decolonising Nature: Strategies for Conservation in a Post-colonial Era.* Earthscan from Routledge, ISBN 978 1 85383749 4.

AHDB Beef & Lamb, Agriculture and Horticulture Development Board, 2018. *Fit for purpose bulls, a blueprint for breeders*. [online] available at https://beefandlamb.ahdb.org.uk/wp-content/uploads/2014/02/BRP-fit-for-purpose-bulls-210214.pdf [accessed 27 Feb 2018].

Albright J. L. and Arave C.W., 1997. *The Behaviour of Cattle.* CABI Publishing, ISBN 0 85199 196 3.

Altmann, J., 1974. Observational Study of Behaviour: Sampling Methods. *Behaviour,* 49 (3/4), pp. 227 – 267.

Aplin, L.M., Firth, J.A., Farine, D.R., Voelkl, B., Crates, R.A., Culina,A., Garroway, C.J., Hinde, C.A., Kidd, L.R., Psorkis, I., Milligan, N.D., Radersma, R., Verhelst, B.L. and Sheldon, B.C., 2015. Consistent individual differences in the social phenotypes of wild great tits, Parus major. *Animal Behaviour*, 108, pp. 117–127.

Arnold, G.W., 1984. Comparison of the time budgets and circadian patterns of maintenance activities in sheep, cattle and horses grouped together. *Applied Animal Behaviour Science,* 13 (1-2), pp. 19–30.

Ausden, M., 2010. *Habitat Management for Conservation – A Handbook of Techniques.* Oxford University Press, ISBN 978 0 19 856873 5.

Ausden, M., and Treweek, J., (1995). 'Grasslands' in Sutherland, W.J. (ed.) and Hill, D.A. (ed.), 1995. *Managing Habitats for Conservation.* Cambridge University Press, ISBN 0 521 44776 3, pp. 197-229.

Bailey, D. and Jensen, D., 2008. Methods of Supplementation May Affect Cattle Grazing Patterns. *Rangeland Ecology & Management*, 61 (1), pp. 131–135.

Berger, A., Scheibe, K-M., Eichhorn, K., Scheibe, A. and Streich, J., 1999. Diurnal and ultradian rhythms of behaviour in a mare group of Przewalski horse (Equus ferus), measured through one year under semi-reserve conditions. *Applied Animal Behaviour Science,* 64, pp. 1–17.

Berger, J., 1986. *Wild Horses of the Great Basin: Social Competition and Population Size.* The University of Chicago Press, ISBN 0 226 04367 3.

Berger, J., Cheng, E., Kang, A., Krebs, M., Li, L., Lu, Z.X., Bushou, B and Schaller, G.B., 2014. Sex differences in ecology of wild yaks at high elevation in the Kekexili Reserve, Tibetan Qinghai Plateau, China. *Journal of Mammalogy,* 95 (3), pp 638–645.

Beynon, S.A., Peck, M., Mann, D.J. and Lewis, O.T., 2012. Consequences of alternative and conventional endoparasite control in cattle for dung-associated invertebrates and ecosystem functioning. *Agriculture, Ecosystems and Environment*, 162, pp. 36–44.

Bluthgen, N., Frund, J., Vazquez, D.P. and Menzel, F., 2008. What do interaction network metrics tell us about specialization and biological traits? *Ecology*, 89 (12), pp. 3387-3399.

Boreham, S., 2013. The geology of the Wicken Vision area, lower Cam valley, Cambridgeshire, UK. *Netherlands Journal of Geosciences,* 92 (1), pp. 47–59.

Bowden, J.M., Karriker, L.A., Stalder, K.J. and Johnson, A.K., 2008. Scan sampling techniques for behavioural validation in nursery pigs. *Animal Industry Report*, AS654, ASL R2342. Iowa State University. DOI: https://doi.org/10.31274/ans_air-180814-852, available at: https://lib.dr.iastate.edu/ans_air/vol654/iss1/91. [Accessed 21 April 2019].

Bowyer, R.T., 2004. Sexual segregation in ruminants: Definitions, Hypotheses, and implications for conservation and management. *American Society of Mammalogists, Journal of Mammology,* 85 (6), pp.1039-1052.

Boy, V. and Duncan P., 1979. Time-Budgets of Camargue Horse I. Developmental Changes in the Time-Budgets of Foals. *Behaviour,* 71 (3/4), pp. 187–202.

Boyd, L. (ed.) and Houpt, K., (ed.) 1994. *Przewalski's Horse: The history and biology of an endangered species.* State University of New York Press, ISBN 0 7914 1890 1.

Boyd, L., and Keiper, R., (2005). ‘Behavioural ecology of Feral Horses’ in Mills, D. and McDonnell, S., *The Domestic Horse. The Evolution, Development and Management of its Behaviour*. Cambridge University Press, ISBN 0 521 89113, pp. 55-82.

Boyd, L. E., 1988. Time budgets of adult Przewalski horses: Effects of sex, reproductive status and enclosure. *Applied Animal Behaviour Science*, 21 (1-2), pp. 19–39.

Boyd, L.E., Carbonaro, D.E. and Houpt, K.A., 1988. The 24-Hour Time Budget of Przewalski Horses. *Applied Animal Behaviour Science,* 21, pp. 5–17.

Boyland, N.K., Mlynski, D.T., James, R. and Brent, L.J.N., 2010. The social network structure of a dynamic group of dairy cows: From individual to group level patterns. *Applied Animal Behaviour Science*, 174, pp. 1–10.

Bragg, J., 2018. Adventurer’s Fen water levels. Unpublished data from the National Trust.

Brouček, J., Uhrinčať, M., Arave, C., Friend, T.H., Šoch, M., Trávniček, J., Tančin, V., Palkovičová, Z., Hanus, A., Raabová, M., Tejml, P., Šťastná, J. and Novak, P., 2013. Influence of Age, Gender, and Sire Line on Young Cattle Behaviour Traits. *Journal of Central European Agriculture*, 14 (1), pp. 432–451.

Burthe, S., Butler, A., Searle, K.R., Hall, S.J., Thackeray, S.J. and Wanless, S., 2011. Demographic consequence of increased winter births in a large aseasonally breeding mammal (Bos taurus) in response to climate change. *Journal of Animal Ecology*, 80 (6), pp. 1134-44.

Buzzard, P.J., Xu, D. and Li, H., 2014. Sexual/aggressive behaviour of wild yak (*Bos mutus* Prejevalsky 1883) during the rut: influence of female choice. *Chinese Science Bulletin*, 59 (2), pp. 2756–2763.

Carey, P., 2017. Wicken Habitat Survey: Alpha codes and Burwell and Guinea Hall Habitat map. National Trust unpublished data.

Chen, S., Ilany, A., White, B.J., Sanderson, M.W. and Lanzas C., 2015. Spatial-Temporal Dynamics of High-Resolution Animal Networks: What Can We Learn from Domestic Animals? *Public Library of Science One*, 10 (6): e0129253.

Cohen, J., 1992. Statistical Power Analysis. *Current Directions in psychological science*, 1 (3), pp. 98-101.

Grafen, A., and Halls, R., 2002. *Modern statistics for the life sciences.* Oxford University Press, ISBN 978 80199252312.

Colston, A., 1997. Conserving wildlife in a black hole. *ECOS*, 18 (1) pp. 61–67.

Colston, A., 2004. Wicken Fen - realising the vision. *ECOS*, 25 (3/4), pp. 42–45.

Colston, A., (2003). ‘Beyond Preservation: the challenge of ecological restoration’, in Adams, W.M, and Mulligan, M., *Decolonizing Nature – Strategies for conservation in a post-colonial era.* Routledge, ISBN 978 1 85383 749 4, pp. 247-267.

Constantine, R., Brunton, D.H. and Dennis, T. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncates*) behaviour. *Biological Conservation*, 117 (2004), pp.299-307.

Cornelissen, P. and Vulink, J. T., 2015. Density-dependent diet selection and body condition of cattle and horses in heterogeneous landscapes. *Applied Animal Behaviour Science*, 163 pp. 28–38.

Côté, S.D., Schaefer, J.A. and Messier, F., 1997. Time budgets and synchrony of activities in muskoxen: the influence of sex, age and season. *Canadian Journal of Zoology*, 75 (10), pp. 1628–1635.

Croft, D.P., Darden, S.K. and Wey, T.W., 2016. Current directions in animal social networks. *Current Opinion in Behavioural Sciences,* 12, pp. 52–58.

Croft, D.P., James, R. and Krause, J., 2008. *Exploring Animal Social Networks.* Princeton University Press, ISBN 978 0 691 12752 1.

Cross, P.C., Lloyd-smith, J.O., Bowers, J.A., Hay, C.T., Hofmeyer, M. and Getz, W.M., 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. *Ann. Zool. Fennici,* 41, pp. 879–892.

Csardi, G., and Nepusz T., 2006. *The igraph software package for complex network research.* Interjournal Complex systems 1695. [online] Available at: http://igraph.org [Accessed 01 Aug 2018].

DEFRA, 2018. *Protected areas designations directory.* [online] Available at: http://jncc.defra.gov.uk/page1527 [Accessed 03 Sept 2018].

DEFRA, 2018. *The UK Biodiversity Action Plan.* [online] Available at: http://jncc.defra.gov.uk/ukbap [Accessed 11 Feb 2018].

de Silva, S., Ranjeewa, A. and Kryazhimskiy, S., 2011. The dynamics of social networks among female Asian elephants. *BMC Ecology*, 11 (1):17.

Demment, M.W. and Van Soest, P.J. 1985. A Nutritional Explanation for Body-size Patterns of Ruminant and Nonruminant Herbivores. *The American Naturalist,* 125 (5), pp. 641–672.

