ZENTRUM
FÜR BIODIVERSITÄT UND NACHHALTIGE LANDNUTZUNG
SEKTION
BIODIVERSITÄT, ÖKOLOGIE UND NATURSCHUTZ

– CENTRE OF BIODIVERSITY AND SUSTAINABLE LAND USE –
SECTION: BIODIVERSITY, ECOLOGY AND NATURE CONSERVATION

Behaviour, interactions and habitat use of European bison (*Bison bonasus*), Exmoor ponies (*Equus ferus*) and Dybowski deer (*Cervus nippon hortulorum*) in a mixed-species enclosure at Tierpark Sababurg

Verhalten, Interaktionen und Raumnutzung von Wisenten (*Bison bonasus*), Exmoor-Ponys (*Equus ferus*) und Dybowski-Hirschen (*Cervus nippon hortulorum*) auf einer weiträumigen Gemeinschaftsanlage im Tierpark Sababurg

Dissertation zur Erlangung des Doktorgrades der
Mathematisch-Naturwissenschaftlichen Fakultäten der
Georg-August-Universität Göttingen

vorgelegt von

Dipl.-Biol.

Michel Delling

aus
Hofgeismar

Göttingen, März 2013

Referentin/Referent:	**Prof. Dr. Rainer Willmann**
1. Korreferentin/Korreferent:	**Prof. Dr. Dr. Matthias Gauly**
2. Korreferentin/Korreferent:	**Prof. Dr. Michael Mühlenberg**
Tag der mündlichen Prüfung:	8. Mai 2013

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1 Introduction

1.1 Wild Animals in Captivity

While collections of living animals have been in existence for thousands of years, the history of the present-day zoo stems from the eighteenth and nineteenth centuries, when zoos were founded in Vienna, Paris and London (IUDZG/CBSG 1993). Those early zoological gardens were built mostly for entertainment and only partly because of scientific interest in exotic animals. Most enclosures were designed to present the animals in a clearly visible way, without regarding the animals' needs for species-appropriate husbandry.

Despite early menageries being the source of much biological information on anatomy and faunal biodiversity, it is only more recently that their potential for research has been recognized and significant biological information accumulated as a result of research activities in zoos (RYDER & FEISTNER 1995).

Nowadays, zoological gardens and wildlife parks are developing more and more into scientific collections – living museums especially for threatened species (IUDZG/CBSG 1993, RABB 1994).

The understanding of modern zoos is to become a network of worldwide centres of species- and nature conservation, in which the animals fulfil the roles of ambassadors for their free-living conspecifics, their natural habitat and the flora and fauna of their original distributional range (SCHUBERT 2006).

Today's zoological institutions also play an important role for education and transfer of knowledge about nature conservation. Because zoos work with a huge diversity of life forms and keep animals in situations where they can be studied relatively easily, they provide opportunities for studying behavioural and demographic issues, reproductive physiology, evolutionary genetics and lots of other topics, which are not readily paralleled (RYDER & FEISTNER 1995). Such studies can provide substantial information about free-living populations and their habitat requirements and thus help in creating effective long-term conservation strategies.

For one of those strategies especially – breeding animals in captivity as a genetic pool for threatened populations – the knowledge about the natural behaviour of the species is essential for its success (SYNDER et al. 1996). This makes the behavioural research in zoological gardens and wildlife parks in comparison to findings from free-living individuals one of the

most important fundaments for the management, welfare and conservation success of species (AVENT 2008).

1.2 Mixed-species exhibits

Keeping wild animals in enclosed areas always results in a reduction in their natural behaviours (MALEK 2009). Thus 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 is culturally developed and social interactions are complex (WIELEBNOWSKI 1998). In order to prevent a rapid and permanent loss of these capacities, not only the enclosure size but also enclosure design and availability of biologically appropriate complexity is relevant (SWAISGOOD & SHEPHERDSON 2005). This can be improved in many ways, for example, by adding substrates such as dirt, litter, mulch, or sand. These substrates increase ‘‘information content’’ of the environment and elicit foraging and investigating behaviour by concealing food, smells, naturally occurring insects, or other wildlife, etc. Barriers and landscaping can provide privacy, promote territorial behaviour, provide escape routes, and thus improve social interactions (HEDIGER 1950, 1968). Trees and other plants offer shade and temperature gradients for choice of microclimate and can also provide hiding places from conspecifics, the public and keepers (SWAISGOOD & SHEPHERDSON 2005).

Where possible, another approach to enrich the daily routine of the animals is keeping different species together. With smaller enclosures, providing suitable behavioural and social enrichment is often problematic, 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).

Keeping different species together in captivity is not a new concept, with early zoos often housing mixed aviaries, aquariums and reptile gardens (ZIEGLER 2002). This was often simply the result of using a single enclosure to hold several species. Mixed-mammal enclosures, however, are a relatively new concept due to a perception in the past of the potential risks, technical demands and problems that can be caused by establishing relationships between species (ZIEGLER 2002).

The earliest reports of open-air mixed-species ungulate exhibits in zoos came from the turn of the nineteenth to the twentieth century, when it became known that natural associations of different species occur in Africa regularly, especially at watering holes (WALTHER 1965).

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 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 (BACKHAUS & FRÄDRICH 1965, THOMAS & MARUSKA 1996). Especially smaller, inconspicuous or reclusive-living species can thus be brought into focus when shown together with well-known or popular species (CROTTY 1981).

1.3 State of research

Zoo-based research on animals in mixed-large-mammal enclosures and the presentation of those species together is a relatively new aspect in zoology. In the early mixed-species exhibits in zoos typically different ungulates were presented together; the co-housing of different primate or carnivore species was not tried until a few decades ago (HAMMER 2002).

The first studies about the problems and benefits of these mixed-species enclosures showed positive (e.g. BARTMANN 1980) as well as negative results (e.g. WALTHER 1965) (see below).

WALTHER (1965) reasoned that although animals may form polyspecific associations in the wild, these relationships vary depending on activity and time.

In zoos, these associations are enforced and not limited in time. Using the example of ungulates he argues that the natural associations occur most around waterholes and are weaker during grazing, thus minimising the aggressive interactions over food. The restricted space in enclosures could therefore lead to food competition not due to food availability but restricted feeding places, thus creating problems for the management (WALTHER 1965).

Even though it could be proved that inter-species aggression can occur not only over food but also especially during the breeding season (e.g. WALTHER 1965, ANDERSEN 1992a, 1992c, WALDER 2007), many researchers found a positive effect on the animals' behaviour. Several surveys showed that often noticeably inactive animals in single-species-enclosures could be brought to increased natural and intra- as well as interspecific behaviours when housed together with other species (e.g. BARTMANN 1979, CROTTY 1981, ZIEGLER 2002).

An investigation of 1262 studies on mixed-species-enclosures in 257 zoos worldwide showed that 91% of the co-housings were successful and even beneficial for the animals' well-being (HAMMER 2001).

Although relationships between species are common and have been studied in free-living fish, birds, ungulates, primates and cetaceans, to name but a few (HEYMANN & BUCHANAN-SMITH 2000), there is comparatively little quantitative data about polyspecific associations in zoos.
Most of what is known today comes from studies on African ungulates, for they are the most commonly co-housed species in zoos all over the world (HAMMER 2001).
Mixed-species enclosures with European mammals are to be found only rarely in zoological gardens or wild animal parks. Equally, the knowledge about these animals and their behaviour in enclosures, particularly when sharing with other species, is only scarce.
The large European herbivores – that is, the European bison, wild horses, deer and others (BUNZEL-DRÜKE et al. 1999) – which were common in Central Europe after the last glacial period before they were displaced by humans, are kept only seldom and are rarely housed in mixed-species exhibits.
As far as is known, the large-scale enclosure at Tierpark Sababurg is the only compound in the world where European bison, wild horses and deer are kept together. As there have not been any scientific studies on this co-housing up to now, there are no findings about the interactions, habitat use and general behaviours of those species with other large herbivores present.
Of these three European animal species, different deer are still the most numerous kept and associated, although most knowledge about deer was derived from field-research (LATHAM 1999).
While intraspecific behaviour of diverse deer species is quite well documented (e.g. FUNK 1981, MERTENS 1984), there is only one study about interspecific actions of different deer in a mixed-deer-species enclosure at ZSL Whipsnade Zoo (Bedfordshire, England) (AVENT 2008).
European bison, as the largest animals of Central Europe, are only rarely kept in zoos and mostly found in the normally more spacious wild animal parks. Although these animals were studied intensely in their natural habitat (e.g. BOROWSKI & KOSSAK 1972, GĘBCZYŃSKA & KRASIŃSKA 1972, CABOŃ-RACZYŃSKA et al. 1983, 1987, DALESZCZYK 2004, 2005, JAROSEVICZ & PIROZNIKOW 2008), there are only sparse investigations on animals in enclosures or breeding centres (VAN DEN BRINK 1980, CHIKUROVA 2008, HOFLING 2009).
The same applies to feral horses. Exmoor ponies being the descendants of the western European wild horse (GATES 1980, BAKER 1993, 2008, WILLMANN 1997), their natural behaviour is quite well documented under free-living conditions (e.g. BAKER 1979, GATES 1980, WILLMANN 1990, 1991, 2008, BAKER 2008, DELLING 2009). The Exmoor ponies'

behaviour in enclosures has been studied in various ways, but not in the context of co-housing with other species (MEINIG 2002, MACKENSEN 2005), though it is known from their natural habitat that interactions with sheep, red and roe deer take place especially on rich pastures or at water holes (GATES 1980, BAKER 2008).

