Dominance In a Mixed-Species Deer Exhibit at ZSL Whipsnade Zoo. A Study Into Supplementary Feeding Methods to Create Greater Equality of Access

Tomos Avent

MSc Conservation Science

September 2008

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science and the Diploma of Imperial College London

Contents

Tables and Figures

14,222 words in Text
1,461 words in Figures and Tables
1,234 words in Appendix

1. Abstract

When multiple species of deer are kept together dominance hierarchies can create differential access to supplementary food. A lower access to food than prescribed can affect fitness whilst higher access can affect behavioural patterns, both potentially serious consequences for management, especially of threatened species. Some studies have shown that increasing the number of food patches has helped to lower the effect of dominance on food access although this has rarely been studied in complex, mixed-species enclosures. It also seems probable that decreasing the size of the earliest presented patches, likely to be taken by the dominant groups, and increasing the proportion of food in subsequent patches, will create greater feeding opportunities for subordinate species. However, for this to be the case, conditions must be such as to prevent dominant groups from breaking up and transferring between patches.

The mixed-species deer group at ZSL Whipsnade Zoo comprises sika deer (*Cervus nippon*), axis deer (*Axis axis*), hog deer (*Axis porcinus*) and fallow deer (*Dama dama*) as well as the threatened swamp deer (*Cervus duvaucelii*). This study aims to examine the dominance hierarchy and its effects on food access and daily behaviour within this deer group. The effects of increasing food patch numbers, and altering the order of patch size presentation is also evaluated. It was found that both sexes of sika deer and axis deer, as well as male fallow deer and hog deer all competed effectively, whilst female fallow deer and swamp deer were lower in the dominance hierarchy. This, however, did not necessarily relate directly to overall food access, the reasons for which are discussed. Differential access to supplementary pellets only affected daily foraging behaviour in swamp deer, the most weakly competitive group, which are probably more vulnerable to small changes in pellet intake. Increasing the number of patches and decreasing the size of the earliest presented patches did not help mitigate the effects of dominance, probably due to the low distance between patches allowing patch transfer and the break up of the most dominant group.

5

2. Introduction

Mixed species exhibits of mammals are growing in popularity in zoos but often bring with them novel interactions that can be difficult to predict and manage (Thomas & Maruska, 1996). One of the major issues that must be addressed is that of feeding, especially when different species compete for the same food type and when animals are given food within an unnaturally small area (McGhee & Baccus, 2006). Feeding competition can manifest itself in two main ways: through scramble competition, where all groups go for the same resource and the foraging opportunities of an individual are limited by those around them; and through contest competition, where dominance hierarchies develop, creating priority access for certain individuals who either aggressively, or simply through passive interference, inhibit others from feeding (see Lomnicki, 1988). In ungulates, both forms of competition will affect feeding (McGhee & Baccus, 2006), but high population densities and low feeding space in captivity will increase the likelihood and importance of contest competition (McGhee & Baccus, 2006).

Deer are commonly kept in mixed species assemblages in zoological parks (ISIS, 2008), estates and farms. In these groups, dominance hierarchies are likely to develop both within and between species. These hierarchies can be subtle and complex, built up over time (Dittrich, 1976), and can have an effect on food access. The nutritional quality and amount of food provided to animals in captivity is normally carefully measured by staff, but in large multi-species groups, it is difficult to evaluate the uptake of individuals or of a single species. Poorly competitive groups may therefore not get the diet prescribed for them by the nutritionists (Dittrich, 1976), and this may have a direct effect on physical condition (Appleby, 1980) and therefore fitness and reproductive ability (Vankova et al., 1999; McGhee & Baccus, 2006). Dominant groups, on the other hand, may over-eat, leaving unnaturally long periods in the day without the need for foraging (Dittrich, 1976). As ungulates in the wild generally dedicate 40-60% of their day to finding and consuming food (Wickstrom et al., 1984), it is argued that this can be detrimental to maintaining natural behavioural patterns (McGhee & Baccus, 2006). These hierarchies, however, can be altered by the spatial distribution of food (Milinski & Parker, 1991).

When feed is placed out within a small area, competition will be increased, lowering the feeding opportunities for subordinate individuals (Bowman & Sowell, 1997; Appleby, 1980). It is therefore recommended that food should be put out in a number of different places so as to decrease levels of competition and create a greater equity amongst species (Thomas & Maruska, 1996; Bowman & Sowell, 1997).

In captivity, if the recommendation to put out food in different places is heeded, the patches are usually put out one at a time, for practical staffing reasons. If hay is being put out, it is often eaten over long periods, and so food distribution time is relatively unimportant. However, patches of pellets are often depleted quickly relative to the time it takes to put them out which may create additional advantages to groups higher up the dominance hierarchy. When the first patch is put out, it is the only food source available, and if feeding methods vary from day to day, sometimes where only one patch is offered, this first patch is likely to be subject to high competition with dominant species controlling access (Bartos et al., 1996). If the quantity of food put out in this first patch is greater than that required by the overall proportion of deer in this dominant group, then individuals would have the potential to consume a greater proportion of the food than allocated leaving less food than was prescribed for the other groups (Landaeta-Hernández et al., 2005). When hierarchies are further complicated by multiple species, and additional competitive differences between sexes within these species, lowly ranking groups could struggle even more with access to food as all patches may be dominated by separate, higher ranking groups.

There is, then, a theoretical relationship between size of initial food patches and effectiveness of feeding methods within multi-species groups. If the relative size of the first few patches is increased, there could be greater tendency for dominant groups to over eat, and the subordinate groups to receive inadequate nutrition. If, however, the first patches were the smallest, as before the first patch put out will initially be the only source of food accordingly will presumably still attract the dominant group. When resource depletion rate is high, it pays to spend as much time as possible foraging (Pruetz & Isbell, 2000). Animals face decisions about where to forage and how long to stay in a patch as it

is becoming depleted (Krebs & Kacelnik, 1991). Therefore, using inferences from the Marginal Value Theorem (Charnov, 1976), as long as there is enough food to keep all individuals in the group feeding, interpatch distance is high, thus requiring energy for patch transfer and lost foraging time, and displacement of other individuals takes energy, it may be beneficial to stay in the current patch. Consequently dominant species would remain at the initial, smaller patches, while subordinate groups would have better access to the larger patches.

ZSL Whipsnade Zoo houses a mixed species deer group of swamp deer (*Cervus duvaucelii*), axis deer (*Axis axis*), sika deer (*Cervus nippon*), fallow deer (*Dama dama*) and hog deer (*Axis porcinus*). Supplementary pellets are provided once a day for the deer in autumn, winter and spring but in the summer the grass is deemed sufficient to meet the deer's dietary requirements. Although keepers have observed biases in access to supplementary feed between species, neither the nature nor the effects of these biases have ever been studied.

2.1 Aims and Objectives

The general aim of this project was to aid management of the mixed deer group at ZSL Whipsnade Zoo by enhancing the understanding of the impact of different distribution methods of supplementary pellets for mixed species ungulate groups.

Specific objectives:
1. Improve understanding of the dominance hierarchy around supplementary pellets between the species, and the sexes within these species, of deer in the mixed species deer paddock at ZSL Whipsnade Zoo.
2. Assess the impact of altering the spatial distribution and presentation order of different sized patches of supplementary pellets on food access of each species, and sex between each species, at the feeding site.

3. Assess the impact of altering the spatial distribution and presentation order of different sized patches of supplementary pellets on the time spent foraging for grass throughout the day for each species, and sex within each species.

Hypotheses

1. There will be differential access to supplementary food pellets between species, and sexes within species, in the mixed species deer exhibit.

2. Increasing the number of food patches will minimise the inequity in feeding between species, and sexes within species. Presenting biggest clumps first will benefit species and sexes within species higher up the dominance hierarchy, whilst putting the smallest clumps out first will benefit species and sexes within species lower down the hierarchy.

3. Methods that alter the proportion of a species, or sex within a species, feeding on the supplementary pellets will also alter proportion of the day spent foraging for that species, or sex within the species.

3. Background

3.1. The Conservation Role of Zoos, with a Focus on Ungulates

Zoological Parks can play an important role in conservation, through contributions to research programmes, education of the general public, financing of in-situ projects, and by acting as an ark for threatened species (see Olney et al., 1994; Wielebnowski, 1998). With regard to their role as an ark, it is important that zoos ensure that animal populations are kept physically and psychologically healthy, whilst maintaining high levels of fitness, genetic viability, and natural behavioural traits (Wielebnowski, 1998). In many mammalian taxa such as ungulates, foraging behaviour and social interactions are complex and culturally developed traits (see Wielebnowski, 1998). In order to prevent a rapid and permanent loss of these traits, they must be factored into ex-situ management (Lyles & May, 1987).

Zoo-based research has played an important role in the conservation of ungulates by working to improve the effectiveness of genetic, demographic and behavioural management of threatened species (Wielebnowski, 1998). Recently, there have also been advancements in methods of artificial insemination and cryobiology in ex-situ centres (Wehnelt & Wilkinson, 2005). For some species, such as the Arabian oryx (*Oryx leucoryx*), much was learnt from studying the individuals in captivity. Research into the best methods of captive breeding helped to boost populations, eventually to a high enough level to allow successful reintroduction (Stanley Price, 1989). The European bison (*Bison bonasus*), Przewalski's horse (*Equus przewalskii*) and the Pere David's deer (*Elaphurus davidianus*) are other ungulate species to have been preserved in captivity following extinction in the wild and then reintroduced into their natural habitat. In other ungulates, teetering populations of Formosan sika deer (*Cervus nippon taioanus*), huemul (*Hippocamelus bisulcus*), addax (*Addax nasomaculatus*), Cuvier's gazelle (*Gazella cuvieri*), mountain gazelle (*Gazella gazella*), dama gazelle (*Nanger dama*), scimitar-horned oryx (*Oryx dammah*) and Abbruzzo chamois (*Rupicapra rupicapra*) have all been increased through captive breeding (Wilson & Stanley-Price 1994; Beck et al., 1994).

Despite numerous successes, zoo-based research has also faced considerable criticism. Rees (2005) argues that insufficient pressure has been exerted on zoos to undertake conservation research programmes and it should be a legal requirement for zoos to undertake conservation-focused research. In addition to this, some authors believe that small sample sizes and relatively unnatural conditions within zoos limit the applicability and relevance of ex-situ research to populations in the wild, and propose that investment into zoo-based research may be better spent on in-situ conservation projects (see Wehnelt & Wilkinson, 2005).

3.2. A Closer Examination of Behavioural Research in Zoos

Animal behaviour can present major hurdles for captive breeding projects (Synder et al., 1996). Zoos have played an important part in undertaking research into behaviour as a facet of successful conservation measures, and Harcourt (1999) draws reference to 'The Behaviour of ungulates and its relation to management', published by the IUCN in 1974, as a model example. However, although it is acknowledged that behavioural work

is common in zoos, Kleiman (1994) argues that when it comes to captive breeding in practice, systematic hypotheses are rarely tested, and that references to behaviour are generally anecdotal or the result of casual observation after problems have occurred.

Behavioural research that attempts to improve management of captive animals may have an impact beyond the focal species. Inferences are often made to the management of similar species and extrapolation of best practice for the management of groups where numbers are so low that there is little time and space for trial and error. In fact, even research on species currently not threatened can be said to have a potential conservation value as any species may become candidates for reintroduction projects in the future (Wielebnowski, 1998).

3.3 Mixed Species Exhibits of Ungulates In Zoos

Housing different species together in captivity is not a new concept, with early zoos often housing mixed aviaries, aquariums and reptile gardens (Ziegler, 2002). These were often simply the result of the practicality of using a single enclosure to hold more than one species. A wide scale use of mixed-mammal enclosures is a relatively new concept however, due to a perception in the past of the potential risks, technical demands and problems that can be caused by establishing new relationships between species (Ziegler, 2002). The rise in popularity of the modern mixed-species exhibit is driven by four main factors; public entertainment and education, space limitations, cost, and animal enrichment (Ziegler, 2002).

Interactions between animals create a more interesting experience for paying members of the public. The association of animals, especially when from the same habitat and geographic region, also provides a good educational tool for children and, if presented properly, also can convey a strong conservation message for people of all ages (Thomas & Maruska, 1996). Zoos are of course more often than not funded by members of the public, and the importance of popular appeal must therefore not be underestimated. Indeed, some of the earliest reports at the turn of the 20th century of open-air mixed-species ungulate exhibits in zoos were driven by visitors' desires to see African grasslands: a sea of antelope and wildebeest filling the vast plains as far as the eye could see (Walther, 1965).

Most zoos will have space limitations, and issues of overcrowding can be another key reason for keeping animals of different species together. Indeed some zoos, such as Burnet Park Zoo in New York, are moving to create mixed species enclosures with the potential for adaptation for 'Species Survival Plan' species at a later date (Moore, 1998). Cost of designing, building and maintaining a singular large enclosure was cited as another good reason to create the mixed species exhibit in Burnet Park Zoo (Moore, 1998).

Providing suitable behavioural and social enrichment is often problematic in zoos, but housing naturally compatible animals together can create a more complex and natural environment encouraging interactions between species and possibly even intensified interactions within species (Ziegler, 2002). As a counterargument to the benefits of enrichment, Walther (1965) reasoned that although animals may form polyspecific associations in the wild, these relationships vary dependant upon activity and time whereas in zoos, the associations are enforced and ever present. Using the example of ungulates he argues that the natural associations are often seen most strongly around waterholes or when animals are lying down. The associations are, however, weaker during grazing, thus minimizing the aggressive interactions over food. In zoos, animals are often forced together to eat, resulting in un-natural competition (Walther, 1965), and thus creating problems for management.

3.4 Polyspecific Associations and Dominance

Relationships between species (polyspecific associations), are common throughout the animal kingdom, and have been noted in fish, birds, ungulates, primates and cetaceans to name but a few (see Heymann & Buchanan-Smith, 2000). They are nearly always formed between intraspecifically social species (Stensland et al., 2003) and are mainly the result of increasing foraging efficiency or predator avoidance (see Ziegler, 2002) although sometimes these associations are simply the bi-product of different species occupying similar areas, due, for example, to a high value feeding area (Stensland et al., 2003).

Dominance hierarchies, where certain individuals or groups have preferential access to a high-value resource, are frequently seen in and between social ungulate species (Appleby, 1980; McGhee & Baccus, 2006). Between species, the high-value resource may be food, with dominant individuals or groups gaining access to the highest value patches (Vahl et al., 2005), and/or protection, as seen in herding ungulates where dominants reside in the safest positions (Hamilton, 1971). Within species, mating opportunities are an additional high-value resource (Appleby, 1980).

Interspecific dominance can manifest itself both agonistically, where species fight (Drews, 1993), or as a form of passive socially-mediated interference where a dominant species can affect the action of a subordinate species simply by being in the same place at the same time (Saito, 1996). It is thought that the latter evolved as a way to minimise the number of costly aggressive interactions (Holand et al., 2004). Mosley (1999) argues that social competition in ungulates is largely a passive process both within and between species. In these cases, passive displacement by dominants and avoidance by subordinates are most important (Barroso et al., 2000, Thouless 1990).

Interspecific dominance can be a function of many factors. In some cases, body size may have the greatest influence (Bassett, 1995; Shelley et al., 2004), whereas increased group size is one way that fallow deer have been observed to compete with red deer (Bartos et al., 1996). In an experiment by McGhee and Baccus (2006), antler size and stage of development in males, and seasonal differences in aggression in females, were the most important factors between axis and fallow deer at high-value food patches. The intricacies of interspecific dominance hierarchies can also be complicated by dominance within the species involved. Age and sex can be additional factors here (see Barrette & Vandal, 1986).