Deng, K., Liu, W. and Wang, D., 2017. Inter-group associations in Mongolian gerbils: Quantitive evidence from social network analysis. *Integrative Zoology*, 12, pp. 446–456.

Donlan, C.J., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., Foreman, D., Martin, P.S., Roemer, G.W., Smith, F.A., Soulé, M.E. and Greene, H.W., 2006. Pleistocene Re-wilding: An Optimistic Agenda for Twenty-First Century Conservation. *The American Naturalist,* 168 (5), pp. 660–681.

Duncan, P., 1980. Time-Budgets of Camargue Horses II. Time-Budgets of Adult Horses and Weaned Sub-Adults. *Behaviour,* 72 (1/2), pp. 26–49.

Duncan, P., 1983. Determinants of the Use of Habitat by Horses in a Mediterranean Wetland. *Journal of Animal Ecology,* 52 (1) pp. 9 –109.

Duncan, P., 1985. Time-Budgets of Camargue Horses III. Environmental Influences. *Behaviour*, 92 (1/2), pp. 188–208.

Dunne, J.A., Williams, R.J. and Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 8, pp. 558-567.

Edouard, N., Duncan, P., Dumont, B., Baumont, R. and Fleurance G., 2010. Foraging in a heterogeneous environment - An experimental study of the trade-off between intake rate and diet quality. *Applied Animal Behaviour Science,* 126, pp. 27–36.

Eigenbrod, F., Adams, W., Hill, C., Macgregor, N., Osborne, P., Clarke, D., Sandbrook, L., Hodge, I., Steyl, I., Thompson, A., van Dijk, N. and Watmough, G., 2017. *A review of large-scale conservation in England, Scotland and Wales.* Natural England Joint Publication, JP019.

English Nature, 2005. *The importance of livestock grazing for wildlife conservation.* English Nature, ISBN 1 85716 8615.

European Commission Environmental, 1992. *The Habitats Directive*. [online] Available at:http://www.ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm [Accessed 03 Sept 2018].

Farine, D.R., 2015. Proximity as a proxy for interactions: issues of scale in social network analysis. *Animal Behaviour,* 104, pp. e1-e5.

Farine, D.R. and Whitehead, H., 2015. Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84, pp. 1144–1163.

Feh, C., 1997. Alliances and reproductive success in Camargue stallions. *Animal Behaviour*, 57, pp. 705–713.

Feh, C., (2005). ‘Relationships and communication in socially natural horse herds’ in Mills, D. and McDonnell, S., *The Domestic Horse. The Evolution, Development and Management of its Behaviour.* Cambridge University Press, ISBN 0 521 89113 2, pp. 83-93.

Firestone, S.M., Christley, R.M., Ward, M.P. and Dhand, N.K., 2012. Adding the spatial dimension to the social network analysis of an epidemic: Investigation of the 2007 outbreak of equine influenza in Australia. *Preventive Veterinary Medicine,* 106, pp. 123-135

Firth, J.A., Voelkl, B., Crates, R.A., Alpin, L.M., Biro, D. Croft, D.P. and Sheldon, B.C., 2017. Wild birds respond to flockmate loss by increasing their social network associations to others. *Proceedings of the Royal Society B*, 284 (1854) 20170299.

Friday, L. and Rowell, T.A., (1997). ‘Patterns and processes’, in Friday, L. (ed.), 1997. *Wicken Fen: the Making of a Wetland Nature Reserve,* Harley Books, ISBN 0 946589 33 x

Gander, A., Rockmann, A. and Strehler, C., 2003. Habitat use by Scottish Highland cattle in a lakeshore wetland. *Bulletin of the Geobotanical Institute ETH,* 69, pp. 3-16.

Goderie, R., Helmer, W., Kerkdijk-Otten, H. and Widstrand, S., 2013. *The Aurochs: born to be wild.* Roodbont Publishers BV, ISBN 978 90 8740 161 0.

Godwin, H., 1929. The “sedge” and “litter” of Wicken Fen. *Journal of Ecology*, 17 (1), pp. 148-160.

Grafen, A., and Halls, R., 2002. *Modern statistics for the life sciences.* Oxford University Press, ISBN 978 80199252312.

Gray, M.E., Cameron, E.Z., Peacock, M.M., Thain, D.S. and Kirchoff, V.S., 2012. Are low infidelity rates in feral horses due to infanticide? *Behavioural Ecological Sociobiology*, 66, pp. 529-537.

Great Fen, 2018. *History of Woodwalton Fen.* [online] Available at: http://www.greatfen.org.uk/heritage/history-woodwalton [Accessed 10 Jan 2018].

Guillemain, M., Fritz, H. and Guillon, N., 2000. Foraging behaviour and habitat choice of wintering Northern Shoveler in a major wintering quarter in France. *Waterbirds: The international journal of waterbird biology*, 23 (3), pp.353-363.

Gutmann, A.K., Spinka, M. and Winckler, C. 2015. Long-term familiarity creates preferred social partners in dairy cows. *Applied Animal Behaviour Science*, 169, pp. 1-8

Gygax, L., Neisen, G. and Wechsler, B. 2010. Socio-Spatial relationships in Dairy Cows. *Ethology*, 116, pp. 10–23.

Hall, L.K., Larsen, R.T.Y., Knight, R.N. and McMillan, B.R. 2018. Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi-arid environment. *Ecosphere*, 9 (1).

Hall, S.J.G and Bunce, R.G.H., 2019. The use of cattle Bos taurus for restoring and maintaining holartic landscapes: Conclusions from a long term study (1946-2017) in northern England. *Ecology and Evolution*, 2019;00:1-11. [online] Available at: https://doi.org/10.1002/ece3.5169. [Accessed 13 May 2019].

Hall, S.J.G and Moore, G.F. 1986. Feral cattle of Swona, Orkney Islands. *Mammal Review*, 16 (2), pp. 89–96.

Hall, S.J.G. 1988. Chillingham Park and its Herd of White Cattle: Relationships between Vegetation Classes and Patterns of Range Use. *Journal of Applied Ecology*, 25, pp.777-789.

Hall, S.J.G. 1989. Chillingham cattle: social and maintenance behaviour in an ungulate that breeds all year round. *Animal Behaviour*, 38, Issue 2, pp. 215-225.

Harris, N.R., Johnson, D.E., McDougald, N.K. and George, M.R., 2007. Social Associations and Dominance of Individuals in Small Herds of Cattle. *Rangeland Ecology and Management*, 60 (4), pp. 339-349.

Harrison, S. and Bruna, E., 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, 22, pp. 225-232.

Harvey, H.J., 2008. The National Trust and nature conservation; prospects for the future. *Biological Journal of the Linnean Society*, 56 (1), pp. 231-248.

Hawkins, D., 2009. *Biomeasurement, A Student's Guide to Biological Statistics.* (Second edition). Oxford University Press, ISBN 978 0 19 921999 5.

Hawkins, D. 2014. *Biomeasurement, A Student's Guide to Biological Statistics.* (Third edition). Oxford University Press, ISBN 978 0 19 965044-6.

Heising, K. and Smid, J., 2013. *Variation in individual behaviour of semi-wild Scottish highland cattle (Bos taurus spp.) in relation to weather conditions, day-time and habitat*. Bachelor thesis of Wildlife Management. Van Hall Larenstein University of Applied Sciences, Leeuwarden.

Hodder, K.H., Bullock, J.M., Buckland, P.C. and Kirby, K.J., 2005. Large herbivores in the wildwood and modern naturalistic grazing systems, *English Nature Research Reports, 648.*

Hughes, F.M.R., Adams, W.M. and Stroh, P.A., 2012. When is Open-endedness Desirable in Restoration Projects? *Restoration Ecology,* 20 (3). pp. 291-295.

Hughes, F.M.R., Stroh, P.A., Adams, W.M., Kirby, K.J., Mountford, J.O. and Warrington, S., 2011. Monitoring and evaluation large-scale, 'open-ended' habitat creation projects: A journey rather than a destination. *Journal for Nature Conservation*, 19, pp. 245–253.

Hughes. R.D., Duncan, P. and Dawson, J., 1981. Interactions between Camargue horses and horseflies (Diptera: Tabanidae). *Bulletin of entomological Research,* 71, pp. 227-242.

IBM Corporation, 2011, *IBM SPSS Statistics for Windows*, Version 20.0, Armonk, New York, IBM Corporation.

Illius, A.W. and Gordon, J.T., 1992. Modelling the Nutritional Ecology of Ungulate Herbivores: Evolution of Body Size and Competitive Interactions. *Oecologia,* 89 (3), pp. 428-434.

Keiper, R. and Berger, J., 1982. Refuge-seeking and pest avoidance by feral horses in desert and island environments. *Applied Animal Ethology*, 9 (2), pp. 111-120.

Kilgour, R.J., 2012. In pursuit of "normal": A review of the behaviour of cattle at pasture. *Applied Animal Behaviour Science,* 138, pp. 1–11.

Kilgour, R.J., Uetake, K., Ishiwata, T. and Melville G.J., 2012. The behaviour of beef cattle at pasture. *Applied Animal Behaviour Science,* 138, pp. 12-17.

Koufopoulos, A.J., 2004. *The Cattle Trades of Scotland, 1603 – 1745,* Ph.D. Thesis - The University of Edinburgh.

Kreuger, K., Flauger, B., Farmer, K. and Hemelrijk, C., 2014. Movement initiation in groups of feral horses. *Behavioural Processes*, 103, pp. 91-101.

Landi, P., Minoarivelo, H.O., Brannstrom, A., Hui, C. and Dieckmann, U., 2018. Complexity and stability of ecological networks: a review of the theory. *Population Ecology*, 60, pp. 319-345.