1.4 Background

1.4.1 Species conservation

Why those three species in combination are such an important area for research can be explained by two major aims of nature conservation. These are to promote the conservation of species and ecosystems, including the ecological interactions and evolutionary processes in which it participates and the environmental services it provides to society (CUARÓN 2005).
The means to accomplish this in modern zoos is by scientific research, captive breeding programs, financial and other support of in situ conservation activities and especially public education at all levels (CUARÓN 2005).
Concerning the importance of breeding and thus enlarging the living populations of rare and endangered animals, keeping European bison, wild horses and Dybowski deer contributes to the conservation regarding the actual population sizes of those species.
The worldwide number of European bison was only 3,200 individuals in the year 2004, of which about 1,800 were free-living and 1,400 in breeding programs (EBPB [European Bison Pedigree Book] 2004, PUCEK et al. 2004). Up until 2009, the population size was increased to about 4,000 individuals owing to intensive breeding efforts (RACZYŃSKI 2009). But only about 60% of the population being propagable due to age, competition or other factors, the effective population-size is far smaller than the number of individuals (KRASIŃSKI 1978, KRASIŃSKA & KRASIŃSKI 2004).
Moreover, the European bison exists in two subspecies or genetic lines which are distinguished in recent populations: the Lowland line (*Bison bonasus bonasus*) and the Lowland-Caucasian line (*B. b. bonasus* and *B. b. caucasicus*), for there are no surviving pure-bred populations of *B. b. caucasicus* (PUCEK et al. 2004). These two subspecies are regarded separately by the IUCN (2012) and classified in different categories of endangerment. While the Lowland-European bison is classified as “Vulnerable”, the Lowland-Caucasian-European bison is categorised as “Endangered” (IUCN 2012). This is due not only to the small

population size of this subspecies, with fewer than 250 individuals, but also to the uniqueness of the extinct pure Caucasian line.

The last free-living European bison were exterminated in 1927 (SCHRÖPFER 2007). Only the efforts of the International Society for Conservation of the European bison founded in Frankfurt/Main on 25–26 August 1923 could save the species from extinction (RACZYŃSKI 2009). The last 56 individuals, of which only 12 were propagable, were collected into breeding centres and founded the whole of today's living population.

Among those 12 European bison, 11 were out of the Lowland line and only one single male („Kaucasus", Studbook-Nr.: 100) belonging to the Caucasian line (SLATIS 1960), so the entire genetic line of this subspecies in existence today is founded by the progeny of this one individual (RACZYŃSKI 2009).

At the moment there are only 6 living propagable males carrying the genes of this special lineage (pers. comm. Dr. Taras Sipko, European Bison Specialist Group SSC/IUCN). One of those is the breeding male at Tierpark Sababurg („Favorit", Studbook-Nr.: 10042), which makes this herd particularly important for the breeding program.

The breeding of Exmoor ponies is another major aim of this institution, which owns 16 animals (spring 2011) forming one of the largest herds in Germany. The early history of these ponies has still to be determined. However, the first written evidence of free-roaming wild horses occurs in the Domesday Book ordered by William the Conqueror in 1086 for the purpose of documenting all inhabitants and possessions of his land (BAKER 1993, 2008). Both habitus and behaviour have remained demonstrably unchanged, because these ponies were not domesticated at any time and crossbreeds with domestic ponies or horses were not robust enough to survive in the climatically rough region of Exmoor (BAKER 1993, 2008). Therefore it is assumed that the Exmoor pony developed almost unaffected by man and is most probably the last post-glacial form of the Northern European wild horse (BAKER 1993, 2008; WILLMANN 1990, 1991, 1999, 2005, 2008).

The total population of Exmoor ponies consists of about 3,000 individuals, which makes it one of the rarest old horse breeds worldwide. But, as with the European bison, the effective population size of propagable animals is much smaller than the number of individuals (BAKER 2008). For this reason, the breeding of these rare animals is controlled by the Exmoor Pony Society, founded in 1921, which keeps the studbook and inspects the breeding animals to ensure the breed survives in its original form (BREWER 1995).

The captive breeding of Dybowski deer is also an important aim in species conservation. Although the worldwide population of Sika deer (*Cervus nippon*) is classified as of 'Least

Concern' (IUCN 2012), the subspecies of the Dybowski deer (*Cervus nippon hortulorum*) was considered to be on the edge of extinction in the wild until 1986, when a 300-individual population was re-discovered along the border between China and Russia (MA 1986, LÜ et al. 2007). Intensive efforts in captive breeding as well as local conservation increased the population size of both free-living and captive animals to about 2,000 individuals worldwide (UECKERMANN 1992, MCCULLOUGH et al. 2009), but further management is essential for the survival of this threatened subspecies (IUCN 2012).

1.4.2 Nature conservation

The second major aim of nature conservation besides species conservation is the preservation of whole ecosystems, their ecological interactions and evolutionary processes (BNatschG, §1). The applied nature conservation tries to preserve ecosystems in their natural form and to restore damaged or destroyed areas to as natural a state as possible (PLACHTER 1995, BUNZEL-DRÜKE et al. 1999).

As to what is defined as "natural", it is taken as a consensus to regard this as the original landscape under all biotic and abiotic influences and site-specific environmental changes if there would have been no human intervention (e.g. HOFMANN 1995, PLACHTER 1995, SCHEIBE et al. 1998b, 2002; BUNZEL-DRÜKE et al. 1999).

One biotic integrant is herbivory, not only of invertebrates but also of (especially large) mammals. Following the hypothesis that man is responsible for the extinction of many animal species in Central Europe, the original landscape and vegetational structure that existed before the overhunting of immigrating humans led to declines in large-mammal populations is to be seen as natural (e.g. MARTIN & KLEIN 1984, DIAMOND 1989, BEUTLER 1992, BUNZEL-DRÜKE et al. 1994, BUNZEL-DRÜKE 1997, 2001).

The results of numerous studies have proved not only the strong influence of large herbivores on the structure and species-composition of the vegetation, but also that they act as key-species creating and sustaining small-scale habitats for multitudinous other species (e.g. SUFFLING et al. 1988, SCHEIBE et al. 1998a, 1998b, BUNZEL-DRÜKE et al. 1999, KRÜGER 1999, KAMPF 2000, SCHARF 2000, VULINK 2001, REDECKER et al. 2002, BUNZEL-DRÜKE & SCHARF 2004, JAROSEVICZ & PIROZNIKOW 2008). Based on this knowledge, in around 1990 the applied nature conservation started to use domesticated ungulates such as horses, cattle or sheep for grazing open areas in the cultural landscape to maintain those habitats in as natural a way as possible (POTT & HÜPPE 1994, BUNZEL-DRÜKE et al. 1999).

Because herbivores use the plant-biomass in different species-specific ways, grazing nature conservation areas with only one species will lead to a merely partial and restricted influence on the vegetation (POTT & HÜPPE 1994, HOFMANN 1995). Therefore, this kind of management should always be conducted with at least two, or prefereably more, species with different food requirements (BUNZEL-DRÜKE et al. 1999).