3.5 Supplementary Feeding and Interspecific Dominance within Mixed Species Groups

Supplementary feeding is common when animals are kept in artificial environments, such as zoos and farms. It is also used to boost wild populations above natural levels for hunting, as in deer estates, and can substitute for lost feeding opportunities in threatened populations.

Ungulates can be provided with supplementary feed in many forms, from hay, silage and root crops, to artificial concentrates in pellets (Putman & Staines, 2004). These pellets can be designed to meet an animal's optimum nutritional requirements and can be adapted to suit management goals (Schmidt & Seivwright, 1997). In domestic livestock and hunting, where production and quality of product is most important, these supplementary pellets often have high vitamin, protein and mineral concentrations; high calcium levels can help deer antler development and pregnant females, for example (Wildlife Institute of India, 2004). Essential nutrients are also important in zoos, as even if animals are given pasture, the quality and quantity of these naturally available nutrients may not be sufficient (Volpelli et al., 2002). Another major problem encountered among animals in captivity is the lack of digestible energy either because of few natural feeding opportunities, or unnaturally high densities of animals on the pasture provided (Putman & Staines, 2004). As mentioned in the introduction, this can be especially important in captive breeding with links to fitness (Vankova et al., 1999; McGhee & Baccus, 2006) and the maintenance of natural behaviour (Dittrich, 1976). When animals eat more supplementary food than is required to compensate for actual loss of forage, the resulting reduction in foraging activity can result in lethargy and apathy.

Dominance hierarchies will create differential access to supplementary feed (McGhee & Baccus, 2006) and the limited space in which food is put out often serves to exacerbate this tendency (Cassinello, 2002). A number of studies have been undertaken on examining intraspecific interactions, but dominance between species around supplementary food is poorly documented. McGhee and Baccus (2006) studied interactions and hierarchies between axis deer (*Axis axis*) and fallow deer (*Dama dama*) around high-quality supplementary feed on a Texan deer ranch. They tested whether one species displaced the other around a feeding site and observed the expenditure of energy required by these displacements. Every twenty minutes, observations were made of a line of supplementary pellets with 25 patches, each about 1.5 m long and spaced about 3.8 m apart. There were115 fallow deer and 165 axis deer in total on the ranch. They compared the sexes of each species against each other. Contact displacements were assumed to be high energy and non-contact, low energy. They found that there was no difference in the number of interspecific displacements over the year, but the number of displacements did

vary dependant upon season, correlated for males with the percentage of individuals in hard antler and for females with seasonal differences in aggression. McGhee and Baccus (2006) argue that this fits with theoretical models where individuals assess value of the food patch and the probability of injury (Enquist & Leimar, 1983) causing rank to fluctuate temporarily if there are offset breeding seasons between species. Antler size also drove intraspecific dominance suggesting that, in the two species of similar sizes, fighting ability, regardless of species, was most important. McGhee and Baccus (2006) also found that non-contact displacements were much more common than contact displacements and that both species showed more intraspecific than interspecific agonistic behaviour.

In a study in a park in the Czech Republic containing 100 red deer (Cervus elaphus) and 130 fallow deer (Darna darna), Bartos et al. (1996) reported that red deer arrived first at supplementary food patches of oats and barley, whilst fallow deer actually delayed their approach, finding spaces in which to forage, possibly as a tactic to reduce the red deer's motivation to fight. However, on arrival at the patch, fallow males attacked all competitors. Although these attacks were not severe, they still resulted in most red deer leaving the patch before food was depleted. Fallow females however, would not join a patch unless competition levels were low.

Supporting the findings of McGhee and Baccus (2006) in their study of axis and fallow deer, Bartos et al. (1996) found there was also variation in food access based upon season. Male red deer visited patches less often after casting their antlers, and when they did attend, rarely displayed aggression against hard-antlered fallow males possibly due to a loss of the ability to defend their food patch or lower levels of sex hormones.

Other research into non-intraspecific dominance in ungulates comes from interbreed hierarchies of livestock around supplementary feed which can have a major effect on production. Landaeta-Hernández et al. (2005) found that Senepol cows were dominant over both Angus and Brahman cows at supplementary feeding patches and suggested genetic and environmental components may be the cause. Senepol are a cross-

breed coming partly from N'Dama cattle which display a remarkable competitiveness for resources and social dominance resulting from 'the extensive and sometimes feral conditions' under which they are produced.

3.6 Distribution of Food and its Relationship to Dominance in Captive Animal Groups

Much of the research into the effects of changing feeding patterns to help alleviate the problems of dominance hierarchies have been carried out on primates, and do not consider interspecific interactions (Gore, 1993). Work by Saito (1996) has shown that greater numbers and sizes of patches and can decrease the effects of rank-related feeding behaviour in Japanese macaques (*Macaca Fuscata)* and this is supported by studies on captive red-capped mangabeys (*Cercocebus torquatus torquatus*) and grey-cheeked mangabeys (*Lophocebus albigena*) (Blois-Heulin & Martinez-Cruz, 2005), Rhesus macaques (*Macaca mulatto)* (Brennan & Anderson, 1988), and away from the primate world, in ruddy turnstones (*Arenaria interpres*) (Vahl et al., 2005). However, this relationship appears not always to have the same relative effect. A study on female vervets (*Chlorocebus aethiops*) by Pruetz and Isbell (2000) showed there were actually increased levels of aggression and more prominent dominance hierarchies in larger food patches. The authors attributed this to the spatial distribution of patches, the larger patches being found in *A.xanthophloea* woodland, where food was spatially clumped compared with the small, more randomly distributed patches in *Acacia drepanolobium* habitat. Mathy and Isbell (2001) go on to suggest that although both patch size and inter-patch distance can have a major influence on dominance, resource depletion time is much more significant in rhesus macaques (*Macaca mulatta*) and renewal rate can also have an important influence.

3.7 A History of Deer Management at ZSL Whipsnade Zoo

Sir Stamford Raffles founded The Zoological Society of London (ZSL) in 1826 to work towards conserving animals and their habitats worldwide (ZSL, 2008). After a visit to the Bronx Zoological Park in New York, the then secretary, Sir Peter Chalmers Mitchell set about creating a wild conservation estate in the countryside (Britishzoos,

2008). In 1926 six hundred acres of farmland on the Dunstable downs near Whipsnade, Bedfordshire, was bought and renovated and stocked by the society, eventually opening to the public on 23rd May 1931 (Britishzoos, 2008).

ZSL Whipsnade Zoo housed deer from its inception, and references of Reeve's muntjac, red deer, and 'graceful Indian deer' were noted in a report by Webb (1931) published in Nature about the zoo's opening. These 'graceful Indian deer' were probably axis deer (*Axis axis*) and fallow deer (*Dama dama*) which were reported in the book 'The Whipsnade Zoo and its Inmates' (Berridge, 1932).

3.8 The Natural History of Deer Housed at ZSL Whipsnade Zoo

<u>Fallow deer</u> (*Dama dama*) range from 84-94 cm at shoulder height and weigh between 49-94 kg for males and from 73-91 cm at shoulder height, and weigh 35-56 kg for females (The British Deer Society, 2008). Males have broad, flattened antlers which can grow to around 70 cm in length (The British Deer Society, 2008). Fallow deer have been introduced into Europe, the Americas, Australia, New Zealand, and Southern Africa for farming, deer parks, and game (Mattiello et al., 1997). The species is listed as Least Concern (IUCN 2007). Fallow can live in open woodland, forest and pasture and generally stay in small, single-sex herds (The British Deer Society, 2008). Sexual segregation and group size vary with habitat (The British Deer Society, 2008). They are active throughout the 24-hour period, peak foraging occurs at dawn and dusk (The British Deer Society, 2008).

<u>Sika deer</u> (*Cervus nippon*) range from 70-95 cm at shoulder and weigh 40-70 kg for males and from 50-90 cm at shoulder and weigh 30-45 kg for females (The British Deer Society, 2008). The males have narrow antlers with less than eight points which can grow up to 28-81 cm in length (Huffman, 2004). They naturally range from Japan and Korea to northern Russia and south eastern China and have been introduced into Europe, North America, and New Zealand (see Huynh et al., 1998). Sika are listed as Least Concern (IUCN 2007). Sika deer live in a wide range of habitats from marshes and swamps to woodlands and agricultural fields (see Huynh et al., 1998). They live in mixed groups of 5–30 animals (see Huynh et al., 1998), but in spring and summer, females and fawns break away, the males often becoming solitary or living in small groups (The

British Deer Society, 2008). They are generally more active at night but do feed throughout the 24-hour period (The British Deer Society, 2008).

Swamp deer (*Cervus duvaucelii*), also known as barasinga deer, are the largest deer in the paddock at around 119-135 cm shoulder height weigh from between 130-145 kg for females and 170-280 kg for males (see Qureshi et al., 2004). The antlers have at least twelve points and can reach one meter long and (see Qureshi et al., 2004). They were once found throughout the North India and Bangladesh but their range has dramatically decreased with estimates of around 5,000 remaining, mostly in Protected Areas (see Maskey et al., 1998). The biggest losses were during 1930's to 1960's due to agricultural encroachment, reclamation of wetlands, grass and timber cutting and unregulated hunting (see Maskey et al., 1998; see Qureshi et al., 2004). They are currently listed as Vulnerable (IUCN 2007). Swamp deer prefer flooded tall grassland but can also live in open forests. Groups of more than twenty individuals are now rarely seen and males are often solitary outside the breeding season (see Maskey et al., 1998). Swamp deer graze during both day and night (see Qureshi et al., 2004).

Axis deer (*Axis axis*) grow up to 90 cm at the shoulder and males weigh about 85 kg (see Sankar & Acharya, 2004). Females are slightly smaller. Antlers have up to three points and can grow to 100 cm long. They are widely found in India, Sri Lanka, Nepal and Bangladesh (see Sankar & Acharya, 2004) and are listed as Least Concern (IUCN 2007). They can live in deciduous woodland, thorn and mangrove forests and plain grassland. Groups can be up to 150 or more individuals (see Sankar & Acharya, 2004) but are generally single-sex outside the rut (see Sankar & Acharya, 2004). Peak feeding times are around dawn and dusk.

Hog deer (*Axis porcinus*) are the smallest deer in the paddock at about 65-75 cm to the shoulder weighing 35-45 kg for males and 60-65 cm at the shoulder and 30-40 kg for females (see Biswas, 2004). Antlers typically have three points and grow from 30 to 45 cm long. The species ranges from Pakistan to as far east as Laos (see Biswas, 2004). They are classed as Near Threatened (IUCN 2007). Hog deer prefer tall grassland, scrub, and cultivated landscapes near forest and wetland (see Biswas, 2004). Hog deer are generally solitary or are found in pairs although groups of around 40-60 have been observed (see Ahsan et al., 1998).

4. Methods

4.1 Study Subjects and Management

The mixed species deer group at ZSL Whipsnade Zoo is in the 'Passage Through Asia' Exhibit. This exhibit comprises 25 swamp deer (*Cervus duvaucelii*) (3 male, 22 female), 63 axis deer (*Axis axis*) (17 male, 46 female), 43 sika deer (*Cervus nippon*) (8 male, 35 female), 70 fallow deer (*Dama dama*) (21 male, 49 female), and 17 hog deer (*Axis porcinus*) (13 male, 4 female). Pelleted food (Monarch Deer Feed, Badminton Feeds ©) is provided to supplement the paddock grass diet in spring, autumn and winter. In the summer, the grass is deemed sufficient to meet the deer's dietary requirements. The pellet diet contains 16.4% crude protein, 4 % oil, 12.5 % fibre and has supplementary vitamin A (10000 iu/kg), vitamin D3 (2000 iu/kg), vitamin E (15 iu/kg) and copper (30 mg/kg).

There was seasonal asymmetry in breeding cycle between deer species at ZSL Whipsnade Zoo. Towards the end of the study period the first births were seen in swamp, hog and fallow deer. The males of these species had recently cast their antlers whilst the male sika deer were casting their antlers during the early-middle of the study period. The axis deer at Whipsnade show seasonal asymmetry within the species. Some males were shedding velvet whilst others were in the early stages of antler development. A few axis deer females also gave birth towards the end of the study period.

4.2 Feeding Methods

The study was carried out from 10th May to 19th June 2008, and the feeding method used on each day was randomised to avoid day to day biases in weather conditions and grass length. There were nine trials of the traditional pellet feeding method, seven trials where pellet was provided in evenly-sized patches, six trials where patch size decreased with presentation order, and eight trials patch size increased with presentation order; details of these feeding treatments are provided below. The planned number of trials for each method was nine but the experiment had to be cut short due to a cull of male axis deer which was brought forward to a day within the study period.

For the purposes of this study, the population of the mixed species group was split up into eight hypothetical catagories: male fallow, female fallow, male sika, female sika, male axis, female axis, hog deer, and swamp deer. Both sexes of hog deer were grouped together, as were both sexes of swamp deer, due to the low total numbers in these two species. Interactions within sexes, and within species in the cases of hog and swamp deer were not studied in this investigation. From here onwards, these categories will be known as 'groups'

Supplementary feeding

For all supplementary feeding methods, the deer were provided with four 25 kg bags each morning at 8:30am in the feeding area (Area 'A', Appendix 1). For an estimation of the amount of food that each group was consuming, the number of deer with their heads down feeding at the supplementary feed was counted. All deer attended the supplementary feeding session and so from this an estimation of the percentage of each group feeding could be made. Aggressive interactions were also recorded, with the group of the winner and loser recorded. However, as shown by Bartos et al. (2002) with a study of deer in open pasture, there were very few aggressive displacements and this data, although useful in explaining other results, was insufficient to allow meaningful analysis. It is attached as Appendix 2. The supplementary pellets lasted no longer than one hour in any of the trials.

4.2.a. Traditional Supplementary Feeding Method

The traditional feeding method used at ZSL Whipsnade Zoo involved spreading pellets in one long line, approximately 25-30 metres long. The keepers were asked to attempt to adhere to this length as closely as possible so as to minimise this variation between trials. Viewed from an elevated position (Area 'B', Appendix 1) using binoculars, the number of individuals of each group with their heads down foraging at the food patch was recorded one minute after the food patch was put out and every two and a half minutes thereafter. The interval of two and a half minutes was used due to the high number of deer foraging, especially in the first twenty minutes after food was put out, and

this was the period of time that it took to record accurately all individuals during the pilot study.

4.2.b. Modified Spatial Distribution of Supplementary Food

To study the effect of increasing the spatial distribution of food, pellets were placed out in four large patches of even sizes (one 25 kg bag of pellets each) approximately 30 metres apart in four corners of a hypothetical square. Keepers would aim to make each clump approximately 15 m^2 and spread the food out evenly within these spaces. Data was collected separately for each clump to maintain a high level of accuracy. The first count was done one minute after the first clump was put out and by the time data was collected for the first clump, the second clump will have been out for a minute and so on for clumps three and four.

4.2.c. Modified Patch Size Presentation Order of Supplementary Food

To investigate the effect of patch size presentation order, the food was provided in four uneven patches of 43 %, 31 %, 19 %, and 7 % of the total supplementary pellet quantity. These percentages were used as they decrease by 12 % on a continuous scale, and were easy for the keepers to distribute with 43 % being one bag plus just over two thirds of a second bag; 31 % being one bag plus just under one third of a second; 19 % being just over two thirds of a bag, and 7 % being just under one third of a bag. One method comprised putting out the biggest patch first, next biggest second, decreasing down to the smallest clump last; the other method required the smallest patch to be presented first, with patch size increasing there on. All clumps were provided within two and a half minutes.