Lau, M.K., Borrett, S.R. Braiser, B., Gotelli, N.J. and Ellison, A.M., 2017. Ecological network metrics: opportunities for synthesis. *Ecosphere*, 8 (8).

Lawton, J.H., Brotherton, P.N.M. Brown, V.K., Elphic, C., Fitter, A.H., Forshaw, J., Haddow, R.W., Hilborne, S., Leafe, R.N., Mace, G.M., Southgate, M.P., Sutherland, W.A., Tew, T.E., Varley, J., and Wynne, G.R., 2010. *Making Space for Nature: a review of England's wildlife sites and ecological network.* [online] Available at: https://webarchive.nationalarchives.gov.uk/20130402170324/http:/archive.defra.gov.uk/environment/biodiversity/documents/201009space-for-nature.pdf [Accessed 10 May 2019]

Staatsbosbeheer, 2018. *Discover Lauwersmeer National Park!* [online] Available at: http://www.np-lauwersmeer.nl/english-information [Accessed 03 Sept 2018].

Lazo, A., 1995. Ranging of feral cattle (Bos taurus) in Donaňana National Park S.W. Spain. *Journal of Zoology*, 236 (3), pp.359 – 369.

Lazo, A., 1994. Social segregation and the maintenance of social stability in a feral cattle population. *Animal Behaviour,* 48, pp. 1133-1141.

Linklater, W.L., 2000. Adaptive explanation in socio-ecology: lessons from the Equidae. *Biological Reviews of the Cambridge Philosophical Society*, 75, pp. 1-20.

Linklater, W.L., Cameron, E.Z., Minot, E.O. and Stafford, K.J., 1999. Stallion harassment and the mating systems of horses. *Animal Behaviour*, 58, pp. 295-306.

Linnane, M.I., Brereton A.J. and Giller P.S., 2001. Seasonal Changes in circadian grazing patterns of Kerry cows (Bos taurus) in semi-feral conditions in Killarney National Park, Co. Kerry, Ireland. *Applied Animal Behaviour Science*, 71, pp. 277-292.

Linnartz, L. and Meissner, R., 2014. *Re-wilding horses in Europe. Background and guidelines - a living document,* Re-wilding Europe, Nijmegen, Netherlands, ISBN 978 90 822514 1 8.

Lorimer, J. and Dreissen, C., 2013. Wild experiments at the Oostvaardersplassen: rethinking environmentalism in the Anthropocene. *Transactions of the Institute of British Geographers,* 39 (2), pp.169-181.

Lorimer, J. and Driessen, C., 2013. Bovine biopolitics and the promise of monsters in the re-wilding of Heck cattle. *Geoforum*, 48, pp. 249-259.

Lorimer, J., Sandom, C., Jepson, P., Doughty, C., Barua, M. and Kirby, K.J., 2015. Re-wilding: Science, Practice and Politics. *Annual Review of Environment and Resources,* 40, pp. 39–62.

MacArthur, R.H. and Wilson, E.O., (1967). *The theory of Island biogeography,* Princeton University Press, ISBN 978-0691088365.

Martin, P. and Bateson, P., 2007. *Measuring Behaviour - an introductory guide.* Oxford University Press, ISBN 978 0 521 53563 2.

Marty, J.T., 2005. Effects of Cattle Grazing on Diversity in Ephemeral Wetlands. *Conservation Biology,* 19 (5), pp. 1626-1632.

May, R.M., 1972. Will a large complex system be stable? *Nature,* 238, pp. 413-414.

McCort, W.D., 1984. Behaviour of Feral Horses and Ponies. *Journal of Animal Science*, 58 pp. 493-499.

McDonnell, S., 1986. Reproductive Behaviour of the Stallion. *Veterinary Clinics of North America Equine Practice,* 2 (3), pp. 535-555.

McDonnell, S., 2003. *A Practical Field Guide to Horse Behaviour - the Equid Ethogram.* Eclipse Press (a division of The Blood Horse Inc.), ISBN 1 58150 090 4.

McDonnell, S.M. and Murray, S., 1995. Bachelor and Harem Stallion Behaviour and Endocrinology, *Biology Reproduction,* Mono 1, pp. 577-590.

Melletti, M. (ed.) and Burton, J. (ed.), 2014. *Ecology, Evolution and Behaviour of Wild Cattle: Implications for Conservation.* Cambridge University Press, ISBN 978 1 10703664 2.

Menard, C., Duncan, P., Fleurance, G., Georges, J. and Lila, M., 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology*, 39, pp. 120-133.

Mills, D. and McDonnell, S., 2005. *The Domestic Horse. The Evolution, Development and Management of its Behaviour*. Cambridge University Press, ISBN 0 521 89113 2

Mittelman, E., 2011. *Social Networks, Pathogen Networks and Gastrointestinal Parasites in a Captive Population of Exotic Ungulates.* Thesis in Animal Biology in the Office of Graduate Studies of the University of California

Monard, A-M and Duncan, P., 1996. Consequences of natal dispersal in female horses. *Animal Behaviour*, 52, pp. 565–579.

Moore, N.W., (1997). 'The Fenland Reserves', in Friday, L. (ed.). *WICKEN FEN The making of a wetland nature reserve.* Harley Books, ISBN 0 946589 33, pp. 3-8.

National Trust, 2011, W*icken Fen National Nature Reserve and Wicken Fen Vision land management plan 2011 to 2015.*

National Trust, 2011. *Wicken Fen Vision.* [online] Available at: https://nt.global.ssl.fastly.net/wicken-fen-nature-reserve/documents/wicken-fen-vision-strategy-document.pdf [Accessed 14 May 2019]

National Trust, 2011. *Wicken Fen Vision: The Grazing Programme Explained*. [online] Available at: https://nt.global.ssl.fastly.net/wicken-fen-nature-reserve/documents/wicken-fen-the-grazing-programme-explained.pdf [Accessed 14 May 2019]

Natural England, 2018. *Designated sites view, Wicken Fen.* [online] Available at: http://www.designatedsites.naturalengland.org.uk/ [Accessed 11 Jan 2018].

Neuhaus, P. and Ruckstuhl, K.E., 2002. Foraging behaviour in Alpine ibex (Capra ibex): consequences of reproductive status, body size, age and sex. *Ethology Ecology & Evolution,* 14 (4).

Noopataya, S., Thongratsskul, S. and Poolkhet, C., 2015. Social Network Analysis of Cattle Movement in Sukhothai Province, Thailand: A Study to Improve Control Measurements. *Veterinary Medicine International*, Vol. 2015 article I.D. 5872352.

Nuňez, C.M.V., Adelman, J.S. and Rubenstein, D.I., 2015. Sociality increases juvenile survival after a catastrophic event in the feral horse (Equus caballus). *Behavioural Ecology*, 26 (1), pp. 138-147.

O'Brien, P.P., Webber, Q.M.R. and Wal, E.V., 2018. Consistent individual differences and population plasticity in network- derived sociality: An experimental manipulation of density in a gregarious ungulate. *Public Library of Science One,* 13 (3) e0193425.

Overmars, W., Helmer, W., Meissner, R. and Kurstjens, G., (2002). 'Natural Grazing, Social Structure and Heredity', in van Duinhoven, G. *Special issue "Grazing and Grazing Animals"*. Expertisecentrum LNV ministerie van Landbouw, Natuurbeheer en Visserij, ISSN 1388-4875

Pasicka, E., 2013. Polish Konik Horse - Characteristics and Historical Background of Native Descendants of Tarpan. *Acta Scientiarum Polonorum Medicina Veterinaria,* 12 (2-4) pp. 25-38.

Phillips C.J.C., 1993. *Cattle Behaviour*. Farming Press Books, ISBN 0 85236 251 X.

Pullin, A.S. and Knight, T.M., 2001. Effectiveness in Conservation Practice: Pointers from Medicine and Public Health. *Conservation Biology*, 15 (1), pp. 50–54.

Putfarken, D., Dengler, J., Lehmann, S. and Härdtle W., 2008. Site use of grazing cattle and sheep on a large-scale pasture landscape: A GPS/GIS assessment. *Applied Animal Behaviour Science,* 111 (1-2), pp. 54-67.

R Core Team, 2017. *R: A language and environment for statistical computing,* R Foundation for Statistical computing, Vienna, Austria. [online] available at https://R-project.org/ [accessed 01 Sept 2018].

Raussi, S., Niskanen, S., Silvonen, J., Hänninen, L., Hepola, H., Jauhianen, L and Veisser, I., 2010. The formation of preferential relationships at early age in cattle. *Behavioural Processes*, 84, pp. 726-731.

Reinhardt, V. and Reinhardt, A., 1981. Relationships in a Cattle Herd (Bos indicus). *Behaviour,* 77 (3), pp. 121-151.

Reinhardt, V. and Reinhardt, A., 1982. Fighting in Cattle. *Behaviour,* 81 (1), pp. 1-13.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. and Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures - a review. *Biological Conservation,* 119, pp. 137–150.

Rowell, T.A., (1997). 'The History of the fen', in Friday, L. (ed.), *Wicken Fen, the making of a wetland nature reserve*. Harley Books, ISBN 0 946589 33 X.

RSPB, 2018. *Landscape Scale Conservation.* [online] Available at: http://www.rspb.org/our_work/conservation/landscape-scale-conservation [Accessed 03 Sept 2018].

Rubin, E.S., Boyce, W.M. and Bleich, V.C., 2000. Reproductive Strategies of Desert Bighorn Sheep. *Journal of Mammalogy*, 81 (3), pp. 769-786.

Ruckstuhl K.E. and Neuhaus, P., 2009. Activity budgets and sociality in a monomorphic ungulate: the African oryx (Oryx gazella). *Canadian Journal of Zoology*. 87, pp. 165-174.

Ruckstuhl, K.E., 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour*, 56, pp. 99-106.