This integration of large herbivores into nature conservation measures is today gaining more and more importance, and in some areas is already well established as a maintenance method for endangered landscapes (e.g. BAERSELMAN & VERA 1995, CORNELISSEN & VULINK 1995, MARTIN 1997, SCHEIBE et al. 1998a, 1998b, REISINGER 1999, SCHARF 2000, BUNZEL-DRÜKE 2001).

Until now, most large-scale grazing projects use the backbred forms of the Tarpan-horse and Heck-cattle (BAERSELMAN & VERA 1995, BUNZEL-DRÜKE 2001).

The original Tarpan *(Equus ferus gmelini*) went extinct in the nineteenth century and all of today's existing specimens descend from domesticated horses (*Equus ferus f. caballus*) selected by breeders to have the outer appearance of Tarpans (JAWORSKI 1997).

The same can almost be said of Heck-cattle, being the attempt of the German zoologists Lutz and Heinz Heck to backbreed the aurochs (*Bos primigenius*) from old and original farm cattle breeds (*Bos primigenius f. taurus*) (HECK, H. 1951, 1980; HECK, L. 1936, 1952b). As it is known today, the aurochs is only a partial ancestor of the European cattle (BOLLONGINO et al. 2006, EDWARDS et al. 2007, STOCK et al. 2009). So, again, this attempt results in domesticated animals that bear only partial resemblence to an extinct species.

It is known that even closely related species can be specialised extremely differently in their feeding habits, diet and habitat use, even while using the same ecological niches (SCHEIBE et al. 1998b, PETRAK 1993). Thus how far these domesticated animals used for grazing projects are able to fulfil the ecological roles of the original large herbivore species of Central Europe is uncertain (SCHEIBE et al. 1998b, PETRAK 1992, 1993).

European bison, wild horses and deer, however, did belong to the natural species community of Central Europe. This means they are far more robust and have adapted to living outside for the whole year with only little management. They also possess more suitable natural traits in size, behaviour, diet and feeding habits for use as grazers in nature conservation areas and for creating as well as sustaining natural habitat structures (PLACHTER 1995, SCHEIBE et al. 1998b, REISINGER 1999).

Even large-scale conservation areas, though, provide only a restricted habitat and it is inevitable that the different species do converge regularly, for example at watering holes

(SCHEIBE et al. 1998b, AVENT 2008). Consequently, knowledge about the habitat requirements, behaviour and interactions between the selected large-herbivore species in advance of such a project is as important as that of their behaviour towards inevitable management measures and visitors (KAULE 1991, BUNZEL-DRÜKE & SCHARF 2004).

Tierpark Sababurg is the only zoological institution worldwide which keeps European bison, Exmoor ponies and Dybowski deer in an approx. 14ha near-natural enclosure. This provides a unique opportunity to study the cohabitation of these species in a large-scale, albeit restricted, area under natural conditions.

The aim of this study is not only to learn more about the behaviour and requirements of these species to improve the management of the remaining populations for species conservation, but also to enhance animal husbandry and welfare to increase breeding successes for this and other zoological institutions.

Furthermore, it has been undertaken in order to provide basic knowledge about the cohabitation of European bison, wild horses and deer to develop the multi-species grazing of large-scale conservation areas with indigenous European species instead of domestic breeds for the benefit of more natural landscape and habitat conservancy.

1.5 Questions

The main questions this study focuses on are intended to provide basic knowledge about European bison, Exmoor ponies and Dybowski deer in captivity.
Thus, the study examines whether the individuals of all three species behave in a natural way, or if their behaviour is influenced by living in an enclosure. Related to this is the question of whether the examined individuals of all three species display a natural social behaviour.
Furthermore, it will be examined how far interspecific interactions between the species occur, and whether these are positive or agonistic. Another aspect that will be investigated is how the examined individuals of all three species use the 14ha-wide enclosure, which areas are preferred or avoided and which enclosure structures are used, and for what purpose. The influence of the seasons and/or different environmental conditions on behaviour, interactions and habitat use will also be analysed.
Another question is whether the cohabitation of European bison, Exmoor ponies and Dybowski deer cause oppression, concurrence or aggression among the species due to the restricted environment, or if they do establish a stable species hierarchy.

Based on the results of the above questions, it will be considered whether there are any necessary improvements in the management at Tierpark Sababurg to be made, and whether this special species combination is suitable to be used for grazing projects in the future.

2 Material and methods

2.1 Investigation area

The present study was conducted at Tierpark Sababurg near Hofgeismar (Hesse, Germany). This wild animal park keeps mainly a large variety of indigenous Central and Northern European species, various old and endangered farm breeds as well as some exotic animals. Founded in 1571, this park, which specialises in expansive, near-natural enclosures, is not only one of the oldest but, with 130ha, also one of the largest zoological institutions of Europe.

About 14ha of the total area are dedicated to the heraldic animals of the park – the European bison with the Exmoor ponies and Dybowski deer as cohabitants.

All three species do have their own stables with attached separating enclosures due to management requirements, but are generally roaming together on the large area constantly throughout the year.

The enclosure mainly contains of undulating grassy areas of different vegetational compositions, vegetated with remaining old woodland-pasture trees as well as groves and shrubs. Dead wood is left in the enclosure for natural decomposition as well as feed and scratching. Three natural rivulets cross the area, one creating two small ponds. The only artificial enclosure content – except fences and stables – is a depositional sandy area for sand bathing.

The whole enclosure is surrounded by paths and is visible from nearly all sites.

Supplemental feeding is offered once a day in the stables in order to control the animals' health, and daily training of separating the animals in case of possible management situations. Feed consisted of seasonably smaller or larger amounts of rolled oats for the Exmoor ponies and Dybowski deer and bruised grain for the European bison. Hay was offered ad libitum on the large common area, as well as mineral and salt licks.

The enclosure contained 16 European bison, 14 Exmoor ponies and 5 Dybowski deer at the beginning of the data collection 16 European bison, 15 Exmoor ponies and 5 Dybowski deer at the end, although there were changes in the individuals.

2.2 Investigation period

Data were collected from March 25th 2010 to March 29th 2011, two times a week, three hours per day, in a pseudo-randomised scheme.
The behaviour and habitat use of the animals was documented for all hours of daylight. Nightly observation was not possible, as there was no night-vision technology available and the area was too spacious to observe the animals without entering the enclosure.
The sample periods were distributed equally over all hours of the day and days of the week throughout all seasons.

2.3 Methods

All observations were conducted after the methods of ALTMANN (1973) and MARTIN & BATESON (2008).

2.3.1 Focal-animal sampling

The observation of the behaviour followed the focal-animal sampling method for documenting the percentages of the shown behaviours per day. Five focus animals of different ages and genders were selected as representatives for every species and observed for the given sample period. All their shown behaviours were documented by a behaviour-classification scheme (Table 11.1, Appendix) after MCDONNELL (2003) (adapted and extended version). This list contains the definitions of the behaviours of all European bison, Exmoor ponies and Dybowski deer – although there are specific behaviours which will only occur in one species.

2.3.2 Behaviour-sampling

All interactions between the three species were documented using the same behaviour-classification scheme, as well as all interactions with visitors and keepers or reactions to environmental or management situations.

2.3.3 Scan-sampling

The habitat use was documented by noting the actual position of every focus animal on a grid map of the enclosure (Figure 11.1, Appendix) every ten minutes of the observation period.

2.4 Equipment

The focus animals were observed with a pair of binoculars from Apollo (7x50). The intervals for recording the positions of the animals were kept with a stopwatch from HANHART („stoppstart“).
The weather data were collected by a TechLine WS-710 weather station.

2.5 Analysis

Data were transferred to Microsoft-Excel© and analysed. The results for the habitat use were graphically depicted with the image editing program Micrografx Picture Publisher©.

3 Results

The results are presented for all three examined species in the following order: behaviour, daily activity rhythms, intra- and interspecific interactions, and habitat use, all in general and under particular environmental circumstances. The abbreviations and definitions of the observed behaviours are listed in Table 11.1 (Appendix).