4.3. Daily Foraging Behaviour

Foraging activity throughout the day, on paddock grass was studied by recording the number of each group with and without their heads down foraging. This was recorded every thirty minutes from 10 am (an hour and a half after the start of supplementary feeding), using binoculars from a car drive through the paddock. This is assumed to give a good estimation of daily foraging in deer. In this case it was important that the number

of individuals not foraging was also recorded, as only approximately 95 % of the paddock could be seen from the road; the deer that were hidden were assumed, possibly inaccurately, to be not feeding. Deer within the mixed species paddock were generally well habituated but at times were disturbed, generally by members of the public leaning out of windows to take pictures. Deer that were disturbed before their activity was judged were discarded from the study for that particular data point. In the pilot study it was noted that disturbed animals were unlikely to go back to their pre-disturbed activity directly after the disturbance so simply waiting a few minutes and recollecting the data would have been inaccurate. However, data would be collected from these individuals half an hour later at the next collection time as it would have been impossible to re-identify accurately the disturbed individual/s.

4.4. Data Analysis

All data analyses were carried out using R version 2.7.1 (R Development Core Team 2008).

Generalized linear models (GLMS), corrected for overdispersion by using a quasibinomial error structure, were used to analyse the mean percentage of each group with their heads down eating for each feeding method. The data was analysed as a whole over the entire feeding period. Analysing all of the data over the whole feeding period gave an indication of the mean percentage of each group that was feeding when food was available. If there were individuals of any species feeding then that would indicate that there were supplementary pellets still available so these data points would be included when calculating this mean. There was very little difference between the average durations of food availability between methods so this should not significantly influence the comparisons between treatments. To work out the intricacies of the hierarchies with the existing 'Line' feeding method, the time was also broken down into time quartiles of; one to five minutes together (Quartile 1), seven and a half to twelve and half minutes together (Quartile 2), fifteen to twenty minutes together (Quartile 3), and finally, all of the remaining scans together (Quartile 4). Analysing each quartile separately allows more inferences into dominance hierarchy rather than total access to food. For example, some

groups may be dominant at the start and get the most food and leave after a certain period of time when they deem the patches to no longer be valuable enough to be feeding at, whereas other groups may stay for longer at the end searching for and eating remaining pellets. To gain a better understanding of changes in the proportion of each group feeding over time, mixed effects models (LMERs) with a quasibinomial error structure, with 'day' and 'time' both included as random effects due to pseudo-replication, were used to generate and compare the gradients of slopes. The 'male fallow deer' group was chosen as a suitable intercept with which to compare all other groups as initial examination of the data suggested that the percentage of deer feeding decreased over time at a rate that was around the median of all groups.

The effect of different feeding methods on each group independently was assessed overall, and again in quartiles using similar GLM analyses this time comparing each of the novel feeding methods to the traditional 'Line' feeding method used at ZSL Whipsnade Zoo.

The effect of different feeding methods on the mean percentage of deer foraging throughout the rest of the day was assessed using GLMs, again with quasibinomial error structures. The R^2 of all models are reported in Appendix 3.

5. Results

Results will be presented in the following order. First, results for the traditional feeding method followed by the effects of modified spatial distribution of supplemental food and modified presentation order of different sized patches. Finally, results of daily foraging patterns will be presented for each species/sex class of deer separately.

To increase readability throughout this section, feeding methods will be known as:

"Line" – When pellets were placed out in one long line (traditional method).

"Even" – When pellets were presented in four evenly sized clumps.
"BtS" – When pellets were presented in clumps of decreasing size (Biggest to Smallest).
"StB" – When pellets were presented in clumps of increasing size (Smallest to Biggest).

5.1 Supplementary Feeding

5.1.a. Traditional Supplementary Feeding Method

Quartile 1 (One to five minutes following food presentation)

Female fallow and swamp deer had the lowest mean percentage of groups feeding in the first quartile with no significant difference between them (Table 1. $P = 0.133$). All of the other groups had significantly higher means than female fallow deer in the first quartile (Table 1. male fallow, $P = 0.002$; female axis $P < 0.005$; male axis, $P < 0.005$; hog, $P = 0.007$; female sika, $P < 0.005$; male sika, $P < 0.005$) with both male and female axis, male fallow and hog deer all with similar means (Table 1) and female and male sika with the greatest means (Table 1).

Quartile 2 (Seven and a half to twelve and a half minutes following food presentation)

The mean percentage of fallow females and swamp deer increased slightly and there was still no significant difference between the two (Table 1. $P = 0.11$). A decrease in hog deer feeding meant that it was no longer significantly higher than female fallow in quartile 2 (Table 1. Figure 1. $P = 0.27$). The mean percentage of both sexes of axis deer feeding decreased by approximately half in the second quartile with the mean of the female axis now significantly lower than the female fallow deer (Table 1. Figure 1. $P = 0.02$) and now no significant difference between the male axis and the female fallow deer (Table 1. $P = 0.47$). Male fallow showed the greatest increase in mean percentage of all groups to now have the second highest mean in quartile two, staying significantly greater than female fallow (Table 1. Figure 1. $P < 0 .005$). The mean percentages of both male and female sika feeding decreased slightly but remained significantly higher than the mean of female fallow deer (Table 1. Both: $P < 0.005$).

Group	Quartile 1 Mean	Quartile 2 Mean	Quartile 3 Mean	Quartile 4 Mean	Overall Mean	Slope
Fallow Female	26.00	29.78	15.80	2.51	14.04	-0.2457
Fallow Male	46.21	52.56	27.34	4.35	24.70	-0.2947
Axis Female	43.16	20.45	1.77	0.06	11.80	-0.5161
Axis Male	49.02	25.71	5.66	0.26	14.59	-0.4714
Sika Female	56.51	49.10	28.57	4.76	26.34	-0.3298
Sika Male	67.59	64.81	46.76	16.85	40.00	-0.2792
Swamp	22.98	26.32	15.94	2.28	12.79	-0.2360
Hog	44.30	36.15	24.25	11.15	23.97	-0.2152

Table 1. Mean percentage of each group feeding during the supplementary feeding session when the food was placed out in a singular long line (traditional supplementary feeding method). The slope column is an estimated gradient of changes in the mean percentage feeding with time over the whole feeding period.

Quartile 3 (Fifteen to twenty minutes following food presentation)

The mean percentage of both sexes of axis deer feeding again dramatically dropped, now both significantly lower than female fallow deer (Table 1. Figure 1. Male, $P = 0.01$; female, $P < 0.005$), the mean of which also decreased but to a lesser extent (Table 1). The decrease in the mean of female fallows feeding was matched by swamp deer (no significant difference, see Table 1. Figure 1. $P = 0.46$). Hog deer did not decrease as sharply as female fallow between quartiles two and three but remained significantly not different (Table 1. Figure 1. $P = 0.13$). The mean percentages of male fallow, and both male and female sika feeding had all decreased but were still significantly greater than the mean percentage of female fallow feeding (Table 1. $P = 0.01$; $P < 0.005$; $P < 0.005$ respectively). The mean percentage of male sika feeding was still clearly the highest (Table 1.).

Quartile 4 (Twenty two and a half minutes onwards following food presentation)

In the final quartile only two groups, male sika, and hog deer had means of over 5 % (Table 1.). These two groups, along with female sika and male fallow, were all significantly higher than female fallow deer (Table 1. $P < 0.005$; $P < 0.005$, $P = 0.01$; $P = 0.06$ respectively). The mean of female fallow deer was still very similar to the swamp

deer mean (Table 1. $P = 0.17$). Both sexes of axis deer were rarely seen feeding in the final quartile, both with means significantly lower than that of the female fallow deer (Table 1. Male, $P = 0.03$; female, $P < 0.005$).

Overall

      Male sika had the highest mean percentage of individuals feeding when the whole feeding period was taken into account and in every quartile (Table 1.). Three other groups, male fallow, female sika and hog deer, had similar means beneath this (Table 1). All four of the species had significantly higher means than female fallow deer (Table 1. All: $P < 0.005$). Hog deer had the shallowest slope gradient over time during the feeding period whereas female and male sika, and male fallow had similar gradients (Table 1 & Figure 1).

      Overall, there was no significant difference between the mean percentage of female fallow and the mean percentages of male and female axis deer feeding (Table 1. $P = 0.82$; $P = 0.18$ respectively) although both axis sexes had significantly steeper gradients over time (Table 1. Figure 1, both: $P < 0.005$). Swamp deer had a significantly lower overall mean percentage of their group feeding than female fallow deer (Table 1. $P = 0.05$) due to lower means, although insignificant separately, for swamp deer in the first two quartiles but there was no significant difference between slopes (Table 1, Figure 1, $P = 0.55$).

5.1.b. Modified Spatial Distribution of Supplementary Food

Structure of overall access

      The male sika had the highest overall mean percentage feeding when the whole feeding period was taken into account (Table 2) followed by male fallow (both significantly higher than female fallow, both: $P < 0.005$). There was no significant difference between the female fallow mean and the means of female sika (Table 2. $P = 0.11$) and hog deer (Table 2. $P = 0.9$) or male axis deer (Table 2, $P = 0.56$). Swamp deer and female axis deer both had a lower overall mean than female fallow deer (Table 2. Swamp = $P < 0.005$; female fallow = $P = 0.14$).

26

Line Data
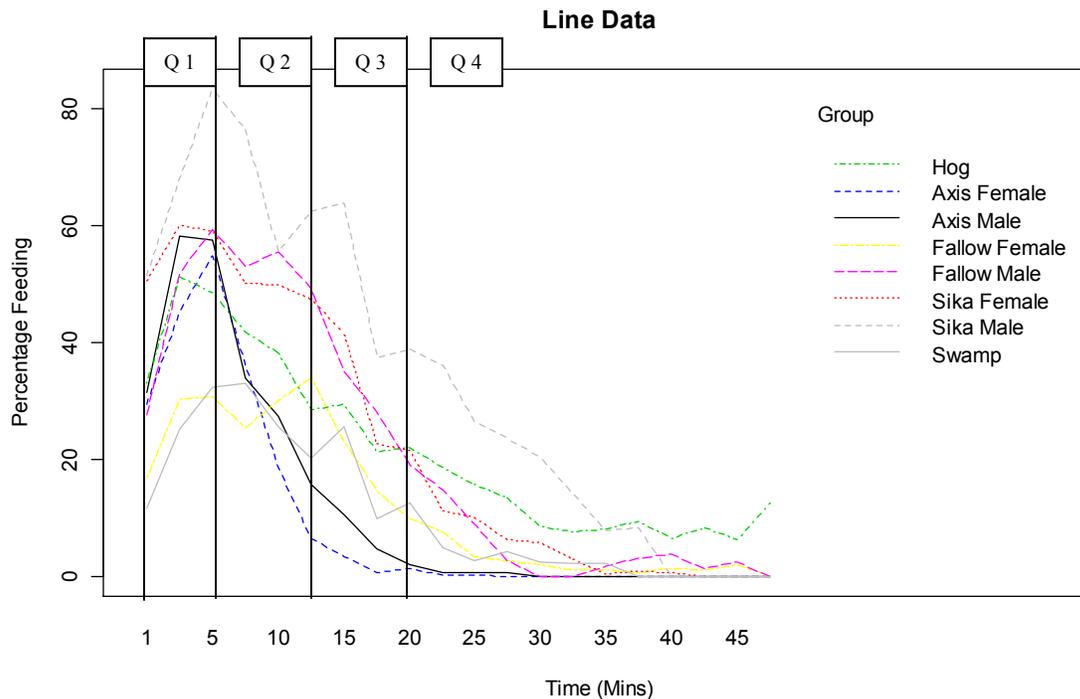
Figure 1. Changes in the mean percentage feeding over time for each group when the food was placed out in a singular long line (traditional feeding treatment). The vertical lines are approximate representations of the boundaries of each quartile. "Q1" is the mean percentage from one minute to five minutes after the food was put out, 'Q2' is 7½ to 12½ minutes, 'Q3' is 15 to 20 minutes and 'Q4' is 22½ minutes onwards.

Inter-group Comparisons Between 'Line' and 'Even' Methods

Altering the spatial distribution of supplementary pellets from the traditional 'line' method to four spaced out evenly sized patches did not have a significant difference on the mean percentage of any of the groups feeding when food was available (Table 2. Female fallow, $P = 0.12$; male fallow, $P = 0.09$; female axis, $P = 0.70$; male axis $P = 0.59$; female sika, $P = 0.20$; male sika, $P = 0.81$; hog, $P = 0.99$; swamp, $P = 0.10$). However, when the data was broken down into different periods of time (quartiles) some groups did show differences between methods. In the first quartile male sika deer had a higher mean percentage of their group with their heads down feeding when the food was distributed into four, spaced-out, evenly sized patches instead of the traditional 'line' method (Table

27

2. Figure 2. $P = 0.01$). Hog deer had a significantly lower mean percentage of the group feeding in this first quartile with this method (Table 2. Figure 2. $P = 0.01$). In the second quartile, female sika had a lower mean percentage of their group feeding when the 'Even' method was used (Table 2. Figure 2. $P = 0.02$). Swamp deer also had a lower mean percentage in the second quartile (Table 2. Figure 2. $P = 0.02$) but a higher mean percentage in the forth quartile (Table 2. Figure 2. $P = 0.04$) when the 'Even' method was used instead of traditional 'Line' method. Male fallow deer had a greater mean percentage feeding in the third and forth quartiles when food was distributed in four even clumps (Table 2. Figure 2. Q3, $P < 0.005$; Q4, $P < 0.005$) and, although marginally insignificant, female fallow deer also had a higher mean percentage of the group feeding in the fourth quartile with this novel method (Table 2. Figure 2. $P = 0.07$). There were no significant differences between methods in any of the quartiles for male axis (Table 2. Figure 2) or female axis deer (Table 2. Figure 2).