De Ruiter, J.R., 1986. The influence of group size on predator scanning and foraging behaviour of wedge-capped capuchin monkeys (Cebus olivaceous). *Behaviour*, 98, pp. 240-58.

Smith, B., 1998. *Moving 'Em,* The Graziers Hui, ISBN 0 9662704 3 6.

Snijders, L., Blumstein, D.T., Stanley, C.R. and Franks, D.W., 2017. Animal Social Network Theory Can Help Wildlife Conservation. *Trends in Ecology and Evolution*, 32 (8), pp. 567-577.

Sosa, S., 2016. The Influence of Gender, Age, Matriline and Hierarchical Rank on Individual Social Position, Role and Interactional Patterns in *Macaca sylvanus* at ‘La Forêt des Singes’: A Multilevel Social Network Approach. *Frontiers in Psychology*, 7:529.

Sosa, S., Pelé, M., Debergue, E., Kuntz, C., Keller, B., Robic, F., Siegwalt-Baudin, F., Richer, C., Zhang, P., Ramos, A. and Sueur, C., 2018. Impact of group management and transfer on individual sociality in Highland cattle (*Bos taurus*). arXiv:1805.11553v2 [g-bio.PE]

Spence, K.L., O'Sullivan, T.L., Poljak, Z., and Greer, A.L., 2017. Descriptive and network analyses of the equine contact network at an equestrian show in Ontario, Canada and implications for disease spread. *BMC Veterinary Research,* 13:191

Stanley, C.R. and Dunbar, R.I.M., 2013. Consistent social structure and optimal clique size revealed by social network analysis of feral goats, *Capra hircus*. *Animal Behaviour,* 85, pp. 771-779.

Stanley, C.R. and Shultz, S., 2012. Mummy's boys: sex differential maternal-offspring bonds in semi-feral horses. *Behaviour*, 149 (3/4), pp. 251-274

Stanley, C.R., Mettke-Hoffman, C., Hager, R. and Shultz, S., 2018. Social stability in semiferal ponies: networks show interannual stability alongside seasonal flexibility. *Animal Behaviour,* 136, pp. 175-184.

Stevens, E.F., 1990. Instability of Harems of feral Horses in Relation to Season and Presence of Subordinate Stallions. *Behaviour*, 112 (3/4), pp. 149–161.

Stone, J., 2006. *Wicken Fen NNR: Reserve Monitoring Programme; Log of soil cores.* Unpublished report for the National Trust.

Strickland, K. and Frère, C.H., 2018. Predictable males and unpredictable females: repeatability of sociability in eastern water dragons. *Behavioural Ecology,* 29 (1), pp. 236-243.

Stroh, P.A., 2012. *Wetland Restoration on Ex-arable Land: the Influence of Seed Banks, Propagule, Dispersal, Grazing and Soil Hydrology,* Ph.D. Thesis: Anglia Ruskin University.

Sutherland, W.J., (1995). 'Introduction and principles of ecological management', in Sutherland, W.J. (ed.) and Hill, D.A. (ed.), 1995. *Managing habitats for conservation,* Cambridge University Press, ISBN 0 521 44776 3.

Takeda, K., Sato, S. and Sugawara, K., 2000. The number of farm mates influences social and maintenance behaviours of Japanese Black cows in a communal pasture. *Applied Animal Behaviour Science*, 67, pp. 181-192.

Taylor, P., 2005. *Beyond Conservation: A wildland strategy.* Earthscan Publications Limited ISBN 1 84407 198 7.

Tolhurst and Oates, 2001. Highland (Kyloe), from *The GAP Breeds Profile Handbook: A guide to the selection of Livestock breeds for grazing wildlife sites*. EnglishNature/GAP/FACT projects ISBN 1 857165705.

Tree, I., 2018. *Wilding: The return of nature to a British farm*. Picador, ISBN 978 1 5098 0509 9.

Tucker, C.B., Rogers, A.R. and Schütz, 2008. Effect of solar radiation on dairy cattle behaviour, use of shade and body temperature in a pasture-based system. *Applied Animal Behaviour Science*, 109 (2008), pp. 141-154.

Van Altena, C., Hemerik, L. and de Ruiter, P.C., 2016. Food web stability and weighted connectance: the complex-stability debate revisited. *Theoretical Ecology*, 9, pp.49-58.

van Vuure, C., 2014. On the origin of the Polish konik and its relation to Dutch nature management. *Lutra*, 57 (2), pp. 111-130.

van Vuure, C., 2005. *Retracing the Aurochs: history, morphology, and ecology of an extinct wild ox.* Pensoft, ISBN 954 642 235 5.

van Vuure, C., 2015. *From Kaikan to Konik.* Semper, ISBN 978 83 7507 185 6.

VanDierendonck, M.C., de Vries, H., Schilder, M.B.H., Colenbrander, B., Þorhallsdóttir, A.G and Sigurjónsdóttir, H., 2009. Interventions in social behaviour in a herd of mares and geldings. *Applied Animal Behaviour Science*, 116 pp. 67–73.

Verdolin, J.L., Traud, A.L., and Dunn, R.R., 2014. Key players and hierarchical organization of prairie dog social networks, *Ecological Complexity*, 19 (2014), pp. 140-147.

Vermeulen, R., 2015. *Natural Grazing, Practices in the re-wilding of cattle and horses.* Re-wilding Europe, Nijmegen, The Netherlands, ISBN 978 90 822514 2 5.

Vulink J. T. and Drost H.J., 1991. A Causal Analysis of Diet Composition in Free Ranging Cattle in Reed-Dominated Vegetation. *Oecologia*, 88 (2) (1991), pp. 167-172.

Vulink, J.T., Drost, H.J. and Jans, L., 2000. The Influence of Different Grazing Regimes on Phragmites and Shrub Vegetation in the Well-Drained Zone of a Eutrophic Wetland. *Applied Vegetation Science*, 3 (1), pp. 73-80.

Waring, George H., 2003. *Horse Behaviour Second Edition*. Noyes Publications/ William Andrew Publishing ISBN 978 0 8155 1484 8.

Warrington, S., 2018. *Wicken Fen Summary of species records.* National Trust unpublished data.

Wasserman, S. and Faust, K., 1994. *Social Network Analysis: Methods and Applications.* Cambridge University Press, ISBN 978 0 521 38707 1.

Watson-Haigh, N.S., Kadarmideen, H.N., and Reverter, A., 2010. PCIT: An R package for weighted gene co-expression networks based on partial correlation and information theory approaches. *Bioinformatics*, 26 (3), pp. 411-413.

Weeks, C.A., Danbury, T.D., Davies, H.C., Hunt, P. and Kestin, S.C., 2000. The behaviour of broiler chickens and its modification by lameness. *Applied Animal Behaviour Science*, 67 (1-2), pp.111-125.

Wey, T., Blumstein, D.T., Shen, W. and Jordán, F., 2007. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, 75, pp. 333-344.

Wey, T.W. and Blumstein, D.T., 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, 79, pp. 1343-1352.

Whitehead, H., 2008. *Analysing Animal Societies: Quantitative Methods for Vertebrate Social Analysis.* The University of Chicago Press, ISBN 13 978 0 226 89523 9.

Wildlife Trusts, The, 2018. *Living Landscapes*. [online] Available at: http://www.wildlifetrust.org/about-us/vision-and-mission/living landscapes [Accessed 03 Sept 2018].

Willisch, C.S. and Neuhas, P., 2009. Alternative Mating Tactics and Their Impact on Survival in Adult Male Alpine Ibex (Capra Ibex Ibex). *Journal of Mammalogy*. 90 (6), pp. 1421–1430.

Yapp, R.H., (1908). ‘Fig 1. Fenland showing position of the four Fenland reserves Map’, in Friday, L. (ed.), 1997. *Wicken Fen, the making of a wetland nature reserve*. Harley Books, ISBN 0 946589 33 X.

Appendices

Appendix I - Years of National Trust land acquisition at Wicken.

Table 1 Years that the National Trust acquired land at Wicken, from 1899 to 2017. Areas of land are identified by their local names, as used in the Management plan for the Reserve (National Trust, Management Plan 2011 – 2015). Dates for certain areas of land are approximate, due to acquisition records being incomplete. Total hectares as of 31st December 2017 = 805.72

Name of Area	Years of acquisition	Hectares
Wicken Fen	1899 - 1926	169.2
Adventurer's Fen (inc. Brett's and Rothschild's)	1907-1924	116.2
Baker's Fen	1993	50.39
Guinea Hall	2000	45.40
Harrison's Farm	1930-1990	21.86
Burwell Fen	2001 - 2008	223.40
Tubney Fen	2005	101.1
Bottisham Fen	2008	56.69
Reach Fen	2011	9.71
Old Bar Drove	2017	2.98
Rand Drove	2017	8.79

Appendix II - Major species groups found at Wicken Fen Nature Reserve.