3.1 Behaviour

3.1.1 Behaviour in general

3.1.1.1 European bison

For an overview of the behaviour of the European bison, Table 3.1 shows the mean daily percentages of the observed behaviours over the complete investigation period.
Feeding took up 47.73% of the day, whereas resting behaviour was shown for 43.05%, including 6.77% and 2.06% respectively for ruminating while resting recumbent and standing. Nearly half the duration of resting behaviour, 20.55%, was spent recumbent.
Locomotion took up 6.79% of the day, and 1.68% was spent on comforting behaviour. Positive social interactions between the European bison occurred mainly as mother-calf relationships and between the bull and cows in heat during the rut, with 0.94% of the day as mean value over the observation period. Agonistic contact appeared more regularly, with an average of 0.78% per day. Since most of this social contact had a very short duration, this behaviour was analysed separately as individual contact. The following social interaction grids (see Table 3.11 and Table 3.12) provide a better overview of the observed interactions. Vigilant behaviour took 0.99% of the day and was mostly shown towards the keepers cars and the keepers themselves regarding non-conspecifics. Concerning general vigilant behaviour, it could be observed mainly from cows with newly born calves. Territorial behaviour and sexual contact both occurred during the rut only, and were infrequent behaviours.

Table 3.1: Mean behaviours of the European bison over the complete investigation period

Behaviour	% / d	Behaviour	% / d	Behaviour	% / d
Ingestion		Social contact		sdc	0.00
fee (in total)	47.73	**soc + (in total)**	0.94	soc	0.00
fee (Hay rack)	3.89	gro	0.00	str	0.10
fee (Stable)	0.42	seo	0.01	scv	0.02
fee (FY E. b.)	2.18	fol	0.16	slc	0.00
fee (TP-Feed)	0.00	sta	0.00	sgc	0.00
gra	37.72	nnc	0.13	seg	0.00
grr	0.01	ncc	0.10	seb	0.00
pic	0.00	nfc	0.17	ske	0.10
bro	0.36	nec	0.06	sdd	0.02
waf	2.06	ngc	0.21	ssh	0.02
nib	0.92	rui	0.00	Vocalisation	
paw	0.01	lii	0.10	squ	0.00
dri	0.16	beg	0.00	whi	0.00
suc	0.00	**soc - (in total)**	0.78	bar	0.00
Resting behaviour		nip	0.00	Territorial behaviour	
res (in total)	43.05	pur	0.00	tim	0.00
rst	11.25	dro	0.21	mar	0.00
rre	20.55	thr	0.31	for	0.02
rly	2.43	thb	0.00	sha	0.00
rur	6.77	thk	0.00	Playing behaviour	
rus	2.06	bit	0.00	plf	0.00
Locomotion		kic	0.00	lop	0.00
loc (in total)	6.79	att	0.00	psb	0.00
sta	3.96	cha	0.00	Sexual behaviour	
sta (suc)	0.62	fla	0.00	sim	0.00
wal	2.18	inc	0.00	ere	0.00
tro	0.02	inf	0.00	mas	0.00
gal	0.02	flg	0.00	saw	0.00
Elimination		avo	0.25	rhm	0.00
def	0.12	Vigilant behaviour		fle	0.08
uri	0.04	**sat (in total)**	0.99	for	0.01
Comforting behaviour		sal	0.00	mou	0.01
com (in total)	1.68	sad	0.50	pen	0.00
rub	0.99	svi	0.06	ine	0.01
rol	0.13	svd	0.01		
scr	0.43	svg	0.01		
atg	0.02	ssc	0.00		
str	0.10	skc	0.17		
spl	0.01	scc	0.00		

3.1.1.2 Exmoor ponies

The Exmoor ponies' behaviour is itemised in Table 3.2, values again in the mean daily percentages of the observed behaviours over the complete investigation period. The ponies used 58.62% of the day for ingestion, mostly with grazing. Resting behaviour occurred for 34.54% of the day, and in contrast to the European bison mainly standing and only little proportions of resting recumbent or lying down. The Exmoor ponies showed locomotion behaviour for 3.87% of the day, of which walking (1.42%) had the highest proportion after standing (1.58%), which was also categorised as locomotive behaviour (MCDONNELL 2003). Comforting behaviour was performed mainly in spring during moulting and in summer, with an average of 1.37% over the observation period .

Positive social contact occurred for 0.86% of the day, agonistic contact for 0.34%. As with the European bison, all social contact was analysed separately as single actions between the individuals due to the short duration. The mutual grooming contact was also regarded separately (see 3.2.2.4 below).

Vigilant behaviour against non-conspecifics could be observed mostly toward the European bison and passing vehicles. General vigilant behaviour was mainly exhibited by mares with newly born foals. All together, vigilant behaviour took 1.09% of the day.

Territorial behaviour was documented as marking behaviour for the stallion only. Playing behaviour could not be found for the focus animals. Sexual behaviour regarding actual mating was not observed within the observation period, although sexual impressing and investigation of excrements was documented for the stallion.

Table 3.2: Mean behaviours of the Exmoor ponies over the complete investigation period

Behaviour	% / d	Behaviour	% / d	Behaviour	% / d
Ingestion		Social contact		sdc	0.00
fee (in total)	58.62	**soc + (in total)**	0.86	soc	0.01
fee (Hay rack)	2.86	gro	0.30	str	0.07
fee (Stable)	0.64	seo	0.01	scv	0.05
fee (FY E.b.)	0.30	fol	0.01	slc	0.00
fee (TP-Feed)	0.04	sta	0.00	sgc	0.00
gra	53.96	nnc	0.16	seg	0.00
grr	0.04	ncc	0.02	seb	0.06
pic	0.00	nfc	0.09	ske	0.03
bro	0.06	nec	0.03	sdd	0.03
waf	0.63	ngc	0.09	ssh	0.01
nib	0.02	rui	0.00	Vocalisation	
paw	0.02	lii	0.08	squ	0.00
dri	0.06	beg	0.06	whi	0.00
suc	0.00	**soc - (in total)**	0.34	bar	0.00
Resting behaviour		nip	0.00	Territorial behaviour	
res (in total)	34.54	pur	0.00	tim	0.00
rst	31.68	dro	0.04	mar	0.01
rre	1.76	thr	0.08	for	0.00
rly	1.10	thb	0.01	sha	0.00
rur	0.00	thk	0.00	Playing behaviour	
rus	0.00	bit	0.00	plf	0.00
Locomotion		kic	0.01	lop	0.00
loc (in total)	3.87	att	0.00	psb	0.00
sta	1.58	cha	0.00	Sexual behaviour	
sta (suc)	0.74	fla	0.00	sim	0.02
wal	1.42	inc	0.01	ere	0.00
tro	0.11	inf	0.00	mas	0.00
gal	0.02	flg	0.01	saw	0.00
Elimination		avo	0.19	rhm	0.00
def	0.06	Vigilant behaviour		fle	0.00
uri	0.09	sat (in total)	1.09	for	0.00
Comforting behaviour		sal	0.00	mou	0.00
com (in total)	1.37	sad	0.55	pen	0.00
rub	0.43	svi	0.04	ine	0.01
rol	0.03	svd	0.00		
scr	0.83	svg	0.01		
atg	0.00	ssc	0.00		
str	0.07	skc	0.22		
spl	0.00	scc	0.01		

3.1.1.3 Dybowski deer

Table 3.3 shows the mean daily percentages of the observed behaviours of the Dybowski deer over the complete investigation period.

The Dybowski deer spent on average 47.22% of the day on food intake, most of which grazing. Resting occurred mainly in the form of resting recumbent (31.68%) and ruminating in this position (12.16%), totalling 43.64% of the day. Locomotion took 4.55% of the Dybowski deer's day, and comforting behaviour 2.44%. This was performed mostly as self-scratching (1.34%) and autogrooming (0.83%).

Positive as well as agonistic social behaviours were shown for 0.43% of the day. As with the other species, these interactions were very short-termed and will be presented as single actions below (3.2.3.3). The Dybowski deer displayed vigilant behaviour for 3.85% of the day, mainly towards visitors and different vehicles including the keepers' cars. General vigilant behaviour without provable reason could be documented for 1.89%. Vocalisations could be observed between hind and deer calf, but only rarely with an average of 0.02% over the complete investigation period. Territorial as well as sexual behaviour could only be documented during shedding of the antlers before the rut.