Group	Feeding Method	Quartile 1 Mean	Quartile 2 Mean	Quartile 3 Mean	Quartile 4 Mean	Overall Mean
Female fallow	Line	26.00	29.78	15.80	2.51	14.04
Female fallow	Even	27.60	35.57	24.30	4.99	18.00
Male fallow	Line	46.21	52.56	27.34	4.35	24.70
Male fallow	Even	46.49	47.17	43.76	11.46	29.96
Female axis	Line	43.16	20.45	1.77	0.06	11.80
Female axis	Even	46.58	23.81	1.76	0.00	12.95
Male axis	Line	49.02	25.71	5.66	0.26	14.59
Male axis	Even	61.34	24.37	5.04	0.00	16.29
Female sika	Line	56.51	49.10	28.57	4.76	26.34
Female sika	Even	49.25	32.65	23.81	6.24	21.86
Male sika	Line	67.59	64.81	46.76	16.85	40.00
Male sika	Even	87.50	63.10	35.12	16.67	41.03
Hog	Line	44.30	36.15	24.25	11.15	23.97
Hog	Even	27.38	34.16	27.88	12.62	21.88
Swamp	Line	22.98	26.32	15.94	2.28	12.79
Swamp	Even	14.94	11.65	9.05	9.12	10.61

Table 2. Mean percentage of each group feeding during the supplementary feeding session when the food was placed four evenly sized clumps and in a line. The overall mean percentage of deer with their heads down when food was available is shown in the 'Overall Mean' column. 'Quartile 1' is the mean percentage from one minute to five minutes after the food was put out, 'Quartile 2' is 7½ to 12½ minutes, 'Quartile 3' is 15 to 20 minutes and 'Quartile 4' is 22½ minutes onwards.
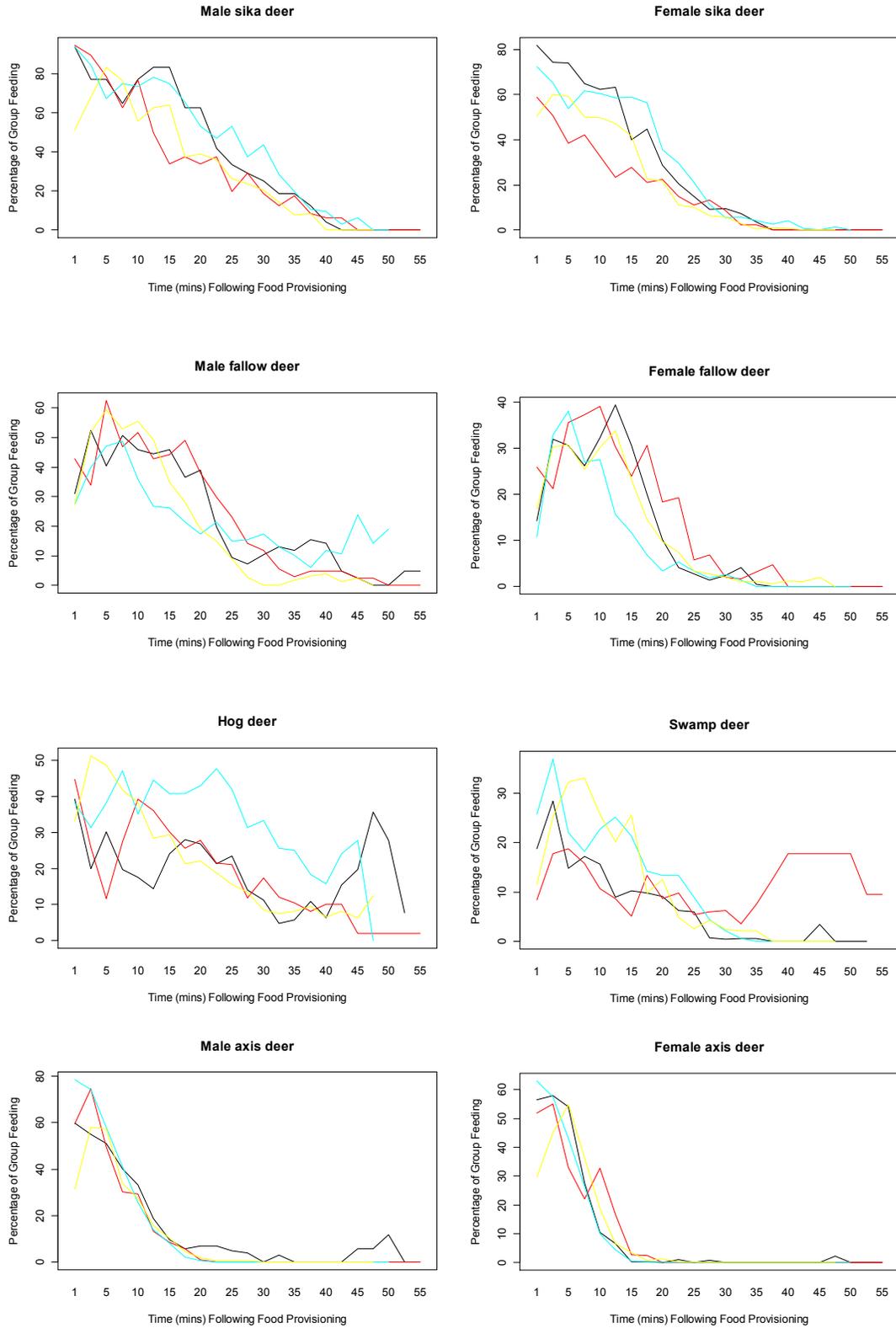
Figure 2. Changes in the mean percentage of each group feeding over time when the food was placed out with the four different feeding methods (Blue = 'Line', Red = 'Even', Black = 'BtS', Blue = 'StB').

To give an indication of how these relationships affect the interplay of groups over time, the changes in the mean percentage of groups feeding over time with four even clumps are graphically depicted together in Figure 3.
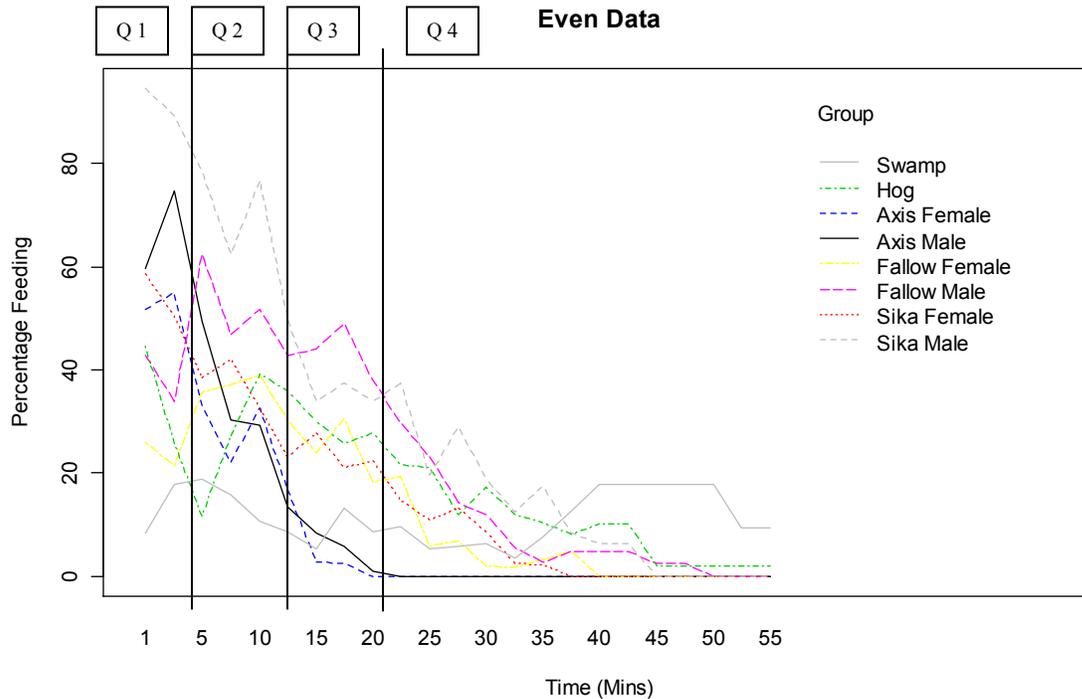
Figure 3. Changes in the mean percentage feeding over time for each group when the food was placed out in four evenly sized clumps. The vertical lines are approximate representations of the boundaries of each quartile. "Q1" is the mean percentage from one minute to five minutes after the food was put out, 'Q2' is 7½ to 12½ minutes, 'Q3' is 15 to 20 minutes and 'Q4' is 22½ minutes onwards.

5.1.c. Modified Patch Size Presentation Order of Supplementary Food
5.1.c.i. Decreasing Patch Sizes ('BtS')

Structure of overall access

Male sika had the greatest overall mean percentage feeding, followed by female sika and male fallow (Table 3), all of which were significantly greater than female fallow deer (Table 3. All: $P < 0.005$). Hog deer had the next highest mean which was again, higher than female fallow (Table 3. $P = 0.02$). Neither sexes of axis deer had significantly

different overall mean percentages feeding to female fallow (Table 3. Male, $P = 0.29$; female, $P = 0.34$). Swamp deer had the lowest overall mean which was significantly lower than female fallow (Table 3. $P < 0.005$).

Group	Feeding Method	Quartile 1 Mean	Quartile 2 Mean	Quartile 3 Mean	Quartile 4 Mean	Overall Mean
Female fallow	Line	26.00	29.78	15.80	2.51	14.04
Female fallow	BtS	25.62	32.65	20.29	1.74	14.81
Male fallow	Line	46.21	52.56	27.34	4.35	24.70
Male fallow	BtS	41.27	47.09	40.48	10.84	28.01
Female axis	Line	43.16	20.45	1.77	0.06	11.80
Female axis	BtS	56.16	14.86	0.24	0.28	12.83
Male axis	Line	49.02	25.71	5.66	0.26	14.59
Male axis	BtS	55.23	30.72	7.52	2.88	18.00
Female sika	Line	56.51	49.10	28.57	4.76	26.34
Female sika	BtS	76.67	63.49	37.78	7.78	35.33
Male sika	Line	67.59	64.81	46.76	16.85	40.00
Male sika	BtS	82.64	75.00	69.44	21.01	50.25
Hog	Line	44.30	36.15	24.25	11.15	23.97
Hog	BtS	29.75	17.25	26.28	14.32	19.73
Swamp	Line	22.98	26.32	15.94	2.28	12.79
Swamp	BtS	20.62	13.93	9.72	1.95	8.80

Table 3. Mean percentage of each group feeding during the supplementary feeding session when the food was placed in a line and in four patches of decreasing size in order of presentation (BtS). The overall mean percentage of deer with their heads down when food was available is shown in the 'Overall Mean' column. 'Quartile 1' is the mean percentage from one minute to five minutes after the food was put out, 'Quartile 2' is 7½ to 12½ minutes, 'Quartile 3' is 15 to 20 minutes and 'Quartile 4' is 22½ minutes onwards.

Inter-group Comparisons Between 'Line' and 'BtS' Methods

Changing the feeding method from the traditional 'Line' method to a method where four patches were presented in an order from largest to smallest in terms of total food proportion ('BtS'), did not have a significant difference on the mean percentage of the group feeding of either male or female axis, male or female fallow, or hog deer when food was available (Table 3. Male axis, $P = 0.28$; female axis, $P = 0.71$; male fallow, $P = 0.27$; female fallow, $P = 0.72$; hog, $P = 0.47$). However, the total mean percentage

feeding was higher for the male sika (Table 3. Figure 2. $P = 0.02$) and female sika (Table 3. Figure 2. $P = 0.02$) groups when the 'BtS' method was used whilst the mean percentage of the swamp group feeding was significantly lower using this new feeding method (Table 3. Figure 2. $P = 0.02$). The differences between methods for the female sika deer were mostly a result of significantly higher mean percentages feeding in the first (Table 3. Figure 2. $P = 0.01$) and second (Table 3. Figure 2. $P = 0.05$) quartiles while the difference between methods for male sika are largely caused by a significantly higher mean percentage of the group feeding in quartile three (Table 3. Figure 2. $P = 0.01$). Swamp deer had lower mean percentages feeding in quartiles two (Table 3. Figure 2. $P = 0.02$) and three (Table 3. Figure 2. $P = 0.05$).

Although the other groups displayed no overall significant differences between these two methods, there were some differences seen when the data was broken down in time quartiles. The mean percentage of hog deer feeding was significantly less with the BtS method compared with the line method in the first quartile (Table 3. Figure 2. $P = 0.05$) but later was significantly greater in the final quartile (Table 3. Figure 2. $P < 0.005$). A higher percentage of male fallow deer were feeding with the 'BtS' method than the 'Line' method in the third quartile (Table 3. Figure 2. $P = 0.02$) and the fourth (Table 3. Figure 2. $P < 0.005$) quartiles. Both female and male axis deer had significantly higher mean percentages of their groups feeding with the 'BtS' method than the line method in the final quartile (Table 3. Figure 2. Female axis, $P = 0.03$; male axis, $P < 0.005$).

Again, to give an indication of how these relationships affect the interplay of groups over time, the changes in the mean percentage of groups feeding over time when fed with the 'BtS' method are graphically depicted together in Figure 4.

5.1.c.ii. Increasing Patch Sizes ('StB')

Structure of overall access

There was no significant difference in the mean percentage of female fallow deer feeding compared with swamp deer (Table 4. $P = 0.10$) or female axis deer (Table 4. $P = $

0.55). The overall means for male axis deer and male fallow deer were significantly higher than the female fallow (Table 4. Both: $P < 0.005$). Male sika deer had the greatest overall mean percentage of individuals feeding and the percentages of hog deer and female sika were joint second highest, all significantly higher than female fallow deer (Table 4. All: $P < 0.005$).
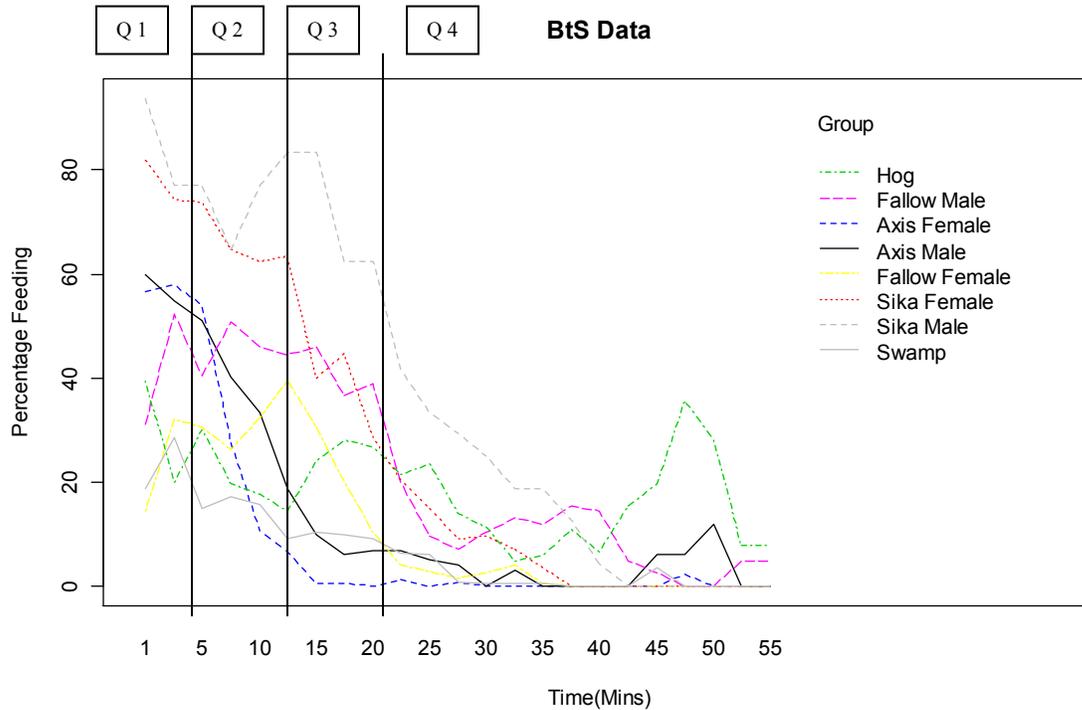
Figure 4. Changes in the mean percentage feeding over time for each group when the food was placed out in four clumps of decreasing size in order of presentation. The vertical lines are approximate representations of the boundaries of each quartile. "Q1" is the mean percentage from one minute to five minutes after the food was put out, 'Q2' is 7½ to 12½ minutes, 'Q3' is 15 to 20 minutes and 'Q4' is 22½ minutes onwards.