Table 1 Numbers of the major species groups found at Wicken Fen Nature Reserve (National Trust, 2010). Total numbers of major species groups = 8,954

Species Group	Number of Species	Notes
Insects		
Coleoptera	1610	Beetles
Dermaptera	2	Earwigs
Diptera	2021	Flies
Ephemeroptera	13	Mayflies
Hemiptera	432	Bugs, aphids, plant hoppers
Hymenoptera - Aculeata	186	Ants, bees and wasps
Hymenoptera - Parasitica	460	Parasitic wasps
Hymenoptera - Symphyta	132	Sawflies
Lepidoptera – Butterflies	35	Butterflies
Lepidoptera – all moths	1223	Macro and micro-moths
Mecoptera	2	Scorpion flies
Megaloptera	2	Alder flies
Neuroptera	14	Lacewings
Odonata	26	Dragonflies and damselflies
Orthoptera	13	Grasshoppers, bush crickets
Phthiraptera	3	Featherlice
Plecoptera	1	Stone flies
Psocoptera	28	Book-lice
Raphidioptera	1	Snake flies
Siphonaptera	11	Fleas
Strepsiptera	3	Twisted wing parasites
Thysanoptera	28	Thrips
Trichoptera	54	Caddis-flies
Thysanura	1	Silverfish
Other Invertebrates		
Mollusca	89	Snails, slugs, bivalves
Crustacea	128	Woodlice, shrimps, waterfleas
Rotifers	41	Rotifers
Collembola	43	Springtails
Arachnida – spiders	258	Spiders
Arachnida - Opiliones	13	Harvestmen
Arachnida – Acari,	42	Mites, Ticks
Arachnida - Pseudoscorpiones	4	Pseudoscorpions
Myriapoda	20	Millipedes, centipedes
Annelida	28	Leeches, worms
Triclads	11	Flatworms
Porifera	8	Freshwater sponge
Nematodes	35	Roundworms, threadworms

Continued…

Appendix II, Table 1 continued. Numbers of the major species groups found at Wicken Fen Nature Reserve (National Trust, 2010). Total numbers of major species groups = 8,954

Species Group	**Number of species**	**Notes**
Lichens	131	
Fungi	560	
Slime moulds	5	
Plants		
Vascular plants	441	Flowers, grasses, trees, ferns
Bryophytes – mosses	112	Moss
Bryophytes – sphagnum mosses	7	Sphagnum mosses
Bryophytes – Liverworts	21	Liverworts
Algae (chlorophyta etc.)	107	Algae
Algae – Diatoms	157	Diatoms
Cyanophyta	23	Blue-green algae
Euglenophyta	15	Single-celled flagellate eukaryote
Characeae	11	Stoneworts
Zooflagellates	19	Single-celled heterotrophic eukaryotes
Oomycota	6	Water moulds, downy mildews
Rhizopoa	12	Amoebas
Ciliates	7	Ciliates
Vertebrates		
Mammals	34	Bats, voles, shrews, deer etc.
Fish	24	Including Spined loach
Amphibians	4	Frog, toad, Smooth and Great-crested newts
Reptiles	3	Grass snake, common lizard, slow-worm
Birds	234	Waders, dabbling ducks, warblers etc.

Appendix III - Summary of nature conservation features of Wicken Fen nature reserve.

Table 1 Summary of nature conservation features of Wicken Fen nature reserve. Habitats and species listed as of international importance are cited in SAC or Ramsar designations. Those of national importance are listed in the United Kingdom's Biodiversity Action Plan (DEFRA, 2018), are Red Data Book listed species or are Red listed birds. Nationally scarce species, local Biodiversity Action Plan species or Amber listed birds are of regional importance.

Feature	**International Importance**	**National Importance**	**Regional Importance**
Geology/Geomorphology			
Undisturbed fenland peat soils		✓	
Habitats			
Molinia meadows on calcareous peat	✓		
Calcareous fens with Cladium mariscus	✓		
Fen and marsh		✓	
Reed swamp		✓	
Open water and ditches		✓	
Carr (wet woodland)		✓	
Floodplain grassland		✓	
Unimproved neutral grassland			✓
Species: plants			
Marsh pea *Lathyrus palustris*		✓	
Fen violet *Viola persicifolia*		✓	
Stoneworts *Charophytes spp*		✓	
Fen dandelion *Taraxacum palustre*		✓	
Fibrous tussock sedge *Carex appropinquata*			✓
Great fen sedge *Cladium mariscus*			✓
Bryophyte community			✓
Species: Mammals, fish, reptiles and amphibians			
Brown hare *Lepus europaeus*		✓	
Otter *Lutra lutra*		✓	
Bats, all species			✓
Great crested newt *Triturus cristatus*	✓		
Spined loach *Cobitis taenia*	✓		
Harvest mouse *Micromys minutus*			✓

Continued…

Appendix III, Table 1 continued. Summary of nature conservation features of Wicken Fen nature reserve.

Feature	**International Importance**	**National Importance**	**Regional Importance**
Species: Birds (breeding species)			
Marsh harrier *Circus aeruginosus*	✓		
Hen harrier *Circus cyaneus* (winter roost)	✓		
Cetti's warbler *Cettia cetti*	✓		
Bearded tit *Panurus biarmicus*		✓	
Song thrush *Turdus philomelus*		✓	
Bullfinch *Pyrrhula pyrrhula*		✓	
Reed bunting *Emberiza schoeniclus*		✓	
Lapwing *Vanellus vanellus*		✓	
Bittern *Botaurus stellaris*		✓	
Gadwall *Anas strepera*		✓	
Pochard *Aythya ferina*		✓	
Water rail *Rallus aquaticus*		✓	
Redshank *Tringa totanus*			✓
Kingfisher *Alcedo atthis*			✓
Species: Invertebrates (abridged)			
Fen and marsh lepidoptera community		✓	
Fen and marsh coleoptera community		✓	
Dragonfly *Odonata* community		✓	
Water beetle *Dryops anglicanus*		✓	
Water beetle *Hydraena palustris*		✓	
Diving beetle *Laccornis oblongus*		✓	
Diving beetle *Dytiscus dimidiatus*		✓	
Diving beetle *Agabus undulatus*		✓	
Longhorn beetle *Lamia textor*		✓	
Ground beetle *Trechus rivularis*		✓	
Crucifix ground beetle *Panageus cruxmajor*		✓	
Leaf beetle *Longitarsus ferrugineus*		✓	
Featherwing beetle *Microptilium palustre*		✓	
Rove beetle *Quedius balticus*		✓	
Reed dagger moth *Simyra albovenosa*		✓	
Reed leopard moth *Phragmataecia castaneae*		✓	
Silver barred moth *Deltote bankiana*		✓	
Flame wainscot moth *Senta flammea*		✓	
Hoverfly *Anasimyia interpuncta*		✓	
Gall fly *Lipara similis*		✓	
Water bug *Microvelia umbricola*		✓	
Plant hopper *Paraliburnia clypealis*		✓	

Appendix IV - List of individual animals followed during data collection.

Table 1 List of individual cattle followed during the course of data collection in 2011. Cattle are listed as per grazing group followed in the study, in descending order of age.

ID code	Name	Age*	Mother	Sex and status	Origin
29601	Black Myra	15	Unknown	Female	Scotland
29901	Malda I	12	Unknown	Lead female	Scotland
20001	Roisin	11	Unknown	Female	Scotland
20101	Griannach	10	Unknown	Female	Scotland
20103	Wendy	10	Unknown	Female	Scotland
20301	Morag II	8	Morag I	Female	Scotland
20302	Malda II	8	Malda I	Female	Scotland
20601	Rue	5	Roisin	Female	Wicken
20602	Rush	5	Wendy	Female	Wicken
20604	Speedwell	5	Morag II	Female	Wicken
20605	Comfrey	5	Griannach	Female	Wicken
20607	Bramble	5	Malda II	Female	Wicken
20608	Rowan	5	Black Myra	Female	Wicken
20701	Bryony	4	Griannach	Female	Wicken
20702	Myrtle	4	Roisin	Female	Wicken
20704	Sorrel	4	Wendy	Female	Wicken
20706	Fat-Hen	4	MaldaII	Female	Wicken
20709	Valerian	4	Morag II	Female	Wicken
20801	Gale	3	Cannach III	Sub-adult female	Wicken
20802	T-Mustard	3	Rowan	Sub-adult female	Wicken
20803	Snowdrop	3	Morag I	Sub-adult female	Wicken
20804	Teasel	3	Speedwell	Sub-adult female	Wicken
20807	Herb-Robert	3	Roisin	Sub-adult female	Wicken
20808	Poppy	3	Rue	Sub-adult female	Wicken

Continued…

Appendix IV, Table 1 Continued…

20810	Daisy cow	3	Bramble	Sub-adult female	Wicken
20901	Ivy	2	Rowan	Sub-adult female	Wicken
20102	Isle	10	Unknown	Lead female	Suffolk
20303	Megan	8	Unknown	Female	Suffolk
10304	Ewan	8	Unknown	Male	Scotland
10603	Billy	5	Morag I	Male	Wicken
10606	Edmund	5	Malda I	Lead male	Wicken
10703	Brett	4	Morag I	Sub-adult male	Wicken
10705	Mitchell	4	Black Myra	Sub-adult male	Wicken
10708	Harrison	4	Malda I	Sub-adult male	Wicken
10805	Tansley	3	Malda II	Sub-adult male	Wicken
10806	Christie	3	Malda I	Sub-adult male	Wicken
10809	Thompson	3	Morag II	Sub-adult male	Wicken
10902	Ernest	2	Isle	Sub-adult male	Wicken
10903	Lapwing	2	Roisin	Sub-adult male	Wicken
10904	Norman	2	Bryony	Sub-adult male	Wicken
21001	Millie	1	Megan	Sub-adult female	Wicken
21002	Hedwig	1	Isle	Sub-adult female	Wicken
11101	Will	2 months	Isle	Male calf	Wicken

*Age as of 31st December 2011

Appendix IV, Table 2 List of individual horses followed during the course of data collection in 2011. Horses are listed in family groups observed as stable from 2004 – 2011. Family groups are ordered by adult male/female, sub-adult male/female and young under one year old.