Table 3.3: Mean behaviours of the Dybowski deer in the complete investigation period

Behaviour	% / d	Behaviour	% / d	Behaviour	% / d
Ingestion		Social contact		sdc	0.01
fee (in total)	47.22	**soc + (in total)**	0.43	soc	0.01
fee (Hay rack)	0.43	gro	0.00	str	0.15
fee (Stable)	1.08	seo	0.01	scv	0.12
fee (FY E.b.)	0.04	fol	0.03	slc	0.01
fee (TP-Feed)	0.34	sta	0.00	sgc	0.01
gra	44.66	nnc	0.13	seg	0.00
grr	033	ncc	0.01	seb	0.02
pic	0.00	nfc	0.05	ske	0.02
bro	0.16	nec	0.02	sdd	0.05
waf	0.43	ngc	0.04	ssh	0.05
nib	0.00	rui	0.00	Vocalisation	
paw	0.00	lii	0.10	squ	0.02
dri	0.06	beg	0.03	whi	0.00
suc	0.02	**soc - (in total)**	0.43	bar	0.00
Resting behaviour		nip	0.01	Territorial behaviour	
res (in total)	43.64	pur	0.00	tim	0.01
rst	0.65	dro	0.05	mar	0.00
rre	29.31	thr	0.02	for	0.00
rly	0.02	thb	0.00	sha	0.04
rur	12.16	thk	0.00	Playing behaviour	
rus	1.50	bit	0.00	plf	0.00
Locomotion		kic	0.00	lop	0.00
loc (in total)	4.55	att	0.00	psb	0.00
sta	2.96	cha	0.00	Sexual behaviour	
sta (suc)	0.07	fla	0.00	sim	0.03
wal	1.45	inc	0.00	ere	0.00
tro	0.08	inf	0.00	mas	0.00
gal	0.01	flg	0.01	saw	0.00
Elimination		avo	0.33	rhm	0.00
def	0.06	Vigilant behaviour		fle	0.00
uri	0.04	**sat (in total)**	3.85	for	0.00
Comforting behaviour		sal	0.04	mou	0.00
com (in total)	2.44	sad	1.89	pen	0.00
rub	0.14	svi	0.63	ine	0.00
rol	0.01	svd	0.15		
scr	1.34	svg	0.07		
atg	0.83	ssc	0.00		
str	0.12	skc	0.45		
spl	0.01	scc	0.17		

3.1.2 Daily activity rhythms

The results above display the mean daily percentages of the observed behaviours. To analyse whether the animals show a particular daily activity pattern, the data were classified for all observed hours. The main behaviours creating an activity pattern being feeding and resting, they were set in contrast for every hour and graphically displayed.

3.1.2.1 European bison

The daily activity rhythm of the European bison over the complete investigation period is shown in Figure 3.1. The mean values from five focus animals in over one year of observation show the tendency of the European bison for feeding in the early morning hours and towards the evening, while the middle of the day is mainly spent resting, mostly recumbent.

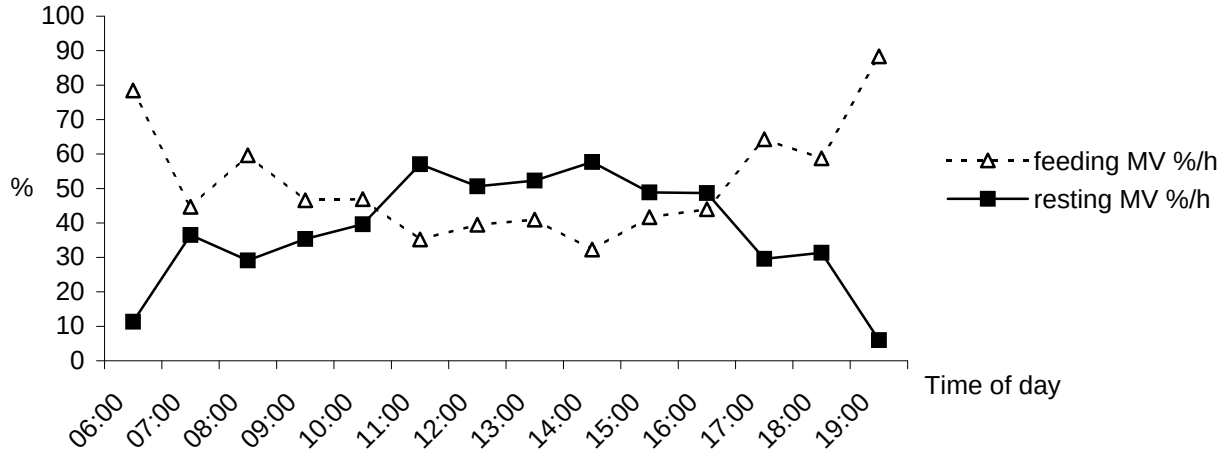

Figure 3.1: Daily activity rhythm of the European bison over the complete investigation period

3.1.2.2 Exmoor ponies

Figure 3.2 indicates the daily activity rhythm of the Exmoor ponies over the complete investigation period. Like the European bison, the Exmoor ponies tend to graze in the early morning hours until the first resting period between 10:00 and 11:00, having a second rest between 13:00 and 14:00 before starting an extensive feeding period until the evening hours.

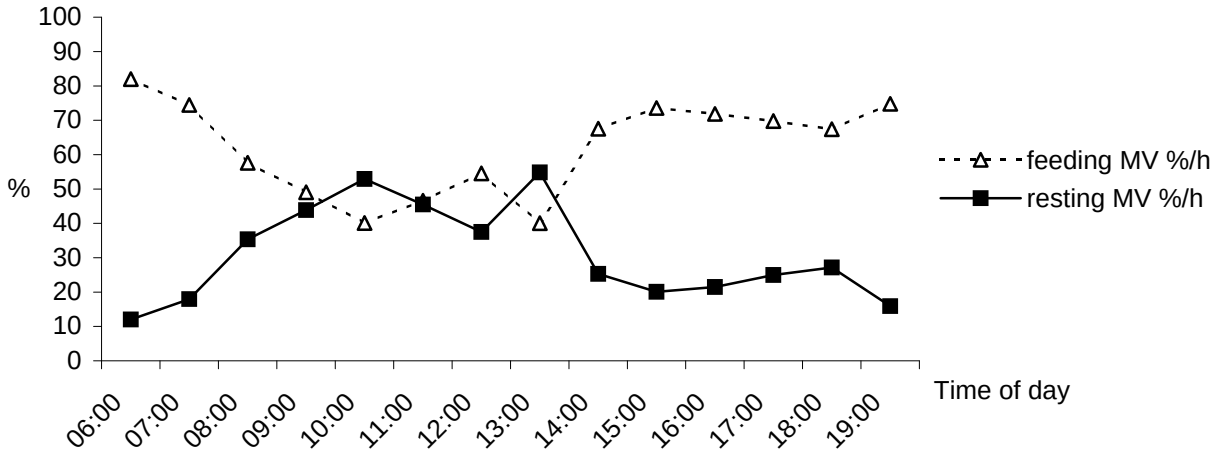

Figure 3.2: Daily activity rhythm of the Exmoor ponies over the complete investigation period

3.1.2.3 Dybowski deer

The Dybowski deer's daily activity rhythm is displayed in Figure 3.3. Feeding in the morning hours is followed by a distinct resting period between 08:00 and 09:00, which leads to several alternating short-termed phases of ingestion and resting behaviour. The next clear feeding periods occur between 16:00 and 17:00 and in the evening hours.

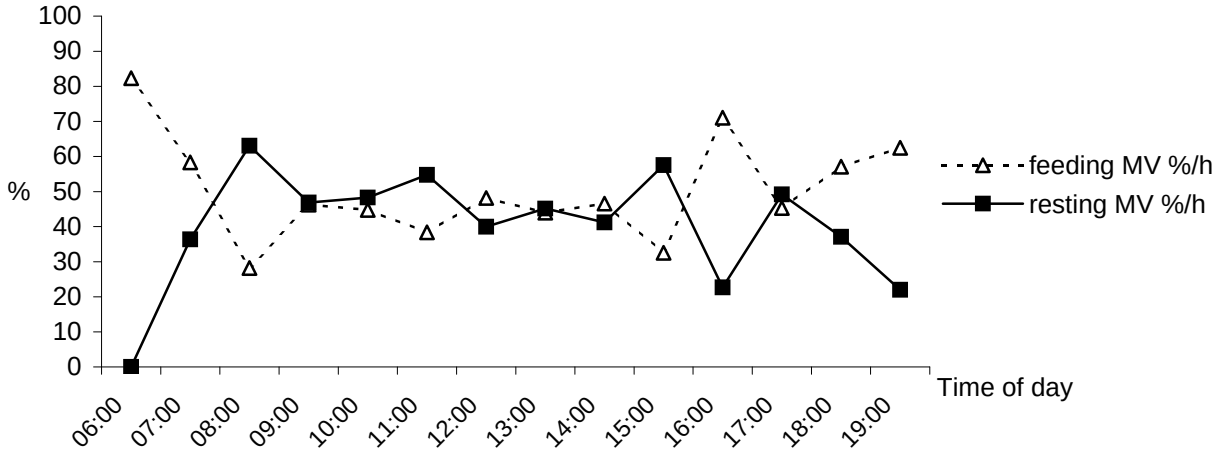

Figure 3.3: Daily activity rhythm of the Dybowski deer over the complete investigation period

3.1.3 Behaviour in different seasons

To demonstrate the behavioural changes in the different seasons and thereby under changing environmental conditions, the animals' behaviour was additionally analysed separately for the separate seasons. For the presentation of the results, only the values of the main behaviours will be diagrammed for clarity reasons. The results are the mean values as percentages of the day for all focus animals of the species studied over the different seasons. For comparison, the results for the complete observation period are included in the tables.