Inter-group Comparisons Between 'Line' and 'StB' Methods

Changing the feeding method from the traditional 'Line' method to a method where clumps were presented in an order from smallest to largest in terms of total food proportion (StB) did not have a significant difference on the mean percentage of female fallow (Table 4. $P = 0.22$), male fallow (Table 4. $P = 0.90$), female axis (Table 4. $P =$

0.84), male axis (Table 4. $P = 0.24$) nor swamp deer (Table 4. $P = 0.16$) feeding. However this new 'StB' method did increase the mean percentages of female sika (Table 4. Figure 2. $P = 0.006$), male sika (Table 4. Figure 2. $P < 0.005$) and hog deer (Table 4. Figure 2. $P < 0.005$) feeding. The overall differences seen by female and male sika deer were largely a product of significant differences in the third (Table 4. Figure 2. Female sika, $P < 0.005$; male sika, $P = 0.03$) and fourth quartiles (Table 4. Figure 2. Female sika, $P = 0.007$; male sika, $P < 0.005$). The overall difference in the mean percentage of hog deer feeding between methods originated from differences in quartiles three (Table 4. Figure 2. $P < 0.005$) and four (Table 4. Figure 2. $P < 0.005$).

Group	Feeding Method	Quartile 1 Mean	Quartile 2 Mean	Quartile 3 Mean	Quartile 4 Mean	Overall Mean
Female fallow	Line	26.00	29.78	15.80	2.51	14.04
Female fallow	StB	27.21	23.38	7.31	1.71	10.82
Male fallow	Line	46.21	52.56	27.34	4.35	24.70
Male fallow	StB	38.10	37.10	21.63	14.36	23.64
Female axis	Line	43.16	20.45	1.77	0.06	11.80
Female axis	StB	54.53	13.59	0.36	0.00	11.82
Male axis	Line	49.02	25.71	5.66	0.26	14.59
Male axis	StB	70.34	26.96	3.68	0.00	17.44
Female sika	Line	56.51	49.10	28.57	4.76	26.34
Female sika	StB	63.81	60.24	50.36	9.68	34.78
Male sika	Line	67.59	64.81	46.76	16.85	40.00
Male sika	StB	81.77	75.52	64.58	28.73	52.16
Hog	Line	44.30	36.15	24.25	11.15	23.97
Hog	StB	35.90	42.23	41.55	28.65	34.47
Swamp	Line	22.98	26.32	15.94	2.28	12.79
Swamp	StB	28.19	22.00	16.29	3.51	13.17

Table 4. Mean percentage of each group feeding during the supplementary feeding session when the food was placed in a line and in four patches of increasing size in order of presentation (StB). The overall mean percentage of deer with their heads down when food was available is shown in the 'Overall Mean' column. 'Quartile 1' is the mean percentage from one minute to five minutes after the food was put out, 'Quartile 2' is 7½ to 12½ minutes, 'Quartile 3' is 15 to 20 minutes and 'Quartile 4' is 22½ minutes onwards.

Of the groups that had no overall significant difference between methods, there were some differences when the data was broken down into time quartiles. Male axis deer performed significantly better with the 'StB' method than the 'Line' method in the

first quartile (Table 4. Figure 2. $P = 0.006$). In the second quartile, the mean percentage of swamp deer feeding was significantly lower when the StB method was used (Table 4. Figure 2. $P = 0.04$.). Male fallow deer had lower percentages feeding in the second quartile (Table 4. Figure 2. $P = 0.016$.) but were significantly higher in the final quartile (Table 4. Figure 2. $P < 0.005$) with the 'StB' method. In the third quartile the mean percentage of female fallow deer feeding was significantly lower with the 'StB' method (Table 4. Figure 2. $P = 0.05$).

As before, to give an indication of how these relationships affect the interplay of groups over time, the changes in the mean percentage of groups feeding over time when fed with the 'StB' method are graphically depicted together in Figure 5.

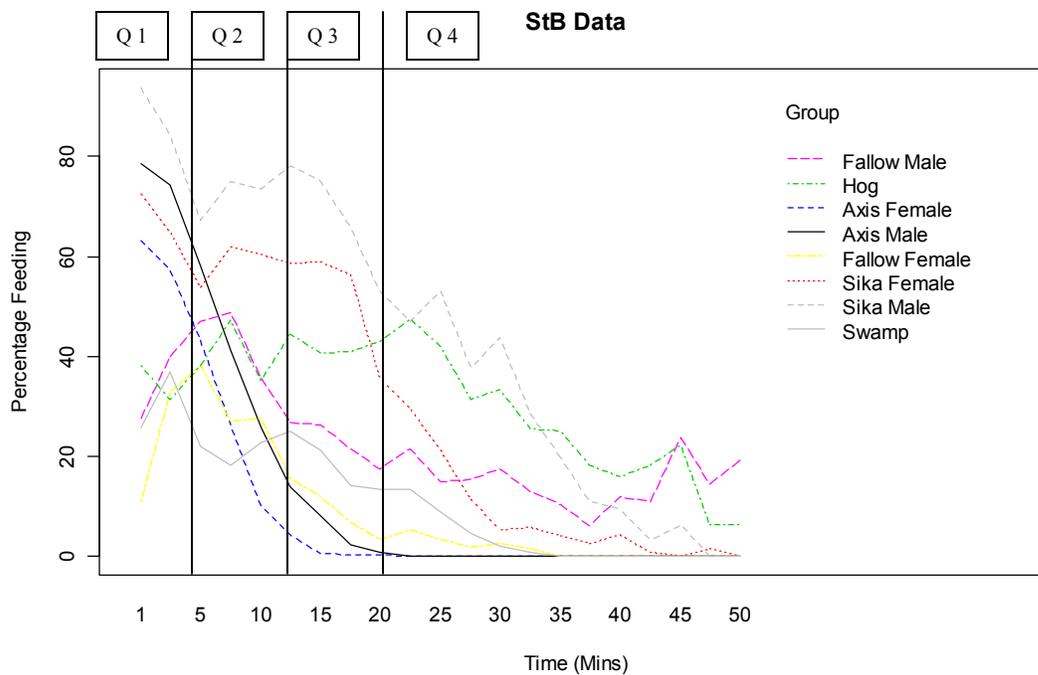Figure 5. Changes in the mean percentage feeding over time for each group when the food was placed out in four clumps of increasing size in order of presentation. The vertical lines are approximate representations of the boundaries of each quartile. "Q1" is the mean percentage from one minute to five minutes after the food was put out, 'Q2' is 7½ to 12½ minutes, 'Q3' is 15 to 20 minutes and 'Q4' is 22½ minutes onwards.

5.2. Daily Foraging

Female fallow deer

The mean percentage of female fallow deer with their heads down foraging on grass throughout the day was not significantly different between when the 'Line' method and the 'Even' and 'BtS' methods were used (Figure 6a. Line mean = 42.4 %; Even, mean = 52.8 %, P = 0.08; BtS, mean = 46.0 %, P = 0.48). Daily foraging activity was however significantly higher when the StB method was used instead of the line method (Figure 6a. mean = 0.53 %, P = 0.02).

Male fallow deer

There was no significant difference in the mean percentage of deer foraging throughout the day between the 'Line' method and the 'Even' and 'BtS' methods (Figure 6b. Line mean = 45.4 %; Even mean = 50.3 %, P = 0.25; BtS mean = 46.7 %, P = 0.77). There was however a significantly higher percentage foraging after the 'StB' method was used (Figure 6b. StB mean = 53.4 %, P = 0.05).
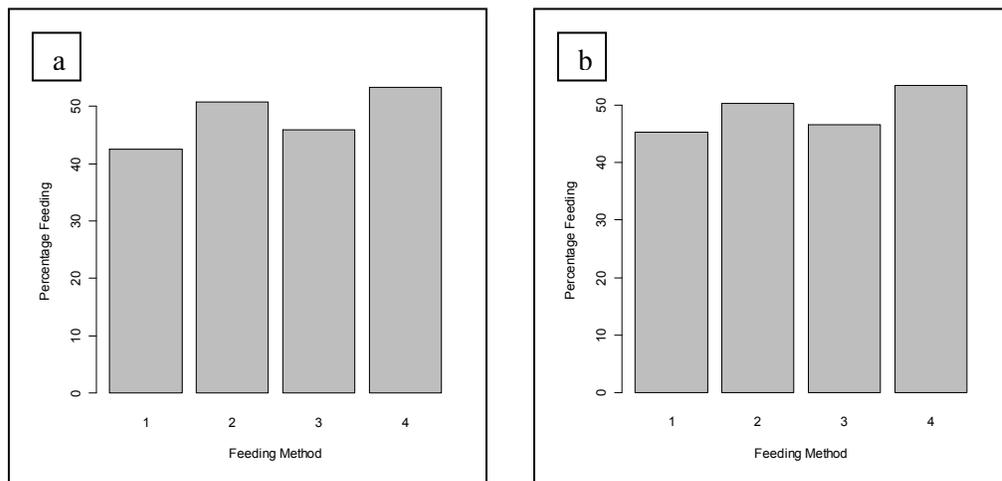

Figure 6a&b. The mean percentage of female fallow deer (a) and male fallow deer (b) feeding throughout the day after being given supplementary pellets with the four different feeding methods. Feeding method 1 is the 'Line' method, 2 is the evenly sized clump method, 3 is the decreasing sized clump method (BtS) and 4 is the increasing size clump method (StB).

Female axis deer

There was no significant difference in daily foraging levels between the 'Line' method and the 'StB' and 'BtS' methods (Figure 7a. Line mean = 26.5 %; BtS mean = 29.9 %, P = 0.39; StB mean = 27.0 %; P = 0.87). After the 'Even' method was used, the mean percentage feeding was significantly higher than when the 'Line' method was used (Figure 7a. Even mean = 34.8 %, P = 0.03).

Male axis deer

There were no significant difference in the mean percentage of the group foraging on grass after the 'Line' method and 'StB' and 'BtS' were used (Figure 7b. Line mean = 28.8 %; BtS mean = 32.2 %, P = 0.45; StB mean = 31.2 %; P = 0.57). The mean percentage feeding was significantly higher however after the 'Even' method than the 'Line' method. (Figure 7b. Even mean = 38.5 %, P = 0.03)

Figure 7a&b. The mean percentage of female axis deer (a) and male axis deer (b) feeding throughout the day after being given supplementary pellets with the four different feeding methods. Feeding method 1 is the 'Line' method, 2 is the evenly sized clump method, 3 is the decreasing sized clump method (BtS) and 4 is the increasing size clump method (StB).

Female sika deer

There was no significant difference in the mean percentage of deer foraging between the 'Line' method and any of the novel treatments (Figure 8a. Line mean = 31.4

%; Even mean = 33.3 %, *P* = 0.68; BtS mean = 29.9 %, *P* = 0.72; StB, mean = 25.2 %, *P* = 0.12).

Male sika deer

There was no significant difference in the mean percentage of deer foraging between the 'Line' method and any of the novel treatments (Figure 8b. Line mean = 32.4 %; Even mean = 33.1 %, *P* = 0.88; BtS mean = 25.4 %, *P* = 0.19; StB, mean = 25.4 %, *P* = 0.15).
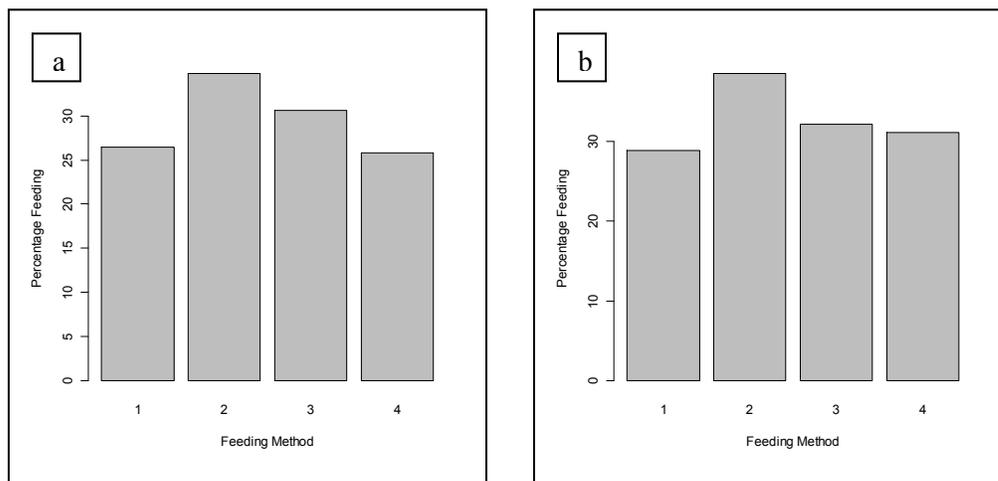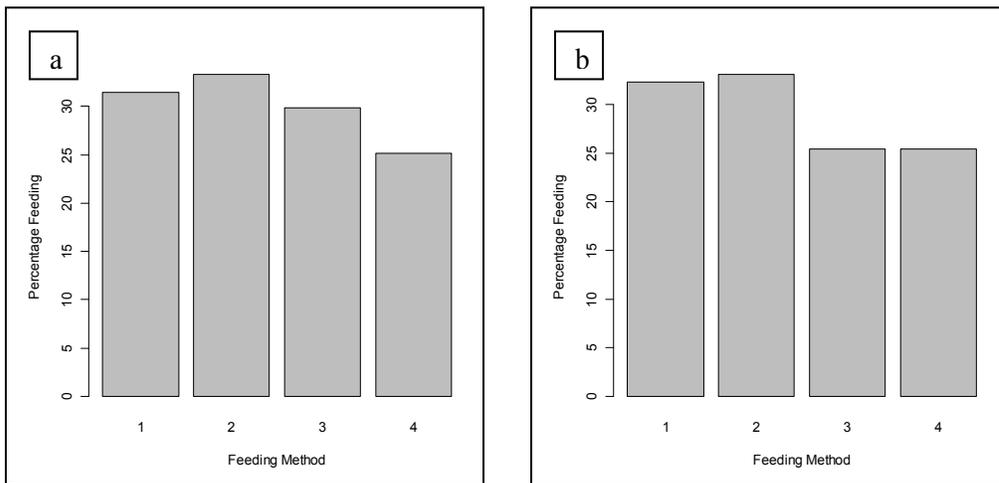

Figure 8a&b. The mean percentage of female sika deer (a) and male sika deer (b) feeding throughout the day after being given supplementary pellets with the four different feeding methods. Feeding method 1 is the 'Line' method, 2 is the evenly sized clump method, 3 is the decreasing sized clump method (BtS) and 4 is the increasing size clump method (StB).

Hog deer

There was no significant difference in the mean percentage of deer foraging between the line method and any of the novel treatments (Figure 9. Line mean = 41.9 %; Even mean = 40.5 %, *P* = 0.59; BtS mean = 39.0 %, *P* = 0.13; StB, mean = 37.7 %, *P* = 0.15).

Swamp deer

There was a significantly greater percentage of swamp deer grazing throughout the day when the supplementary pellets were put out using the 'Even' and 'BtS' methods

compared to the 'Line' method (Figure 10. Line, mean = 45.2 %; Even, mean = 53.7 %, $P = 0.04$; BtS, mean = 54.4 %, $P = 0.03$). There was no significant difference between the 'Line' and the 'StB' methods (Figure 10. StB, mean = 38.9 %, $P = 0.18$).