ID code	Name	Age*	Mother	Sex and status	Origin
59901	Orlik	12	Orna	Lead male	Holland
50202	Nurag	9	Napia	Lead male	Holland
50401	Hanty	7	Napia	Male	Wicken
50501	Forest	6	Orada	Male	Wicken
69301	Nadia	18	Natka	Lead female	Holland
60003	Napia	11	Nadia	Female	Holland
60102	Oriola	10	Opravda	Female	Holland
60601	Gracie	5	Oriola	Female	Wicken
60702	Sashka	4	Oriola	Female	Wicken
60201	Kroka	9	Kurka	Female	Holland
51003	Chiron	1	Gracie	Sub-adult male	Wicken
51001	Basil	1	Napia	Sub-adult male	Wicken
51005	Nimbus	1	Nadia	Sub-adult male	Wicken
61102	Holly	8 months	Napia	Female foal	Wicken
61101	Daisy	8 months	Gracie	Female foal	Wicken
61108	Lily	5 months	Sashka	Female foal	Wicken
61106	Sky	6 months	Kroka	Female foal	Wicken
51103	Bert	8 months	Oriola	Male foal	Wicken
51109	George	4 months	Nadia	Male foal	Wicken
50701	Charlie	4	Orada	Lead male	Wicken
60002	Nanja	11	Nagana	Lead female	Holland
60101	Kaluna	10	Kola	Female	Holland
60909	Yara	2	Krieka	Female	Wicken
51004	Spod	1	Nanja	Sub-adult male	Wicken
51107	Jack	5 months	Kaluna	Male foal	Wicken
51105	Ernie	6 months	Nanja	Male foal	Wicken
50603	Eric	5	Krieka	Lead male	Wicken
50803	Gus	3	Orada	Lead male	Wicken
50801	Ralph	3	Napia	Male	Wicken

Continued…

Appendix IV, Table 2 continued…

50802	Sam	3	Oriola	Male	Wicken
60001	Krieka	11	Kawa	Lead female	Holland
60605	Esther	5	Nanja	Female	Wicken
50908	Ted	2	Esther	Sub-adult male	Wicken
51007	Ellis	1	Krieka	Sub-adult male	Wicken
61006	Polly	1	Esther	Sub-adult female	Wicken
51110	Flynn	3 months	Esther	Male foal	Wicken
50602	Tindal	5	Napia	Lead Male	Wicken
60804	Octavia	3	Nadia	Lead female	Wicken
60901	Meg	2	Krieka	Female	Wicken
61104	Jess	8 months	Meg	Female foal	Wicken
50905	Bob	2	Orada	Male	Wicken
50902	Tam	2	Kaluna	Male	Wicken
50907	Lychnis	2	Nadia	Male	Wicken
50903	Winston	2	Oriola	Male	Wicken
50904	Howard	2	Nanja	Male	Wicken
50906	Gypsy	2	Gracie	Male	Wicken
61002	Willow	1	Orada	Female	Wicken
50502	Peat	6	Napia	Unaffiliated male	Wicken
50604	Pip	5	Kaluna	Unaffiliated male	Wicken

Appendix V - Seasonal data collection dates for 2011.

The following four tables detail seasonal data collection dates for 2011. This includes daily start and finish times along with which species/group type were followed on each occasion. Each species/group type was followed for one hour a day for a total of six days before moving to the next. Time is recorded as per the 24 hour clock.

Table 1 Winter (January, February and December) scan sampling dates in 2011. Total individual hours of observation = 35.5.

<table>
<tr><th>Date</th><th>Species/group type</th><th>Start time</th><th>Finish time</th><th>Total hours per day observed</th></tr>
<tr><td>04/01</td><td rowspan="6">Horse, mixed sex</td><td>07:30</td><td>08:00</td><td>0.5</td></tr>
<tr><td>05/01</td><td>10:00</td><td>11:00</td><td rowspan="5">1.0</td></tr>
<tr><td>06/01</td><td>10:00</td><td>11:00</td></tr>
<tr><td>07/01</td><td>11:15</td><td>12:15</td></tr>
<tr><td>08/01</td><td>12:10</td><td>13:10</td></tr>
<tr><td>11/01</td><td>13:50</td><td>14:50</td></tr>
<tr><td>12/01</td><td>Cattle, female</td><td>09:10</td><td>10:10</td><td>1.0</td></tr>
<tr><td>13/01</td><td>Cattle, mixed sex</td><td>10:45</td><td>11:45</td><td>1.0</td></tr>
<tr><td>14/01</td><td>Cattle, female</td><td>11:35</td><td>12:35</td><td>1.0</td></tr>
<tr><td>15/01</td><td>Cattle, mixed sex</td><td>12:55</td><td>13:55</td><td>1.0</td></tr>
<tr><td>18/01</td><td>Cattle, female</td><td>12:45</td><td>13:45</td><td>1.0</td></tr>
<tr><td>19/01</td><td>Cattle, mixed sex</td><td>14:10</td><td>15:10</td><td>1.0</td></tr>
<tr><td>20/01</td><td rowspan="6">Horse, mixed sex</td><td>07:45</td><td>08:45</td><td rowspan="6">1.0</td></tr>
<tr><td>21/01</td><td>10:15</td><td>11:15</td></tr>
<tr><td>22/01</td><td>10:25</td><td>11:25</td></tr>
<tr><td>01/02</td><td>11:00</td><td>12:00</td></tr>
<tr><td>02/02</td><td>13:35</td><td>14:35</td></tr>
<tr><td>03/02</td><td>14:20</td><td>15:20</td></tr>
<tr><td>04/02</td><td>Cattle, mixed sex</td><td>07.45</td><td>08:45</td><td>1.0</td></tr>
<tr><td>05/02</td><td>Cattle, female</td><td>10:45</td><td>11:45</td><td>1.0</td></tr>
<tr><td>08/02</td><td>Cattle, mixed sex</td><td>10:20</td><td>11.20</td><td>1.0</td></tr>
<tr><td>09/02</td><td>Cattle, female</td><td>12:35</td><td>13:35</td><td>1.0</td></tr>
</table>

Continued….

Appendix V, Table 1 continued…

10/02	Cattle, mixed sex	12:30	13:30	1.0
11/02	Cattle, female	13.20	14.20	1.0
12/02	Horse, mixed sex	08:00	09:00	1.0
15/02		10:25	11:25	
16/02		10:50	11:50	
17/02		12:00	13:00	
18/02		13:45	14:45	
19/02		13:20	14:20	
14/12	Cattle, male	08:00	09:00	1.0
15/12	Cattle, male	11:30	12:30	1.0
16/12	Cattle, female	10:00	11:00	1.0
17/12	Cattle, male	11:30	12:30	1.0
21/12	Cattle, female	14:10	15:10	1.0
23/12	Horse, mixed sex	10:30	11:30	1.0

Appendix V, Table 2 Spring (March, April, May) scan sampling dates in 2011. Total individual hours of observation = 51.75. See introduction to Appendix V for further details

Date	Species/group type	Start time	Finish time	Total hours per day observed
01/03	Cattle, mixed sex	08:30	09:30	1.0
02/03	Cattle, female	08:40	09:40	1.0
03/03	Cattle, mixed sex	10:20	11:20	1.0
04/03	Cattle, female	11:00	12:00	1.0
05/03	Cattle, mixed sex	12:50	13:50	1.0
08/03	Cattle, female	13:20	14:20	1.0
09/03	Horse, mixed sex	07:30	08:30	1.0
10/03		09:50	10:50	
11/03		09:05	10:05	
12/03		11:00	12:00	
14/03		13:40	14:40	
16/03		13:20	14:20	
17/03	Cattle, female	08:00	09:00	1.0
18/03	Cattle, mixed sex	09:40	10:40	1.0
19/03	Cattle, female	10:25	11:25	1.0
28/03	Cattle, mixed sex	12:00	13:00	1.0
30/03	Cattle, female	12:10	13:10	1.0
31/03	Cattle, mixed sex	13:20	14:20	1.0
01/04	Horse, mixed sex	07:00	08:00	1.0
02/04		09:15	10:15	
05/04		10:30	11:30	
06/04		12:45	13:45	
07/04		15:00	16:00	
08/04		18:45	19:45	
09/04	Cattle, mixed sex	07:30	08:30	1.0
12/04	Cattle, female	10:20	11:20	1.0
13/04	Cattle, mixed sex	12:00	13:00	1.0
14/04	Cattle, female	12:45	13:45	1.0
15/04	Cattle, mixed sex	15:30	16:30	1.0

Continued…

Appendix V, Table 2 continued…

<table>
<tr><td>16/04</td><td>Cattle, female</td><td>11:45</td><td>12:45</td><td>1.0</td></tr>
<tr><td>17/04</td><td>Cattle, mixed sex</td><td>18:00</td><td>19:00</td><td>1.0</td></tr>
<tr><td>25/04</td><td rowspan="6">Horse, mixed sex</td><td>06:30</td><td>07:30</td><td rowspan="6">1.0</td></tr>
<tr><td>29/04</td><td>09:30</td><td>10:30</td></tr>
<tr><td>29/04</td><td>14:45</td><td>15:45</td></tr>
<tr><td>30/04</td><td>11:10</td><td>12:10</td></tr>
<tr><td>30/04</td><td>15:30</td><td>16:30</td></tr>
<tr><td>03/05</td><td>17:45</td><td>18:45</td></tr>
<tr><td>04/05</td><td>Cattle, female</td><td>06:05</td><td>07:05</td><td>1.0</td></tr>
<tr><td>05/05</td><td>Cattle, mixed sex</td><td>08:50</td><td>09:50</td><td>1.0</td></tr>
<tr><td>07/05</td><td>Cattle, mixed sex</td><td>12:40</td><td>13:40</td><td>1.0</td></tr>
<tr><td>10/05</td><td>Cattle, female</td><td>15:05</td><td>16:05</td><td>1.0</td></tr>
<tr><td>11/05</td><td>Cattle, mixed sex</td><td>19:00</td><td>20:00</td><td>1.0</td></tr>
<tr><td>12/05</td><td rowspan="4">Horse, mixed sex</td><td>06:45</td><td>07:45</td><td rowspan="2">1.0</td></tr>
<tr><td>13/05</td><td>09:15</td><td>10:15</td></tr>
<tr><td>14/05</td><td>10:40</td><td>11:25</td><td>.75</td></tr>
<tr><td>24/05</td><td>13:25</td><td>14:20</td><td>1.0</td></tr>
<tr><td>25/05</td><td>Cattle, female</td><td>08:45</td><td>09:45</td><td>1.0</td></tr>
<tr><td>26/05</td><td>Horse, mixed sex</td><td>18:45</td><td>19:45</td><td>1.0</td></tr>
<tr><td>27/05</td><td>Cattle, female</td><td>10:30</td><td>11:00</td><td>0.5</td></tr>
<tr><td>28/05</td><td>Horse, mixed sex</td><td>15:30</td><td>16:30</td><td>1.0</td></tr>
<tr><td>30/05</td><td>Cattle, female</td><td>13:25</td><td>14:25</td><td>1.0</td></tr>
<tr><td>31/05</td><td>Cattle, mixed sex</td><td>06:20</td><td>07:20</td><td>1.0</td></tr>
</table>

Appendix V, Table 3 Summer (June, July, August) scan sampling dates in 2011. Total individual hours of observation = 37.75. See introduction to Appendix V for further details.