3.1.3.1 European bison

Table 3.4 lists the main behaviours of the European bison in the different seasons. Compared to the mean values over the complete observation period, the daily time spent on feeding is increased from March to May and again from September to November, then decreased from December to February. The time spent resting changed in the opposite way, while the results for locomotion and comforting behaviour remained relatively constant. The only exception is an increased value for comforting behaviour from June to August. Social interactions were highest from June to November regarding positive social contact. Agonistic contact was highest from September to November.

Table 3.4: Main behaviours of the European bison in different seasons

% / d	MV	MV March - May	MV June - August	MV September - November	MV December - February
fee	47.73	52.59	47.23	54.02	36.40
res	43.05	38.00	41.85	34.02	53.48
loc	6.79	5.88	6.60	7.67	7.12
com	1.68	1.48	2.68	1.16	1.26
soc +	0.94	0.05	1.67	1.89	0.10
soc -	0.78	0.48	0.79	1.45	0.39

3.1.3.2 Exmoor ponies

The Exmoor ponies' main behaviours, as shown in Table 3.5, varied more in the different seasons. Having low values for the daily time spent for ingestion from June to August, the daily time invested for feeding was clearly increased from March to May and from September to November. Correlative, the daily resting periods increased from June to August and

decreased from March to May and from September to November. Comforting behaviour was observed mostly during the summer months June to August, as was positive and agonistic social contact.

Table 3.5: Main behaviours of the Exmoor ponies in different seasons

% / d	MV	MV March - May	MV June - August	MV September - November	MV December - February
fee	58.62	68.08	41.34	72.57	52.96
res	34.54	25.18	52.39	19.79	40.30
loc	3.87	3.29	2.96	4.81	4.52
com	1.37	1.53	2.08	1.23	0.51
soc +	0.86	0.69	1.35	1.16	0.15
soc -	0.34	0.23	0.58	0.47	0.06

3.1.3.3 Dybowski deer

The main behaviours of the Dybowski deer in the different seasons are presented in Table 3.6. Feeding took up the lowest amount of time in summer from June to August and the highest from December to February, although the overall variations were lesser than in the other species. The resting periods changed in the opposite order.

Locomotion increased continually over the year, having the largest proportion from December to February. Comforting behaviour occurred the most from June to August, as did all social interactions.

Table 3.6: Main behaviours of the Dybowski deer in different seasons

% / d	MV	MV March - May	MV June - August	MV September - November	MV December - February
fee	47.22	45.19	41.85	49.78	52.98
res	43.64	49.20	49.62	41.34	36.64
loc	4.55	2.39	3.63	5.57	6.86
com	2.44	2.62	3.14	2.61	1.23
soc +	0.43	0.01	0.94	0.42	0.29
soc -	0.43	0.08	0.89	0.50	0.18

3.1.4 Daily activity rhythms in different seasons

Resulting from the different behaviours during the seasons, the animals also show alterations in their daily activity rhythms. As in Chapter 3.1.2, the activity rhythms are graphically displayed by setting in contrast the mean values of feeding and resting for every observed hour in the analysed season.

3.1.4.1 European bison

From March to May, the European bisons' daily activity rhythm (Figure 3.4) showed slight alternating periods of feeding and resting until 12:00. This was followed by a more distinct ingestion phase towards the evening, interrupted by a resting period from 15:00 to 16:00.

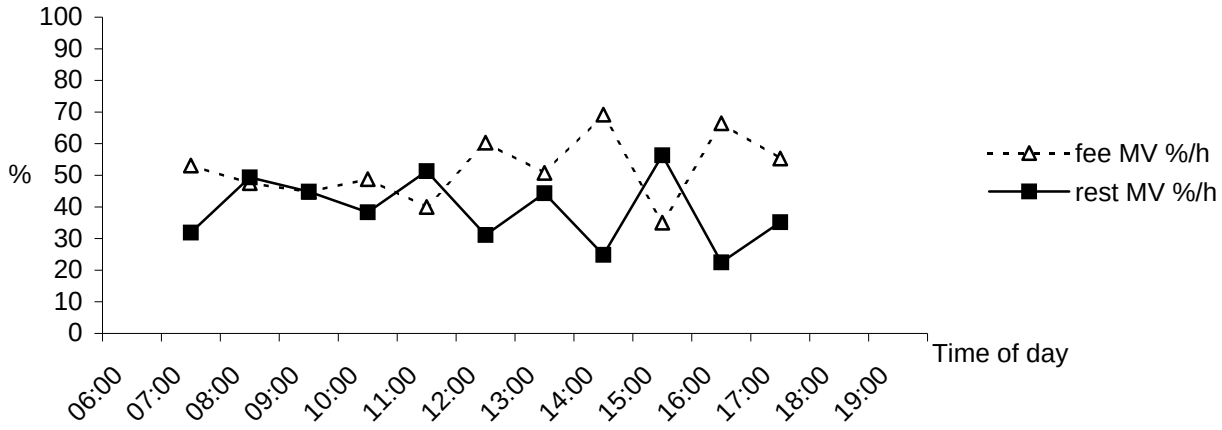

Figure 3.4: Daily activity rhythm of the European bison from March to May

Figure 3.5 displays the daily activity rhythm of the European bison in the summer season from June to August. Here, the animals showed a regular alternation of feeding and resting periods. Resting occurred mainly from 10:00 to 11:00 and 13:00 to 17:00, whereas feeding lasted mainly from 11:00 to 13:00 and in the early morning and evening hours.

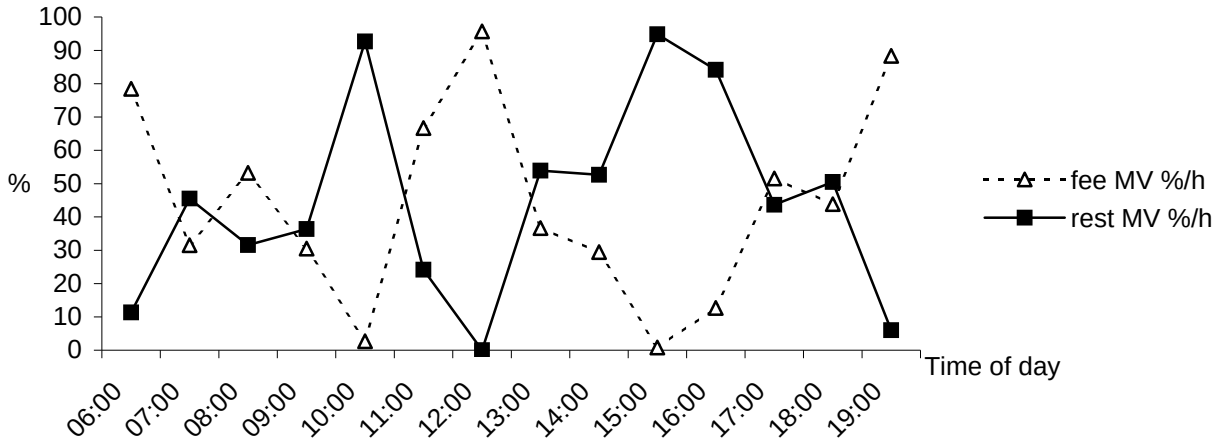

Figure 3.5: Daily activity rhythm of the European bison from June to August

As in March to May, feeding dominated the daily rhythm of the European bison from September to November (Figure 3.6). Only a single, if extended, period of resting occurred from 11:00 to 15:00.