Figure 9. The mean percentage of hog deer feeding throughout the day after being given supplementary pellets with the four different feeding methods. Feeding method 1 is the 'Line' method, 2 is the evenly sized clump method, 3 is the decreasing sized clump method (BtS) and 4 is the increasing size clump method (StB).
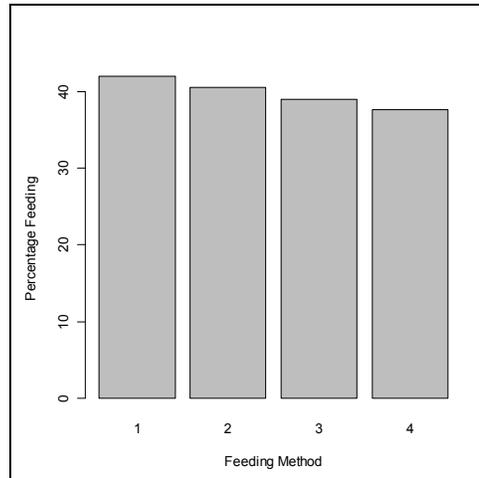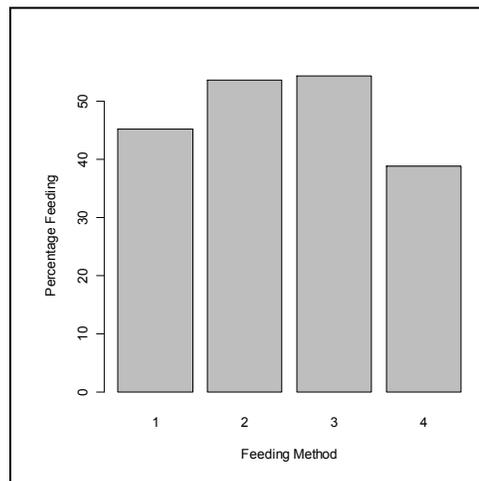

Figure 10. The mean percentage of swamp deer feeding throughout the day after being given supplementary pellets with the four different feeding methods. Feeding method 1 is the 'Line' method, 2 is the evenly sized clump method, 3 is the decreasing sized clump method (BtS) and 4 is the increasing size clump method (StB).

For the interest of managers, a graph depicting the changes in foraging levels throughout the day for each species is included as Appendix 4.

6. Discussion

6.1. Traditional Feeding Method

When multiple species of ungulates are kept together, and competition around feeding is high, it is expected that dominance hierarchies will develop creating differential access to this food (McGhee & Baccus, 2006). At ZSL Whipsnade, the mixed deer group are traditionally fed supplementary pellets in a line about 25-30 metres long. The percentage of deer with their heads down feeding at the supplementary feeding site was recorded for each species every two and a half minutes as an estimate of food access. There were high enough numbers of fallow deer, sika deer and axis deer to break down these species into sex for a more in-depth analysis.

6.1.a. The Dominance Hierarchy and Links to Pellet Access

Both sexes of sika deer had the highest proportions all the groups feeding during the first five minutes after the pellets were put out, with the males remaining the most successful group in every quartile and the females remaining in the top three groups. As a consequence, the male sika group had the highest overall access to the supplementary pellets and the female sika group were second. This certainly suggests a high degree of interspecific dominance which is supported by the fact that sika deer were involved in 14 of all 16 interspecific exchanges and came out on top in each contest (Appendix 2).

High proportions of both sexes of axis deer feeding were observed in the first five minutes but were coupled with the most rapid decreases of any of the groups feeding, resulting in a low overall pellet access. This could be the sign of strongly competitive groups with low demands for supplementary feed, possibly related to the seasonally high

availability of forage during the study period. Similar studies when food is scarcer in winter may give better insights into this. It could also be due to displacement. Male fallow deer were equally competitive as axis deer directly after the food was put out but did not have such sharp declines over time. In fact their level of drop off was slow enough for their overall access to be at a similar level to the female sika group. The fact that the percentage of the group feeding was higher in the second five minutes than the first five suggests that they could be in part responsible for the axis exodus. Male fallow deer have been seen to delay their approach to feeding sites when they are in direct competition with red deer in an attempt to reduce the red deer's motivation to fight, later displacing the red deer with aggressive encounters (Bartos et al., 1996). However, it is unlikely that the male fallow displaced the axis as there were no competitive interactions between the groups (Appendix 2) and they both coexisted and fed well during the first five minutes. The increase observed is more likely to be the result of the increased space provided by the voluntarily exiting axis deer. Female fallow deer were one of the most poorly competitive groups directly after the food was presented but, as with the male fallow group, numbers feeding increased as axis deer started to leave. Further observations by Bartos et al. (1996) found that female fallow deer would only join food patches when competition levels were low, which supports the idea that the increase is dependant upon opportunism rather than competitive interference.

Hog deer competed well during early stages with numbers decreasing at the slowest rate over time of all groups. Swamp deer had the significantly lowest access to food overall and did not compete well during the early stages suggesting that they have the lowest position in the interspecific hierarchy.

It seems that, at this time of the year, the effects on food access of a group's position in the hierarchy are of different levels of importance for different species. Sika, the most dominant species, are benefiting, gaining the highest overall access, whilst swamp deer, the weakest competitors, are suffering, having the lowest overall proportions feeding. However, neither sex of axis deer seem to have a high demand for food and have low overall access despite a high competitive ability directly after food is put out. Both

41

sexes of fallow deer seem to benefit as a result and the females, especially, have higher levels of overall access than their early competitive performance suggests. Hog deer seem to be able to compete well and have an ability to maintain high levels of feeding as the food patch is depleted, which results in a high overall access to food.

6.1.b. Mechanisms of Dominance

Body Size

Bassett (1995) and Shelley et al. (2004) have found evidence that a larger body size can affect a species' position within dominance hierarchies. However, there is not a great deal of size difference between sika, axis and fallow deer despite differential competitive abilities and the largest species, swamp deer, is the lowest ranking species whilst the smallest species, hog deer, compete well. Hog deer, in fact, may be assisted by their smaller body size, with Thomas and Markusa (1996) arguing that larger animals tend to accept and do not dominate smaller animals, citing the combination of bongos (*Tragelaphus eurycerus isaaci*) and yellow-backed duikers (*Cephalophus sylvicultor*) as an example of this.

Group Size

Larger group sizes have been seen to aid competitive ability at food patches in ungulates (Clutton-Brock el al., 1982; Risenhoover & Bailey 1985). With the exception of hog deer, which were often solitary or in small groups, the sexes within each species generally formed their own groups. Cohesion between sexes within each species varied, but axis deer appeared to maintain a singular multi-sex herd throughout (*personal observation*). This may help explain their high competitive abilities during early stages. Fallow deer have been seen to gain increased food access as a function of large group sizes when competing against red deer (Bartos et al., 1996; Bartos et al., 2002) and at Whipsnade, both male and female fallow deer have the largest of all the sex specific groups. However, they display a greater degree of sexual segregation than axis deer (*personal observation*) and so this may not give them direct advantages over axis deer; however, both species probably gained advantages from their larger group size relative to

the swamp deer group, which had the smallest group size of all species. Both sika sexes had the smallest sex specific groups suggesting that their high competitive abilities are derived in other ways.

Tactics and Aggression

Some studies suggest that natural selection can cause genetic variability for aggressiveness (see Maynard Smith & Harper, 1988). Studies on cows have suggested that varying levels of natural aggression, a function of evolutionary environment, can play an important role in dominance between breeds (Landaeta-Hernández et al., 2005).

Sika deer have small group sizes in the wild, with some males even solitary (The British Deer Society, 2008) which suggests that they may have evolved mechanisms, such as aggression, to help them compete over high value patches. As sika deer are involved in, and win, the majority of interspecific encounters, this may be the case. The actual levels of aggression may not even be truly represented by this interaction data as Enquist and Leimar (1987) state that levels of aggression can be subdued when competition is relatively low and, Mosley (1999) suggested that species of ungulates which have been held together for long periods of time, as is the case at ZSL Whipsnade Zoo, form stable structures of dominance hierarchy as a mechanism to avoid high levels of aggressive encounters.

Swamp deer are naturally found in small groups in tall natural grassland (see Maskey et al., 1998). When this is compared with fallow deer for example, which have spent the last thousand years kept in unnaturally high numbers for hunting purposes in Europe (Mattiello et al., 1997), it is easy to see how swamp deer may not have evolved the same levels of competitive aggression. Swamp deer are more likely to be dependant upon tactically finding and exploiting gaps left by dominant deer as the resource value decreases, which is supported by the low levels of decline in numbers over time. Hog deer also seem to use tactics to increase their food access. A study by Schmidt & Hoi (1999) on red deer stags reported that smaller individuals can be 'sneaky' and find gaps between individuals at supplementary feeding sites. The smaller body size and increased

tolerance from larger species may help them to be more effective at this tactic than the swamp deer.

<u>Sex</u>

Overall there seemed to be a generally higher competitive ability for males in every group where it was testable. This was to be expected and was similarly observed by Mattiello et al. (1997) with fallow deer (*Dama dama*) and Barrette and Vandal (1986) in caribou (*Rangifer tarandus*).

<u>Seasonality</u>

McGhee and Baccus (2006) showed that the seasonal differences in competitive ability between axis and fallow deer were largely a result of asymmetries in breeding cycles. Around half of the male axis deer were shedding velvet during the study period whilst fallow deer had already cast before the start of data collection. This may have offered the male axis deer an advantage over male fallow deer but, as females also competed well, it was unlikely to have a major influence. Sika deer cast their antlers only a few weeks later than fallow deer and so this is again unlikely to be a major factor in differences between these groups. It is unlikely that there would have been seasonally-related hormonal differences between species during this period.

6.2 Altering Feeding methods

6.2.a. Increasing Number of Patches

Increasing the number of feeding sites has been shown to decrease biases in access to food caused by dominance hierarchies (Blois-Heulin & Martinez-Cruz, 2005; Bowman & Sowell, 1997). However, changing food distribution from a single line to four evenly-sized patches, approximately 30 metres apart, did not have the effect on feeding access between deer groups as predicted. The groups that gained highest overall access in the line feeding method continued to do so when the number of patches was increased and no groups had significantly different mean percentages of their groups feeding between the two methods. In fact, the group highest up the dominance hierarchy, male

sika actually did better in the earliest stages, whilst the lowest ranking group, swamp deer, do even worse at the start when the number of patches available is increased.

Much of the theory behind the effectiveness of this method in mitigating the effects of interspecific dominance in food access between species is based upon groups staying together, thereby leaving other food patches for subordinate groups (Thomas & Maruska, 1996; Bowman & Sowell, 1997). This seems true for both sexes of the fallow and axis groups as their competitive abilities seem partly reliant upon their high group size. However, if a species is highly dominant, and this dominance is not derived from a high group size, then it may pay to move away from the strong competition within that group to weaker competition in other groups (Milinski & Parker, 1991), This seemed to be the case with male sika deer, thus suggesting that this important assumption is violated by a key species. This then spreads out competition instead of leaving patches more open to subordinate groups. In fact, the average number of interactions per trial went from two for the traditional treatment, to 3.4 for the even patches (Appendix 2).

Interestingly female fallow deer, the other most poorly competitive group during early stages with the traditional 'Line' method, did not suffer in the same respect as the swamp deer group. This is probably a by product of the fragmentation of male sika deer, creating fewer gaps, on which the poorly competitive swamp deer seem dependant. Female fallow deer however, seem to be using their large group size and higher natural aggression to try and create gaps instead of having to wait for them to appear Within the 'Line' and the 'Even' method female fallow were involved in 14 interactions compared to just five involving swamp deer, and although they always loose, it suggests that they are at least attempting to compete.

Hog deer suffered directly after the food was put out in this new method compared to the traditional 'Line' method. If, as predicted earlier, they do use 'sneaky' tactics to get food, this could be reliant upon the gaps in food access being close together so they are easy to find and require low energy to access. Patch transfer to find gaps

45

would thus decrease foraging opportunity (Mathy & Isbell, 2001), especially at these early stages.

A very interesting observation from this data is the feeding performance of deer towards the end of the feeding period. Swamp deer, the least competitive group overall, had a significantly higher mean percentage feeding in the final quartile when food was put out in patches, as did female fallow, the second poorest competitor early on. As patches become depleted they lose value and so are less important to defend. If all of the remaining food is in one area however, only a few individuals that may not have achieved a high access earlier can restrict access for subordinates whilst more dominant individuals are needed for the same level of control when the food is spatially distributed. Despite this late surge from these subordinate groups, it was not enough to compensate for lack of feeding opportunities early on the make this new method beneficial overall.

6.2.b. Effects of Patch Size Presentation Order

When food is presented in multiple patches, it stands to reason that the first patch of food will be taken by the most dominant group as it is the only patch available at that point in time. This was observed during pilot studies at Whipsnade. Therefore, it was hypothesised that changing the proportional value of these early patches may serve to alter access for groups in different positions of the dominance hierarchy. Larger patches first would favour dominant groups as they could control and restrict access whilst smaller patches first, as long as depletion rates, interpatch distances (see Krebs & Kacelnik, 1991) and the costs of competitive displacements are high (see Enquist & Leimar, 1983), may favour subordinate groups.

6.2.b.i. Decreasing Patch Sizes

As expected, the structure of overall access to food between groups remained similar to the structure seen when food was presented with the traditional 'Line' feeding method and the most dominant groups, male and female sika, had significantly higher

mean percentages feeding overall. Much of the benefit for males was found in the late middle sections suggesting that they are monopolising the first, larger patch as predicted and reaping the rewards of a high value patch whilst other patches are becoming depleted. This increase is directly correlated in time with a lower percentage of the least competitive group, swamp deer, feeding which would be expected due to the fewer gaps available to exploit. However, female fallow deer, the other weakest group, do not suffer so much, possibly again due to their more active approach in gaining access which is supported by the percentage of interactions involving female fallow deer increasing from 19 % (7 of 36) in the 'Line' method to 34 % (11 of 32) in this novel 'BtS' method (Appendix 2).

6.2.b.ii. Increasing Patch Sizes

Contrary to predictions, there was very little difference in the order of overall access to food between groups when this new method was used. Male sika again had the highest overall mean percentage feeding, and the predicted increase in access for the female fallow and swamp deer groups, which seem to be the poorest competitors, was not achieved.

Both male and female sika deer increased their overall feeding levels, with both sexes generally doing better in the latter stages when compared to the 'Line' method. This implies that when the first, smaller patch was depleted, they moved to other patches and became dominant over other deer there. However, in the first five minutes there were a greater number of interactions involving sika deer with this method than in the 'Line' method (Appendix 2). This suggests that the transfer from the first patch occurred early on, and, again, the male sika group probably dispersed. Interactions were generally simple displacements instead of energetically expensive, antagonistic encounters and so the low energy cost and risk of serious injury would not act as a deterrent against moving to other patches when presented. It is also clear that the distance between patches was not great enough to be an impediment for movement between patches.

Accordingly, the swamp deer group and the female fallow group had lower percentages feeding in the mid-sections, the time when the poorer groups should have been benefiting most.

6.3 Effects of Supplementary Feeding Method on Daily Foraging

If the proportion of a group accessing supplementary food can be significantly increased by a certain feeding method then there may be subsequent effects on daily foraging (see Putman & Staines, 2004). However, the low occurrence of large-scale differences in access to supplementary pellets between methods for many of the groups makes this difficult to assess.

Both male and female sika deer gained significantly higher overall access in the 'StB' an 'BtS' feeding methods but this did not amount to differences in the proportions of each group foraging throughout the day. Both fallow sexes had higher daily foraging when the 'StB' method was used but there was no difference overall in pellet access for either species. Male fallow had a higher overall access to supplementary pellets with the 'Even' and 'BtS' methods but this showed no knock-on effect to daily foraging and there were no significant differences in hog daily foraging between the 'Line' and the other methods despite a significantly higher overall mean percentage feeding on supplementary pellets with the 'StB' method. Both sexes of axis deer had higher mean daily foraging after the 'Even' method was used instead of the 'Line' method but there were no differences in pellet access in any quartile, let alone overall.