<table>
<tr><th>Date</th><th>Species/group type</th><th>Start time</th><th>Finish time</th><th>Total hours per day observed</th></tr>
<tr><td>02/06</td><td>Cattle, female</td><td>14:45</td><td>15:45</td><td>1.0</td></tr>
<tr><td>03/06</td><td>Cattle, mixed sex</td><td>18:45</td><td>19:45</td><td>1.0</td></tr>
<tr><td>04/06</td><td rowspan="5">Horse, mixed sex</td><td>06:00</td><td>07:00</td><td rowspan="5">1.0</td></tr>
<tr><td>07/06</td><td>08:20</td><td>09:20</td></tr>
<tr><td>08/06</td><td>12:10</td><td>13:10</td></tr>
<tr><td>09/06</td><td>14:30</td><td>15:30</td></tr>
<tr><td>10/06</td><td>18:15</td><td>19:15</td></tr>
<tr><td>21/06</td><td>Cattle, mixed sex</td><td>06:30</td><td>07:30</td><td>1.0</td></tr>
<tr><td>22/06</td><td>Cattle, female</td><td>08:30</td><td>09:30</td><td>1.0</td></tr>
<tr><td>23/06</td><td>Cattle, mixed sex</td><td>12:30</td><td>13:30</td><td>1.0</td></tr>
<tr><td>24/06</td><td>Cattle, female</td><td>14:45</td><td>15:45</td><td>1.0</td></tr>
<tr><td>25/06</td><td>Cattle, mixed sex</td><td>15:30</td><td>16:30</td><td>1.0</td></tr>
<tr><td>30/06</td><td rowspan="10">Horse, mixed sex</td><td>10:00</td><td>10:45</td><td>0.75</td></tr>
<tr><td>01/07</td><td>18:00</td><td>19:00</td><td rowspan="3">1.0</td></tr>
<tr><td>02/07</td><td>15:15</td><td>16:15</td></tr>
<tr><td>05/07</td><td>15:05</td><td>16:05</td></tr>
<tr><td>06/07</td><td>15:20</td><td>15:35</td><td>0.25</td></tr>
<tr><td>23/07</td><td>07:30</td><td>08:00</td><td>0.5</td></tr>
<tr><td>26/07</td><td>10:35</td><td>11:05</td><td>0.5</td></tr>
<tr><td>27/07</td><td>13:00</td><td>14:00</td><td rowspan="3">1.0</td></tr>
<tr><td>28/07</td><td>10:50</td><td>11:50</td></tr>
<tr><td>29/07</td><td>15:00</td><td>16:00</td></tr>
<tr><td>30/07</td><td>Cattle, female</td><td>06:15</td><td>07:15</td><td>1.0</td></tr>
<tr><td>30/07</td><td rowspan="3">Cattle, mixed sex</td><td>08:30</td><td>09:30</td><td rowspan="3">1.0</td></tr>
<tr><td>02/08</td><td>14:30</td><td>15:30</td></tr>
<tr><td>02/08</td><td>16:30</td><td>17:30</td></tr>
<tr><td>03/08</td><td>Cattle, female</td><td>17:15</td><td>18:15</td><td>1.0</td></tr>
</table>

Continued…

Appendix V, Table 3 Continued…

16/08	Horse, mixed sex	07:00	08:00	1.0
17/08		11:00	11:45	0.75
18/08		12:00	13:00	1.0
19/08		13:50	14:35	0.75
20/08	Cattle, female	10:30	11:30	1.0
20/08	Horses, mixed	16:10	16:55	0.75
23/08		15:30	15:45	0.25
23/08		17:15	17:30	0.25
24/08	Cattle, mixed	06:30	07:30	1.0
25/08		11:30	12:30	
26/08		11:00	12:00	
27/08		14:15	15:15	
30/08		15:30	16:30	
31/08		17:15	18:15	
31/08		18:45	19:45	

Appendix V, Table 4 Autumn (September, October, November) scan sampling dates in 2011. Total individual hours of observation = 37.

Date	Species/group type	Start time	Finish time	Total hours per day observed
01/09	Horse, mixed	09:45	10:30	0.75
02/09		06:30	07:30	1.0
03/09		11:15	11:30	0.25
13/09		14:25	15:10	0.75
14/09		15:30	16:15	0.75
15/09		19:15	19:30	0.25
16/09	Cattle, mixed	08:00	09:00	1.0
17/09	Cattle, female	10:00	11:00	1.0
20/09	Cattle, mixed	14:00	15:00	1.0
21/09	Cattle, female	14:00	15:00	1.0
22/09	Cattle, mixed	16:00	17:00	1.0
23/09		17:00	18:00	
24/09	Horse, mixed	08:15	08:45	0.5
27/09		09:30	10:30	1.0
01/10	Cattle, mixed	09:00	10:00	1.0
07/10	Cattle, mixed	13:00	14:00	1.0
08/10	Cattle, female	10:15	11:15	1.0
08/10	Cattle, mixed	14:15	15:15	1.0
11/10		09:00	10:00	
15/10	Cattle, female	12:15	13:15	1.0
18/10	Cattle, mixed	12:50	13:50	1.0
19/10	Horse, mixed	08:45	09:15	0.5
20/10		11:05	11:35	0.5
21/10		10:10	10:55	0.75
22/10		12:30	13:00	0.5
25/10		13:00	14:00	1.0
26/10		12:20	13:05	0.75
27/10	Cattle, mixed	08:30	09:30	1.0
28/10	Cattle, female	10;45	11:45	1.0
29/10	Cattle, mixed sex	11:00	12:00	1.0

Continued…

Appendix V, Table 4 Continued…

08/11	Cattle, female	11:00	12:00	1.0
09/11	Cattle, mixed	12:40	13:40	1.0
10/11	Cattle, female	13:30	14:30	1.0
16/11	Horse, mixed	12:10	13:10	1.0
17/11		12:30	13:15	0.75
18/11		13:10	14:10	1.0
19/11	Cattle, mixed	09:00	10:00	1.0
22/11		10:10	11:10	
23/11		10:30	11:30	
24/11	Cattle, female	13:50	14:50	1.0
25/11	Cattle, mixed	10:00	11:00	1.0
26/11		11:00	12:00	

Appendix VI - Example completed field sheet

These sheets were used out in the field to record the behaviour and the identity of the first three nearest neighbours for all individuals in that day's study group. Four sheets were filled in for each day's data collection hour. The sheets had the same layout for the horses and cattle. Total number of cattle field sheets completed during data collection = 360, total number completed for the horses = 288 (overall total = 648).

Datasheet shown over the page

Appendix VI, Table 1 Example completed field sheet from January 2011.

Time Budget	Date;	6/1/11	Start;	10.30	Finish;	10.44		Notes:										
	Standing graze	Walking graze	Browse	Stand Alert	Stand immob	Stand doze	Ster recum	Ster recum eyes clsd	Lat recumb	Lat recum eyes clsd	Walking	Run	Drink	Other	NN1	NN2	NN3	Compt
Hanty				✓											Forest	–	–	W bank
Nadia											✓				Napia	–	–	102
Nurag														TF	Gawn	–	–	102
Octavia		✓													–	–	–	102
Polly	✓														Ellis	–	–	W bank
Kaluna	✓														Vanja	–	–	101
Anita's Gracie														SG	Winter	Forest	–	W bank
Tindal				✓											–	–	–	101
Forest				✓											–	–	–	102
Gypsy Spirit	✓														–	–	–	102
Peat		✓													Chiron	–	–	101
Basil	✓														Orlik	Nadia	Kroka	102
Spod					✓										Charlie	–	–	101
Sashka											✓				Chiron	Snot	–	102
Augustus (Gus)					✓										–	–	–	102
Ted (Scabbers)			✓												–	–	–	102
Sam														TF	Nurag	–	–	102
Ralph														SG	Tammy	–	–	102
Chiron Pavel	✓														Peat	–	–	101
Napia											✓				Nadia	–	–	102
Winston	✓														–	–	–	102
Kroka	✓														Basil	–	–	102
Tam	✓														–	–	–	102
Oriola											✓				–	–	–	102
Pipit (Pip)											✓				–	–	–	101
Lychnis														RC	Gawn	–	–	102
Orlik											✓				Forest	Gracie	–	W bank
Krieka	✓														Estar	–	–	101
Bob	✓														–	–	–	101
Eric	✓														Gus	–	–	101
Howard	✓														–	–	–	101
Charlie	✓														Spod	–	–	101
Auyara (Yara)					✓										–	–	–	101
Willow	✓														–	–	–	102
Nanja	✓														Kaluna	–	–	101
Esther											✓				Krieka	–	–	101
Nimbus	✓														–	–	–	102
Meg	✓														–	–	–	101
Ellis														SG	Polly	–	–	W bank

Appendix VII - Behavioural definitions

Table 1 Table of behavioural definitions used during the course of the research to identify and record maintenance behaviours. This table was constructed during 2010 using in field observations with reference to McDonnell (2003) and Boy and Duncan (1979).