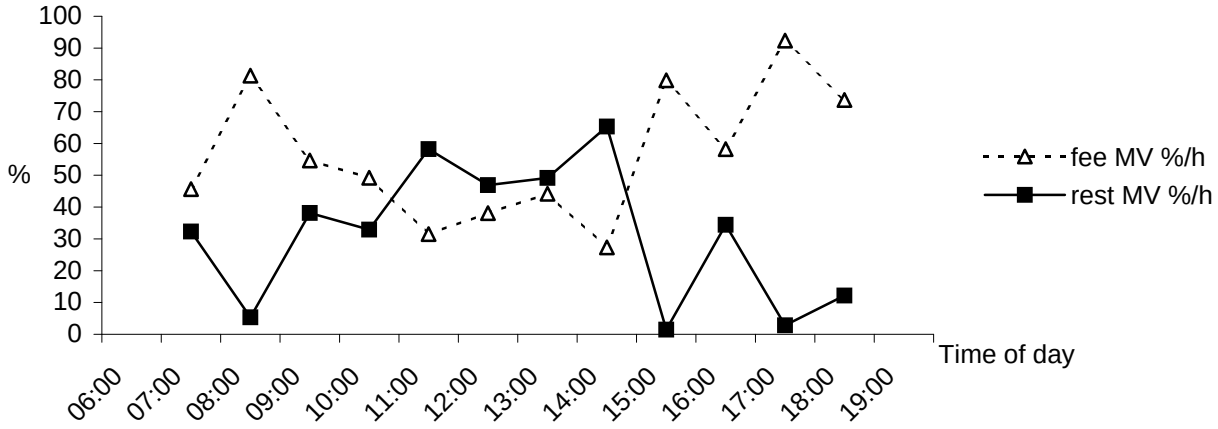

Figure 3.6: Daily activity rhythm of the European bison from September to November

In winter from December to February, the European bison extended this resting phase to the rest of the daily observation period (Figure 3.7). A distinct feeding period only occurred in the morning hours from 09:00 to 11:00.

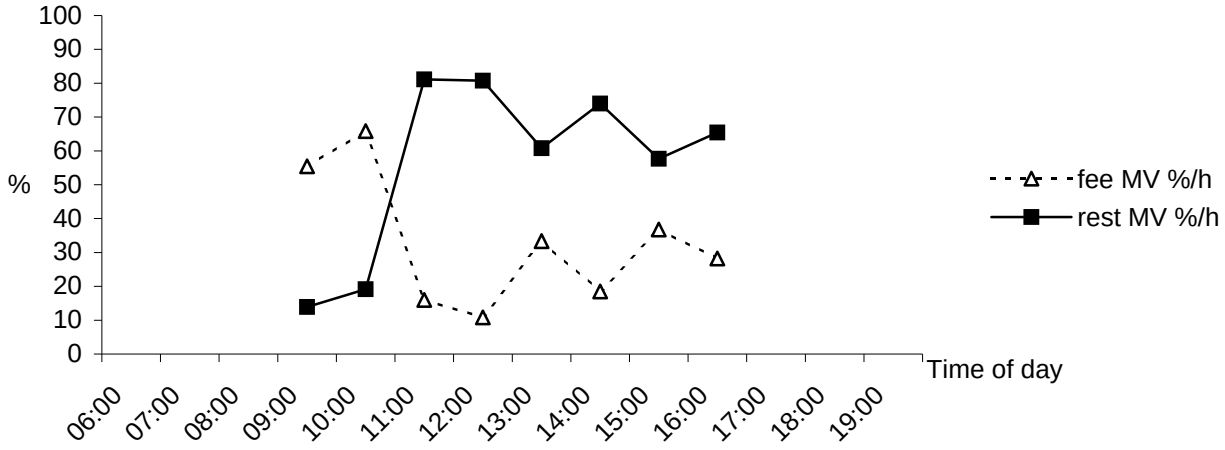

Figure 3.7: Daily activity rhythm of the European bison from December to February

3.1.4.2 Exmoor ponies

The Exmoor ponies' daily activity rhythm from March to May shows clear alternating periods of feeding and resting over the whole day (Figure 3.8). However, the values for the resting phases only exceed those for feeding from 10:00 to 11:00.

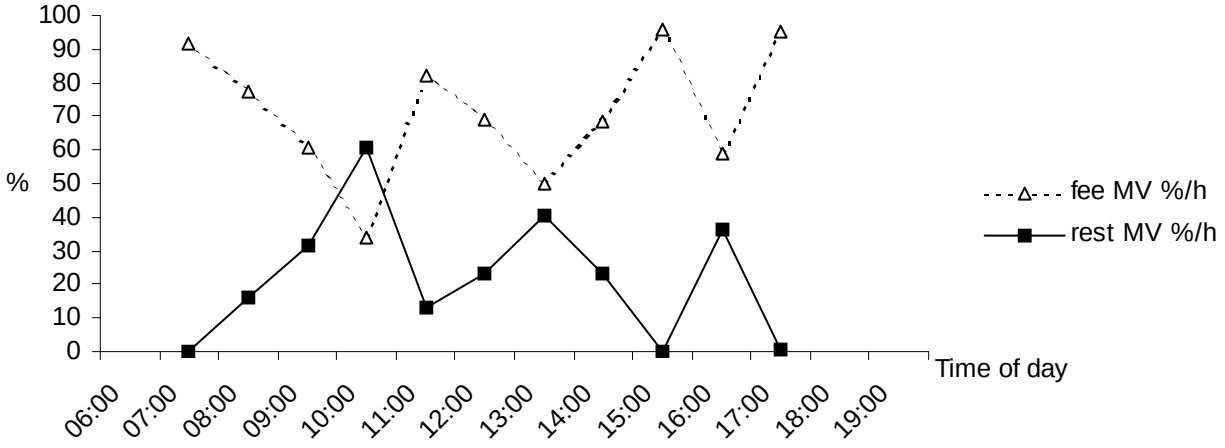

Figure 3.8: Daily activity rhythm of the Exmoor ponies from March to May

The opposite could be documented for the summer season from June to August (Figure 3.9). Extensive feeding periods in the early morning hours and towards the evening indeed

remained, but resting dominated the Exmoor ponies' day. Feeding only occurred between 16:00 and 17:00, and sometimes also between 11:00 and 12:00.

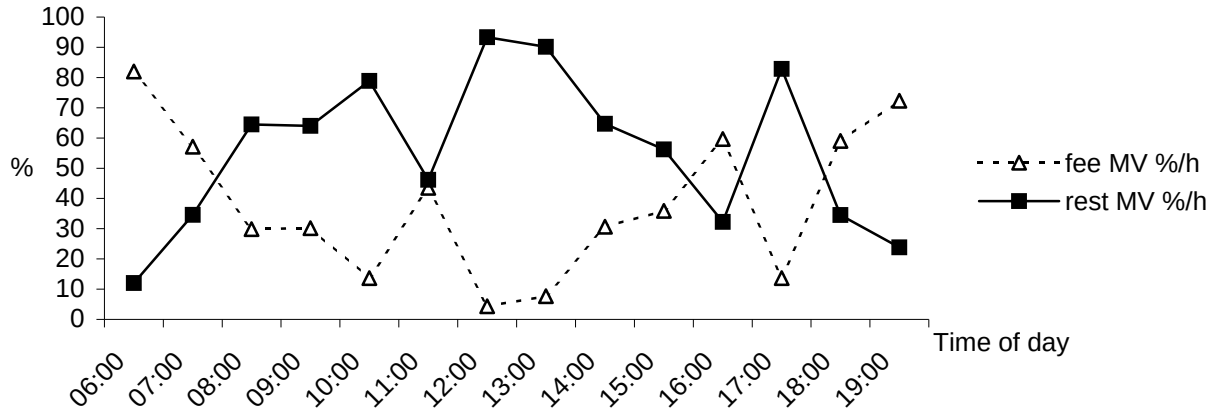

Figure 3.9: Daily activity rhythm of the Exmoor ponies from June to August

The daily activity rhythm of the Exmoor ponies from September to November (Figure 3.10) resembles the activity pattern from March to May (Figure 3.8), although the feeding periods are not that obvious. From September to November, the ponies fed for most of the daytime, with only one resting period between 09:00 and 10:00.