The lack of any relationship in these species suggests that the degree of change created by the novel feeding methods was not great enough to exact different daily foraging levels. With the axis deer, this would be expected as they left the feeding site early with each method and so presumably ate their optimum amount. There was however one important link between pellet access and daily foraging. The swamp deer had a significantly lower percentage feeding over the supplementary feeding period with the 'BtS' method which translated to a significantly higher mean percentage foraging

throughout the day. This might be because smaller gross gains are relatively higher net gains for a species with low access.

6.4 Conclusions, Management Recommendations and Future Research

There is clearly differential access to supplementary pellets amongst species, and sexes within those species, in the mixed deer paddock at ZSL Whipsnade Zoo. Sika deer seemed dominant and showed higher levels of aggression than other species. Axis deer also competed well early on but the numbers feeding decreased rapidly implying that they have a low food demand at this time of the year. There appears to be a high difference in competitive abilities between sexes of fallow deer. Although male fallow competed well early on, the female fallow group did not, and seemed to be dependant upon spaces created by exiting axis deer. Members of the hog deer group generally foraged independently, and slotted into gaps between species seemingly tolerated by dominant groups. This resulted in a high access to the pellets, which also continued later on in the supplementary feeding bout. Swamp deer are apparently the species which should cause most concern for management. They were the least competitive group and got the lowest overall access to the supplementary pellets of all groups. It seemed that their low levels of aggression and a small group size, with very few males, hinders their competitive ability.

These findings are of course just a snapshot in time. Dominance hierarchies may be subject to seasonal changes due to asymmetries in breeding systems and differing levels of competition. Increasing competition later on in the year is likely to impact swamp deer to an even greater degree, and, if axis stay at the feeding site for longer when the supplementary feed has a greater relative value then this could also heavily impact upon female fallow deer which were seen to benefit when the axis left. It would be important to study if the increased pellet allocation in the winter is great enough to prevent this. The deer are also given hay later on in the year, which depletes at a slower rate and as a result creates lower levels of competition. It would be interesting to know if

these more poorly competitive groups are more reliant upon this type of supplementary food.

Mitigating the effects of the dominance hierarchy on access to food is not a straight forward task. Increasing the number of food patches did not have the desired effect. This seemed partly to do with the break up of the male sika group but it is also likely that, due to the large numbers of groups and the competitive strength of both axis sexes and male fallow deer, as well as the sika groups, four patches would not have been enough to bring about the sort of change that was predicted.

Producing smaller patches first did not help to mitigate effects either. Seemingly, the patches were too close to deter dominant groups from moving to patches of higher value or breaking up to dominate different patches. It is recommended that the distance between patches should be increased to make it more energetically viable to stay in one place and keep members of the male sika group together. As depletion rates of pellets are high, and the deer paddock at Whipsnade is large, I believe this could have a great influence on increasing access for subordinate groups as long as it was practical for keepers to implement. Observing which groups go to which patches on the basis of presentation order would then allow the proportional food quantity of each patch to be adjusted as necessary to best serve the needs of each group.

The success of novel methods should be judged upon increases in access for the weakest competitive, swamp deer and female fallow groups. It is unlikely that changes in feeding methods would be greatly detrimental to the dominant groups, However, the feeding performance of hog deer should be monitored as they seem to suffer a little directly after the food was put out in separate patches due to having to travel further to find gaps in which to forage. However, they do show a strong ability to feed later into the feeding session and so changes in methods would probably not have a great impact.

The effects on daily foraging are still unclear. Small changes in pellet access may have an impact upon the foraging of lower ranking deer but due to the low levels of

changes in access between methods, conclusions are difficult to draw. If small decreases in pellet access result in increases of daily foraging levels for poorly competitive species, as this data suggest is the case with swamp deer, this stresses the importance of altering feeding methods to ensure that subordinate species are not suffering as a result. This is especially important for the swamp deer group at Whipsnade, due to the threatened conservation status of the species; low levels of food access can affect fitness of individuals, which is particularly undesirable within a threatened species. The evidence from this study suggests that the idea that other animals can become 'bored' or lethargic with increased access may be discounted as all species spent a significant proportion of their days foraging and increasing food access did not seem to affect this. If recommendations are followed and result in greater changes in access then further studies would give greater insights into this.

It is clear from this study that dominance hierarchies between multiple species are complex and it is not always obvious how they will affect access to supplementary food. Effective management is important in zoos, especially in captive breeding programmes of threatened species where the maintenance of optimum fitness is vital and the implications of management failure can be severe. It species of ungulates are kept together in mixed species exhibits, close attention should be paid to interspecific dominance, and its subsequent effects on food access.

6.5. Study Limitations

The scope for wide scale changes to feeding methods was limited by there being only one observer and by the practical constraints of management at the zoo. If food were to be put out in more patches, more observers would have been needed to record that data accurately and any request to the keepers to make wide-scale differences to management based purely on unproven hypotheses would probably have been resisted. The power of the data would have been improved by a greater number of trials.

The percentage of the groups with their heads down feeding was used as an estimation of pellet access but different species can have different bite rates (Vankova et al., 1999) which will affect actual food intake. Studying this would make an interesting addition to the project. It must also be remembered that due to the low numbers, both sexes were grouped together in the data for hog and swamp deer groups but were compared directly with data for separate sexes of other species and so the insights gained for these species are more limited. The percentage of each group made up of yearlings might also affect competitive ability and it was assumed that this percentage was similar throughout groups. However, neither this assumption, nor the difference between adults and yearlings in terms of food access were quantified.

The low differences in changes to foraging restricted the inferences that could be made from the daily foraging data and assumptions were made that foraging levels would be accurately represented from 10:00 am to 5:00 pm. As dusk and dawn are thought to be the most important foraging periods for most deer, extending the hour of the study period would test this, but this was impossible due to restrictions on access after closing time at ZSL Whipsnade Zoo.

7. Acknowledgements

8. References

Ahsan, M.F., Huynh, D.H., Khien, H.M., Duc, T.V. & Qureshi, O. (1998) Hog Deer (Axis porcinus). In: Wemmer, C. (ed.) Deer: Status Survey and Conservation Action Plan. Gland, IUCN

Appleby, M.C. (1980) Social rank and food access in red deer stags. *Behaviour*, 74, 294-309

Barrette, C. & Vandal, D. (1986) Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour*, 97, 118-145

Barroso, F.G., Alados, C.L. & Boza, J. (2000) Social hierarchy in the domestic goat: effect on food habits and production. *Applied Animal Behaviour Science* 69, 35–53

Bartos, L., Vankova, D., Miller, K.V. & Siler, J. (2002) Interspecific competition between whitetailed, fallow, red and roe deer: a comparison of time spent grazing on an open pasture. *Journal of Wildlife Management.* 66, 522–527.

Bartos, L., Vankova, D., Siler, J. & Losos, S. (1996) Fallow deer tactic to compete with red deer over food. *Aggressive behaviour*. 22, 375-385

Basset, A. (1995) Body size-related coexistence: an approach through allometric constraints on homerange use. *Ecology.* 76, 1027–1035.

Beck, B.B., Rapaport, L.G., Stanley-Price, M.R. & Wilson A.C. (1994) Re-introduction of captive born animals. In: P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds). Creative conservation: interactive management of wild and captive animals. London, Chapman & Hall

Berridge W.S. (1932) The Whipsnade Zoo and its Inmates. London. A & C Black

Berteaux, D., Crête, M., Huot, J., Maltais, J. & Ouellet, J.-P. (1998) Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment *Oecologia.* 115, 84-92

Biswas, T. (2004) Hog Deer. In: Ungulates of India. Wildlife Institute of India [Online] available from: http://www.wii.gov.in/envis/ungulatesofindia/assam_2.htm [Accessed 13th June 2008]

Blois-Heulin, C. & Martinez-Cruz, B. (2005) Influence of food dispersion on feeding activity and social interactions in captive *Lophocebus albigena* and *Cercocebus torquatus torquatus*. *Primates*. 46, 77–90

Bowman, J.G. & Sowell, B.F. (1997) Delivery method and supplement consumption by grazing ruminants: a review. *Journal of Animal Science*. 75, 543-550.

Brennan, J. & Anderson, J.R. (1988) Varying Responses to Feeding Competition in a Group of Rhesus Monkeys (Macaca mulatta). *Primates.* 29(3), 353-360

British Zoos (no author) [Online] Available from: http://www.britishzoos.co.uk/whipsnade/ visited 27/08/08 [Accessed 12th August 2008]

Cassinello, J. (2002) Food access in captive *Ammotragus*: the role played by hierarchy and mother-infant interactions. *Zoo Biology.* 21 (6), 597 – 605

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology.* 9, 129-136.

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

Dittrich, L. (1976) Food presentation in relation to behaviour in ungulates. *International Zoo Yearbook.* 2 (1), 288-299

Drews, C. (1993) The concept and definition of dominance in animal behavior. *Behaviour* 125, 283–313.

Enquist, M. & Leimar, O. (1983) Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology* 102, 387–410.

Enquist, M. & Leimar, O. (1987) Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology.* 127, 187-205.

Gore, M.A. (1993) Effects of food distribution on foraging competition in rhesus monkeys (*Macaca mulatto*) and hamadryas baboons (*Papio hamadryas*). *Animal Behaviour.* 45, 773-786.

Hamilton, W.D. (1971) Geometry for the Selfish Herd. *Journal of theoretical biology.* 31, 295-311

Hanley, T.A. (1997) A nutritional view of understanding and complexity in the problem of diet selection by deer (*Cervidae*). *Oikos.* 79 (2) 209-218

Harcourt, A.H. (1999) The behavior–conservation interface. *Trends in Ecology and Evolution.* 14 (12), 490

Heymann, E.W. & Buchanan-Smith, H.M. (2000) The behavioural ecology of mixed-species troops of *callitrichine* primates. *Biological Review*, 75, 169–190.

Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M.E., Røed, K.H., Nieminen, M. & Weladji1, R.B. (2004) Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *Journal of Zoology*. 263, 365–372

Huffman, B. (2004) [Online] Available from: www.ultimateungulate.com [Accessed 18th July 2008]

Huynh, D.H., Duc, T.V., Khien, H.M., Helin, S., Endi, Z. & Izawa, M. (1998) Sika deer *Cervus nippon*. In: Wemmer, C. (ed). Deer: Status Survey and Conservation Action Plan. Gland. IUCN

ISIS - International Species Information System (2008) Species Holdings [Online] Available from: http://app.isis.org/abstracts/abs.asp [Accessed 26th August 2008]

IUCN (2007) 2007 IUCN Red List of Threatened Species. [Online] Available from: www.iucnredlist.org. [Accessed 28th August 2008].

Kleiman, D.G. (1994) Animal behaviour studies and zoo propagation programs. *Zoo Biology* 13, 411-412

Krebs, J.R., & Kacelnik, A. (1991) Decision making. In Krebs, J., & Davies, N. (eds.), Behavioural ecology. 3rd edition. Oxford. Blackwell Scientific Publishers.

Landaeta-Hernández, A.J., Chenoweth, P.J., Randles, R., Littell, R., Rae, O & Chase, C.C. (2005) Identifying the social dominance order in a mixed breed herd: A practical methodology *Revista Científica*. 15 (2), 148-154,

Latham, J. (1999) Interspecific interactions of ungulates in European forests: an overview. *Forest Ecology and Management*, 120 (1-3), 13-21

Lomnicki A. (1988) Population ecology of individuals. Princeton. Princeton University Press.

Lyles A.M. & May, R.B. (1987) Problems in leaving the ark. *Nature* 326, 245-246

Milinski, M. & Parker, G.A. (1991) Competition for resources. In Krebs, J., & Davies, N. (eds.), Behavioural ecology. 3rd edition. Oxford. Blackwell Scientific Publishers.

Maskey, T.M., Schaaf, C.D., Singh, A. & Qureshi, Q. (1998) Swamp deer or barasingha *Cervus duvauceli*. In: Wemmer, C. (ed). Deer: Status Survey and Conservation Action Plan. Gland. IUCN

Mathy, J.W. & Isbell, L.A. (2001) The relative importance of size of food and interfood distance in eliciting aggression in captive rhesus macaques (*Macaca mulatta*) *Folia Primatol* 72, 268-277

Mattiello, S., Mattiangeli, V., Bianchi,L. & Carenzi, C. (1997) Feeding and social behavior of fallow deer (*Dama dama L.*) under intensive pasture confinement. *Journal of Animal Science* 75, 339-347

Maynard Smith, J. Harper, D.G.C. (1988) The evolution of aggression: Can selection generate variability? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.* 319 (1196), 557-570

McGhee, J.D. & Baccus, J.T. (2006) Behavioral interactions between axis and fallow deer at high-value food patches. *The Southwestern Naturalist.* 51(3), 358–367

Moore, D.E. (1998) Husbandry and breeding of North American ungulates in a zoo. *International Zoo Yearbook.* 36 234-246

Mosley, J.C. (1999) Influence of social dominance on habitat selection by free-ranging ungulates. In Launchbaugh, K.L, Mosley, J.C. & Sanders, K.D (eds.) Grazing behavior of livestock and wildlife. Idaho. Idaho Forest, Wildlife and Range Experiment Station Bulletin 70. University of Idaho. [Online]. Available from: http://www.cnrhome.uidaho.edu/documents/mosley.pdf&pid=74886&doc=1. [Accessed 16th May 2008]

Olney, P.J.S., Mace, G.M. & Feistner, A.T.C. (1994) Creative Conservation. Interactive Management of Wild and Captive Animals. London. Chapman & Hall.

Pruetz, J.D. & Isbell, L.A. (2000) Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioural Ecology and Sociobiology* 49, 38–47

Putman, R.J. & Staines B.W. (2004) Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. *Mammal Review* 34 (4), 285–306

Qureshi, Q., Sawarkar, V.B., Rahmani, A.R. & Mathur, P.K. (2004) Swamp Deer or Barasingha. In: Ungulates of India. Wildlife Institute of India [Online] available from: http://www.wii.gov.in/envis/ungulatesofindia/index.html [Accessed 13th June 2008]

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rees, P.A. (2005) Will the EC Zoos Directive increase the conservation value of zoo research? *Oryx.* 39, 128–131.

Risenhoover, K.L. & Bailey, J.A. (1985) Relationships between group size, feeding time, and agonistic behavior of mountain goats. *Canadian journal of zoology.* 63, 2501 2506.

Sankar, K. & Acharya, B. (2004) Spotted deer or Chital. In: Ungulates of India. Wildlife Institute of India [Online] available from: http://www.wii.gov.in/envis/ungulatesofindia/index.html [Accessed 13th June 2008]

Saito, C. (1996) Dominance and feeding success in female Japanese macaques (*Macaca Fuscata*): effects of food patch size and inter-patch distance. *Animal Behaviour*. 51, 967–980

Schmidt K.T. & Hoi, H. (1999) Feeding tactics of low-ranking red deer stags at supplementary feeding sites. *Ethology*. 105, 349-360

Shelley, E.L., Tanaka, M.Y.U., Ratnathican, A.R., Blumstein, D.T. (2004) Can Lanchester's laws help explain interspecific dominance in birds? *The Condor*. 106, 395–400

Stanley Price, M.R. (1989) Animal Re-introductions: The Arabian Oryx in Oman. Cambridge, Cambridge University Press

Stensland, E., Angerbjörn, A., Berggren, P. (2003) Mixed species groups in mammals. *Mammal Review*. 33 (3) 205–223

Synder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.M., Toone, W.D. & Miller, B. (1996) Limitations of captive breeding in endangered species recovery. *Conservation Biology*, 10 (2), 338–348.