Behaviour	**Description**
Away from herd	Animal 250m beyond the furthest individual within the herd boundary
Browse	Pluck leaves or fruit from trees or shrubs using lips and tongue
Cud	(Cattle only) Regurgitate food bolus into mouth, repetitively chew bolus in mouth, swallow and regurgitate bolus at least twice
Drink	Place muzzle on water source, suck water through mouth
Lateral recumbency	Lying flat on one side, legs usually extended away from body, doing nothing else
Lateral recumbency, eyes closed	Lying in lateral recumbency with eyes closed
Other	Any other behaviour performed by animals not detailed in ethogram
Run	Animal moving forward at speed in any gait other than walk
Stand alert	Standing, ears pointing forward, head high, attention focussed on an object
Stand immobile	Standing, doing nothing else, eyes open, ears floppy, standing with weight distributed over all four legs
Standing cud	(Cattle only) Standing, weight spread equally over all four legs, cudding
Standing doze	Standing, doing nothing else, eyes half shut or shut, bottom lip drooping, weight distributed over three legs, one hind leg relaxed
Standing graze	Stand in one spot, intake grass or herbs using lips and tongue, five or more mouthfuls taken in one spot
Sternal cud	(Cattle only) Lying in sternal recumbency, cudding
Sternal recumbency	Lying on floor, legs tucked under body, one or two legs may be extended forwards, lying upright on brisket
Sternal recumbency eyes closed	Lying in sternal recumbency with eyes shut
Walk	Animal taking 10 or more steps without grazing or stopping
Walking graze	Intake grass or herbs using lips and tongue, one or two mouthfuls taken at each spot with two or more strides taken between feeding spots
Water cud	(Cattle only) Stand in water for five minutes or more, cudding, eyes open, weight distributed over all four legs
Water stand immobile	Stand in water for five minutes or more, doing nothing else, eyes open, weight distributed over all four legs

Appendix VIII – Animal Degree calculations

Table 1a Individual degree for mixed sex cattle degree, in summer (1st March – 31st August) and winter (1st January – 28th February and 1st September – 31st December). Asymmetric association matrices were constructed for each group in each season, and these were exported as comma delimited files into R (R core team, 2017) where individual degree was calculated using igraph package. Degree is a direct count of how many associations an individual has. Individuals ranked in descending order of degree. (n = 17)

Summer				**Winter**			
ID code	**Degree**	**Sex**	**Age category**	**ID code**	**Degree**	**Sex**	**Age category**
20303	13	♀	Adult	10703	13	♂	Sub-adult
10705	12	♂	Sub-adult	10809	13	♂	Sub-adult
10708	12	♂	Sub-adult	10902	13	♂	Sub-adult
10806	12	♂	Sub-adult	10904	13	♂	Sub-adult
10902	12	♂	Sub-adult	20303	12	♀	Adult
21002	12	♀	Sub-adult	21001	12	♀	Sub-adult
10903	11	♂	Sub-adult	20102	11	♀	Adult
10904	11	♂	Sub-adult	10903	10	♂	Sub-adult
20102	11	♀	Adult	21002	10	♀	Sub-adult
21001	11	♀	Sub-adult	10606	9	♂	Adult
10603	10	♂	Adult	10705	9	♂	Sub-adult
10606	10	♂	Adult	10708	9	♂	Sub-adult
10703	10	♂	Sub-adult	10805	9	♂	Sub-adult
10805	10	♂	Sub-adult	10806	9	♂	Sub-adult
10809	9	♂	Sub-adult	10304	6	♂	Adult
10304	6	♂	Adult	10603	5	♂	Adult
				11101	5	♂	Young

Appendix VIII, Table 1b Individual degree for female cattle, summer and winter. For further details, refer to Table 1a, Appendix VIII. Individuals ranked in descending order of degree. (n = 26).

Summer				**Winter**			
ID code	**Degree**	**Sex**	**Age category**	**ID code**	**Degree**	**Sex**	**Age category**
20807	14	♀	Sub-adult	20101	14	♀	Adult
20607	12	♀	Adult	20709	14	♀	Sub-adult
20901	12	♀	Sub-adult	20103	13	♀	Adult
20103	11	♀	Adult	20901	13	♀	Sub-adult
20302	11	♀	Adult	20605	12	♀	Adult
20709	11	♀	Sub-adult	20701	12	♀	Sub-adult
29901	11	♀	Adult	20807	12	♀	Sub-adult
20101	10	♀	Adult	29601	12	♀	Adult
20601	10	♀	Adult	29901	12	♀	Adult
20605	10	♀	Adult	20604	11	♀	Adult
20704	10	♀	Sub-adult	20810	11	♀	Sub-adult
29601	10	♀	Adult	20001	10	♀	Adult
20604	9	♀	Adult	20301	10	♀	Adult
20702	9	♀	Sub-adult	20702	10	♀	Sub-adult
20810	9	♀	Sub-adult	20802	10	♀	Sub-adult
20001	8	♀	Adult	20804	10	♀	Sub-adult
20301	8	♀	Adult	20706	9	♀	Sub-adult
20602	8	♀	Adult	20302	8	♀	Adult
20802	8	♀	Sub-adult	20602	8	♀	Adult
20803	8	♀	Sub-adult	20607	7	♀	Adult
20808	7	♀	Sub-adult	20801	7	♀	Sub-adult
20608	6	♀	Adult	20808	7	♀	Sub-adult
20706	6	♀	Sub-adult	20601	6	♀	Adult
20801	5	♀	Sub-adult	20608	6	♀	Adult
20804	4	♀	Sub-adult	20704	6	♀	Sub-adult
20701	3	♀	Sub-adult	20803	6	♀	Sub-adult

Appendix VIII, Table 1c Individual degree for horses, in summer and winter. For further details, refer to Table 1a, Appendix VIII. Individuals ranked in descending order of degree. (n = 49).

Summer				**Winter**			
ID code	**Degree**	**Sex**	**Age category**	**ID code**	**Degree**	**Sex**	**Age category**
51003	28	♂	Sub-adult	50502	27	♂	Adult
51005	28	♂	Sub-adult	50907	27	♂	Sub-adult
50802	25	♂	Sub-adult	51003	25	♂	Sub-adult
50902	25	♂	Sub-adult	50906	24	♂	Sub-adult
51001	25	♂	Sub-adult	50401	23	♂	Adult
50401	24	♂	Adult	50802	23	♂	Sub-adult
50906	24	♂	Sub-adult	50803	23	♂	Sub-adult
50604	23	♂	Adult	50904	23	♂	Sub-adult
50801	23	♂	Sub-adult	50908	23	♂	Sub-adult
50908	23	♂	Sub-adult	60909	23	♀	Sub-adult
51004	23	♂	Sub-adult	60601	22	♀	Adult
60909	23	♀	Sub-adult	50501	21	♂	Adult
61006	23	♀	Sub-adult	50602	21	♂	Adult
69301	23	♀	Adult	50604	21	♂	Adult
50905	22	♂	Sub-adult	50801	21	♂	Sub-adult
50907	22	♂	Sub-adult	50905	21	♂	Sub-adult
50501	21	♂	Adult	60702	21	♀	Sub-adult
50803	21	♂	Sub-adult	61002	21	♀	Sub-adult
51007	21	♂	Sub-adult	61006	21	♀	Sub-adult
60201	21	♀	Adult	50902	20	♂	Sub-adult
50602	20	♂	Adult	51005	20	♂	Sub-adult
50903	20	♂	Sub-adult	59901	20	♂	Adult
50904	20	♂	Sub-adult	60901	20	♀	Sub-adult
60003	20	♀	Adult	50903	19	♂	Sub-adult
61102	20	♀	Young	51004	19	♂	Sub-adult
60001	19	♀	Adult	51007	19	♂	Sub-adult
60702	19	♀	Sub-adult	69301	18	♀	Adult
61002	19	♀	Sub-adult	60003	17	♀	Adult

Continued…

Appendix VIII, Table 1c Continued…

50502	18	♂	Adult	60201	17	♀	Adult
51103	18	♂	Young	50202	16	♂	Adult
61101	18	♀	Young	60101	16	♀	Adult
50603	17	♂	Adult	60102	16	♀	Adult
60901	17	♀	Sub-adult	51001	15	♂	Sub-adult
50202	16	♂	Adult	51103	15	♂	Young
59901	16	♂	Adult	60605	15	♀	Adult
60601	16	♀	Adult	50603	14	♂	Adult
60804	16	♀	Sub-adult	50701	14	♂	Sub-adult
60101	15	♀	Adult	60001	14	♀	Adult
60102	15	♀	Adult	60804	14	♀	Sub-adult
60605	15	♀	Adult	61106	13	♀	Young
50701	14	♂	Sub-adult	61101	12	♀	Young
60002	14	♀	Adult	61102	12	♀	Young
51107	11	♂	Young	60002	10	♀	Adult
61108	10	♀	Young	61108	10	♀	Young
51105	7	♂	Young	51105	9	♂	Young
61106	7	♀	Young	51107	9	♂	Young
61104	6	♀	Young	51109	7	♂	Young
51109	5	♂	Young	61104	5	♀	Young
				51110	4	♂	Young