The British Deer Society (2008) [online] Available from: http://www.bds.org.uk/ [Accessed 28th July 2008]

Thomas, W.D. & Maruska, E.J. (1996): Mixed species exhibits with mammals. In: Kleiman, D. G., Allen, M. E., Thompson, K. V. & Lumpkin, S. (Eds). Wild mammals in captivity: principles and techniques. Chicago, University of Chicago Press.

Thouless, C.R. (1990) Feeding competition between grazing red deer hinds. *Animal Behaviour*. 40 (1), 105-111.

Vahl, W.K., Lok, T., van der Meer, J., Piersma, T. & Weissing, F.J. (2005) Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology*. 16(5), 834-844,

Vankova, D., Bartos, L., Miller, K.V. & Brandl, P. (1999) Behavior of white-tailed and fallow deer during winter supplemental feeding. *Folia Zoologica* 48, 87–92.

Volpelli, L.A., Valusso, R. & Piasentier, E. (2002) Carcass quality in male fallow deer (*Dama dama*): effects of age and supplementary feeding. *Meat Science*. 60, 427–432

Walther, F. (1965) Ethological aspects of keeping different species of ungulates together in captivity. *International Zoo Yearbook*. 5 (1), 1-13

Webb, W.M. (1931) Whipsnade Zoological Park. *Nature.* 127, 835-836

Wehnelt, S. & Wilkinson, R. (2005) Forum research, conservation and zoos: the EC Zoos Directive – a response to Rees. *Oryx.* 39 (2) 132-133

Wickstrom, M.L., Robbins, C.T., Hanley, T.A., Spalinger, D.E., Parish, S.M. (1984) Food intake and foraging energetics of elk and mule deer. *The Journal of Wildlife Management*, 48 (4), 1285-1301

Wielebnowski, N. (1998) Contributions of behavioural studies to captive management and breeding of rare and endangered mammals. In: Caro, T.M., (ed.) Behavioral Ecology and Conservation Biology. Oxford, Oxford University Press

Wildlife Institute of India 2004 [Online] Available from: http://www.wii.gov.in/envis/ungulatesofindia/ [Accessed 28th July 2008]

Wilson A.C. & Stanley-Price M.R. (1994) Reintroduction as a reason for captive breeding. In: P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds). Creative conservation: interactive management of wild and captive animals. London, Chapman & Hall

Ziegler, T. (2002) Selected mixed species exhibits in Zoological Gardens. *Primate Report.* 64, 5-89

ZSL 2008 [Online] Available from: http://www.zsl.org/info/about-us/ visited 27/08/08 [Accessed 4th August 2008]

9. Appendices

9.1. Appendix 1 – Map of the mixed species deer paddock at ZSL Whipsnade Zoo with the feeding area (Area 'A') and the viewing area from which data was collected (Area 'B').

FENCE LINE

AREA 'A'

AREA 'B'
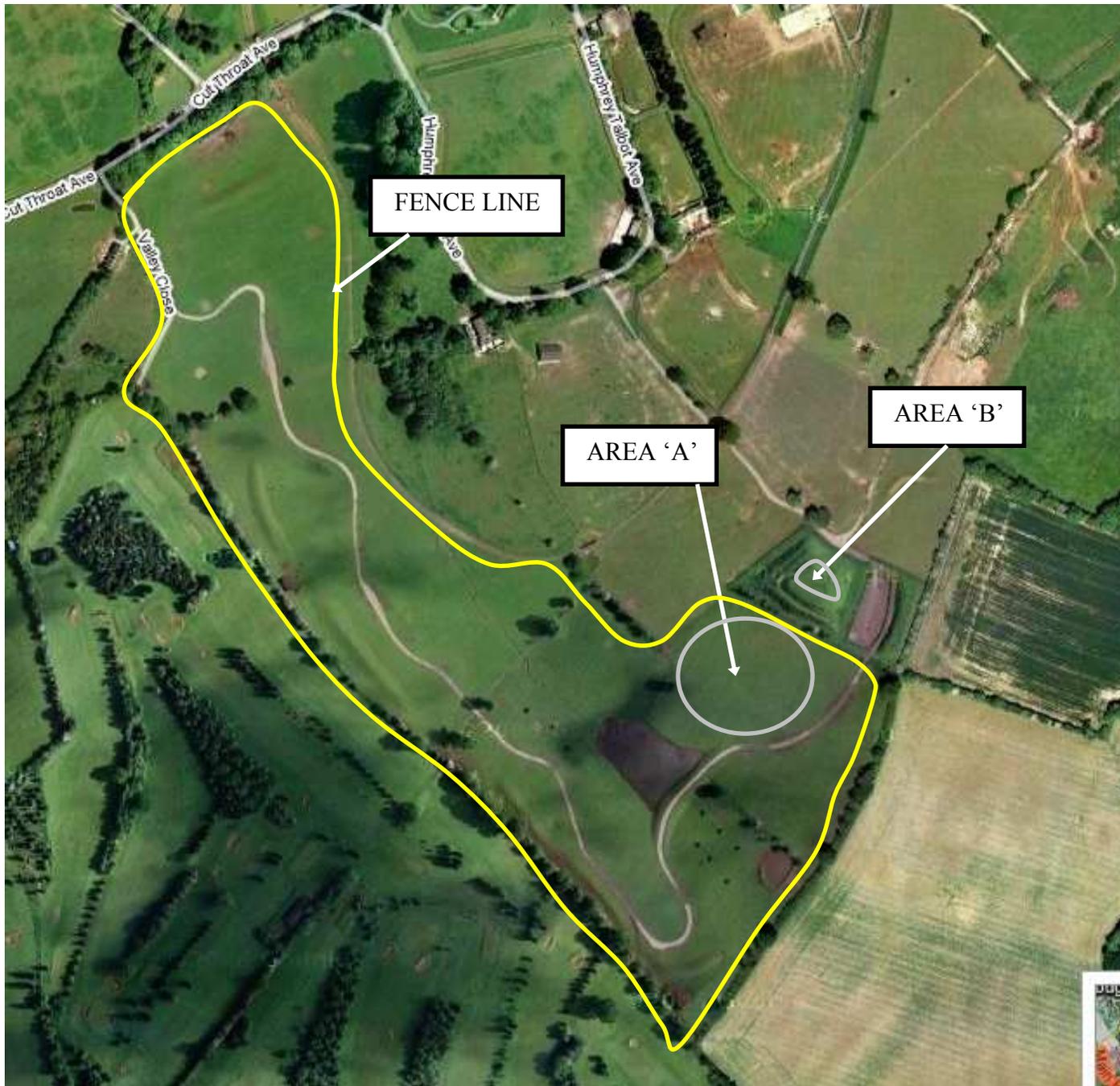
Picture credit – 2008 Google© Maps UK (http://maps.google.co.uk/maps, 2008)

9.2 Appendix 2 – A record of all of the interactions in each quartile with each feeding method. If an individual displaced more than one of the same group then the number displaced prefixes the code. Groups are coded as follows: Male sika = 'MS'; Female sika = 'FS'; Male Axis = 'MA'; Female Axis = 'FA'; Male Fallow = 'MF'; Female Fallow = 'FF'; Hog = 'H'; Swamp = 'SW'.

Traditional Feeding Method ('Line')

Quartile 1		**Quartile 2**		**Quartile 3**		**Quartile 4**	
Winner	Looser	Winner	Looser	Winner	Looser	Winner	Looser
MA	FF	MA	MA	MS	MS	MA	MA
MS	H	FS	FS	MS	MS	MS	MS
MF	SW	H	H	MS	FF	MS	MS
MS	MF	MS	FS	MS	MS	MS	5FF
MS	FF	MS	FS	FS	H	MS	7FF
MS	FS	MS	2FS	MS	MS		
FS	FS	FS	FS	MS	MS		
MS	2SW			MS	4H		
MA	FA			MA	MF		
MA	MA			MF	SW		
MS	MS			MS	3FF		
				MS	3MF		
				MS	FF		

Modified Spatial Distribution of Supplementary Food ('Even')

Quartile 1		**Quartile 2**		**Quartile 3**		**Quartile 4**	
Winner	Looser	Winner	Looser	Winner	Looser	Winner	Looser
MS	MS	MS	MS	MS	MS	MS	MS
MF	FS	FS	FF	MS	FF	MS	H
FA	FA	MA	FS	H	SW	MS	MS
MA	FA	MS	MF	MS	FS	MF	H
MS	FS	MA	FF	FS	MS	SW	SW
MS	MA	FS	FF			MS	FF
MS	MS	FA	FA				
MS	MS	FS	SW				
MS	MA	MS	FS				
MA	MF						
MS	MS						
FS	FF						
MS	MS						
FS	FS						
FS	FF						

Decreasing clump sizes ('BtS')

Quartile 1

Winner	Looser
MS	MS
MS	H
FS	FS

Quartile 2

Winner	Looser
MA	MF
MS	MS
MS	FS
MS	MS
MA	FF
MA	FF
MS	FS
MA	MA
MA	FF
MS	2FF
MS	2MF
MA	MF
MS	FS
MA	3MF
MA	3FF
MS	MF
MS	3MF
MA	FF

Quartile 3

Winner	Looser
MS	FF
MS	2MF
MS	H
MS	FF
FS	FF
FS	MF
MS	MF

Quartile 4

Winner	Looser
MS	3MF
MS	3FF
MS	FF
MS	MF

Increasing clump sizes ('StB')

Quartile 1

Winner	Looser
MA	MA
MA	FF
MA	MF
MS	2MF
MA	MS
MS	SW
MA	FA
FS	MF
MS	MS
FA	SW
MS	MS
MS	MA
MS	MS
MS	FS
FS	H
MS	2FS
MS	MA
MS	FA

Quartile 2

Winner	Looser
MA	MF
MS	2SW
MS	3MA
MS	3FA
MS	MF
MA	FA
MS	MS
MA	5MF

Quartile 3

Winner	Looser
MS	H
MS	MF
MF	3H
FS	MS
MS	2MF

Quartile 4

Winner	Looser
MS	2MF
MS	2FF
MS	MF
MS	MF
MS	MS
MS	FS

9.3. Appendix 3 – Model statistics (F values, multiple R-squareds and degrees of freedom for all models.

Supplementary feeding

GLMs for studying differential access between groups for the 'Line' method: Overall – F = 0.48. R^2 = 0.002248, df = 1492; Quartile 1 – F = 0.42. R^2 = 0.01121. df = 262; Quartile 2 - F = 0.57. R^2 = 0.01505. df = 262; Quartile 3 - F = 0.21. R^2 = 0.005493. df = 262; Quartile 4 - F = 0.05. R^2 = 0.0005604. df = 262

GLMs comparing differential overall access for other methods: 'Even', F = 0.36. R^2 = 0.002148. df =1162; 'BtS', F = 0.70. R^2 = 0.004891. df =1002; 'StB', F = 1.105. R^2 = 0.005565. df =1382

GLMs for comparing methods for the female fallow group: Overall – F = 0.03665. R^2 = 0.0002216. df = 496; Quartile 1 – F = 0.001345. R^2 = 4.692e-05. df = 86; Quartile 2 - F = 0.05342. R^2 = 0.00186. df = 86; Quartile 3 - F = 0.05743. R^2 = 0.001999. df = 86; Quartile 4 - F = 0.002543. R^2 = 3.376e-05. df = 226

GLMs for comparing methods for the male fallow group: Overall – F = 0.05744. R^2 = 0.0003473. df = 496; Quartile 1 – F = 0.0339. R^2 = 0.001181. df = 86; Quartile 2 - F = 0.1244. R^2 = 0.004319. df = 86; Quartile 3 - F = 0.3182. R^2 = 0.01098. df = 86; Quartile 4 - F = 0.03775. R^2 = 0.0005008. df = 226

GLMs for comparing methods for the female axis group: Overall – F = 0.0008044. R^2 = 4.866e-06. df = 496; Quartile 1 – F = 0.06617. R^2 = 0.002303. df = 86; Quartile 2 - F = 0.02324. R^2 = 0.00081. df = 86; Quartile 3 - F = 0.0001107. R^2 = 3.86e-06. df = 86; Quartile 4 - F = 3.255e-06. R^2 = 4.321e-08. df = 226

GLMs for comparing methods for the male axis group: Overall – F = 0.01096. R^2 = 6.629e-05. df = 496; Quartile 1 – F = 0.1572. R^2 = 0.005453. df = 86; Quartile 2 - F = 0.0173. R^2 = 0.0006032. df = 86; Quartile 3 - F = 0.001804. R^2 = 6.294e-05. df = 86; Quartile 4 - F = 0.000572. R^2 = 7.593e-06. df = 226

GLMs for comparing methods for the female sika group: Overall – F = 0.2808. R^2 = 0.001696. df = 496; Quartile 1 – F = 0.189. R^2 = 0.006549. df = 86; Quartile 2 - F = 0.3988. R^2 = 0.01372. df = 86; Quartile 3 - F = 0.2524. R^2 = 0.008726. df = 86; Quartile 4 - F = 0.01308. R^2 = 0.0001736. df = 226

GLMs for comparing methods for the male sika group: Overall – F = 0.3174. R^2 = 0.001916. df = 496; Quartile 1 – F = 0.08446. R^2 = 0.002938. df = 86; Quartile 2 - F = 0.05703. R^2 = 0.001985. df = 86; Quartile 3 - F = 0.3405. R^2 = 0.01174. df = 86; Quartile 4 - F = 0.1463. R^2 = 0.001939. df = 226

GLMs for comparing methods for the hog group: Overall – F = 1.117. R^2 = 0.003352. df = 496; Quartile 1 – F = 0.1443. R^2 = 0.002454. df = 86; Quartile 2 - F = 0.2616. R^2 = 0.004439. df

= 86; Quartile 3 - F = 0.4349. R^2 = 0.007358. df = 86; Quartile 4 - F = 1.094. R^2 = 0.007146. df = 226

GLMs for comparing methods for the swamp group: Overall – F = 0.01221. R^2 = 3.677e-05. df = 496; Quartile 1 – F = 0.03614. R^2 = 0.0006157. df = 86; Quartile 2 - F = 0.05418. R^2 = 0.0009227. df = 86; Quartile 3 - F = 0.01029. R^2 = 0.0001753. df = 86; Quartile 4 - F = 0.001417. R^2 = 9.321e-06. df = 226

Daily foraging

GLMs for comparing methods for each group: Female fallow, F = 0.1314. R^2 = 0.0008834. df = 446; male fallow, F = 0.09078. R^2 = 0.0006103. df = 446; female axis, F = 0.08193. R^2 = 0.0005508. df = 446; male axis, F = 0.08619. R^2 = 0.0005794. df = 446; female sika, F = 0.05501. R^2 = 0.0003699. df = 446; male sika, F = 0.05597. R^2 = 0.0003763. df = 446; hog, F = 0.3817. R^2 = 0.001276. df = 446; swamp, F = 0.3269. R^2 = 0.001093. df = 446

9.4. Appendix 4 – Changes in the proportions of each species foraging throughout the day from 10:00am to 5:00pm