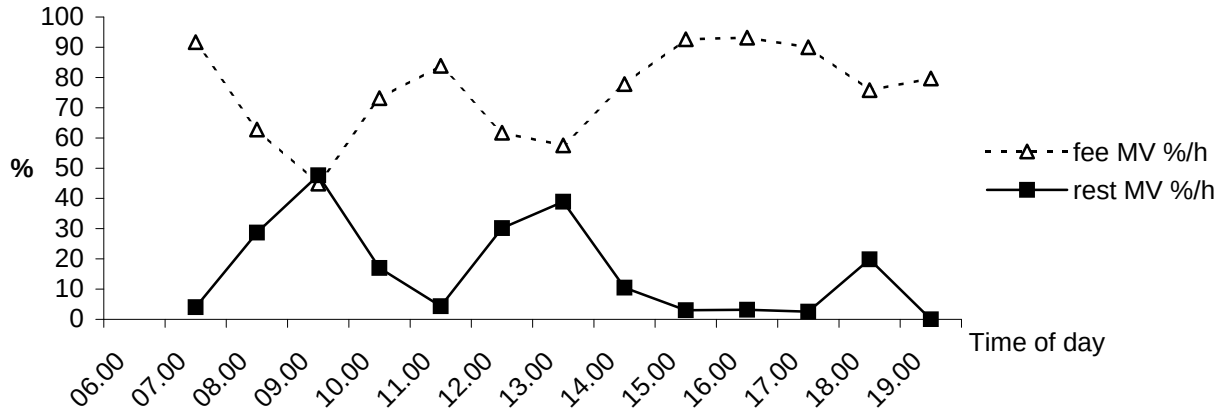

Figure 3.10: Daily activity rhythm of the Exmoor ponies from September to November

Regarding the Exmoor ponies' activity rhythm in winter from December to February (Figure 3.11), as with the European bison (Figure 3.7), there is a clear scheduling of the day. Starting with a short and weakly distinct feeding period, the first half of the day was completely

dedicated to resting until 14:00. Then feeding dominated the rest of the daily observation period.

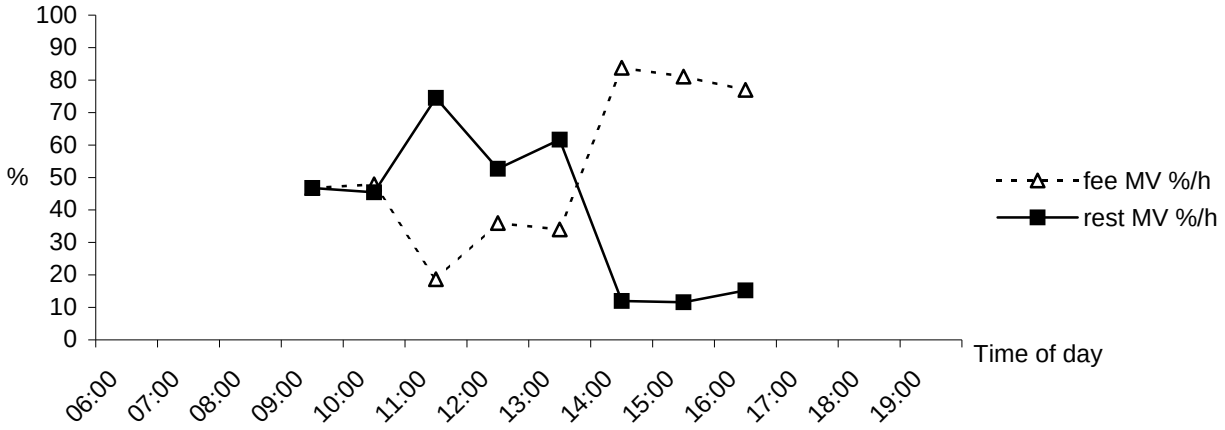

Figure 3.11: Daily activity rhythm of the Exmoor ponies from December to February

3.1.4.3 Dybowski deer

The daily activity rhythm of the Dybowski deer from March to May is shown in Figure 3.12. After feeding in the early morning hours, the morning was spent resting. After a feeding period from 12:00 to 13:00, the afternoon was also dominated by resting behaviour until 16:00.

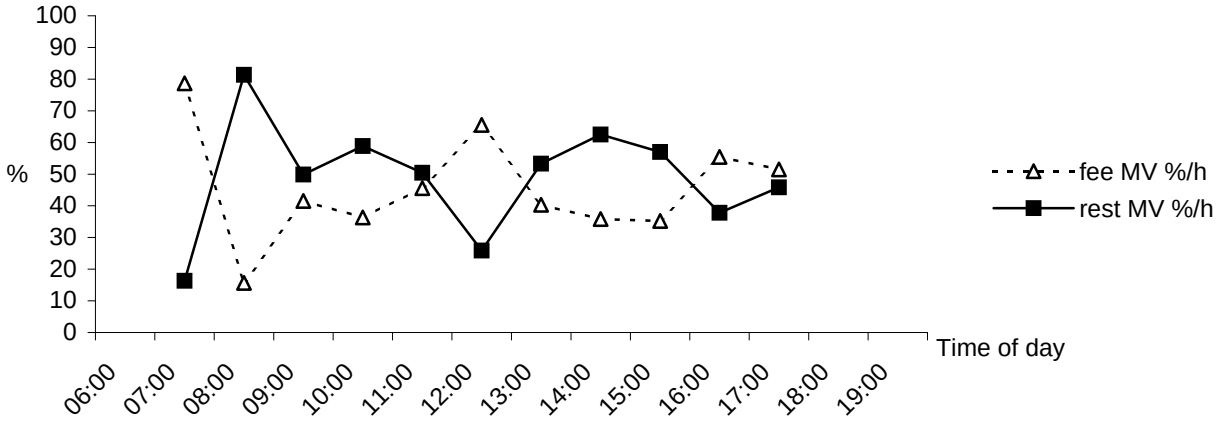

Figure 3.12: Daily activity rhythm of the Dybowski deer from March to May

From June to August, the Dybowski deer's daily activity rhythm changed only in the temporal specificity (Figure 3.13). The deer extended the first feeding period from 10:00 to 12:00 and started feeding again at 15:00. The resting periods remained in the morning from 07:00 to 10:00 and in the afternoon from 12:00 to 15:00.

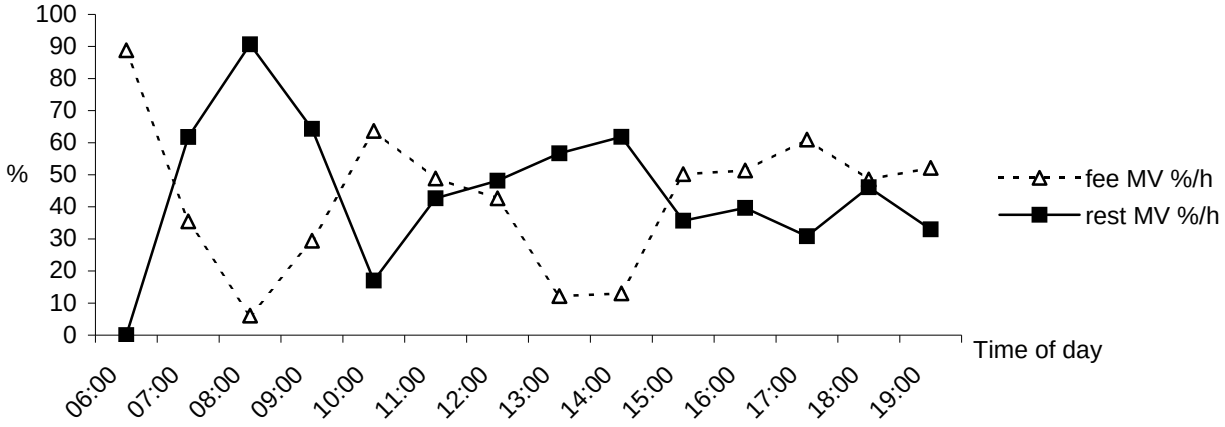

Figure 3.13: Daily activity rhythm of the Dybowski deer from June to August

Figure 3.14 displays the daily activity rhythm of the Dybowski deer from September to November. In this season, the mornings' feeding period lasted until 11:00 followed by resting behaviour until 14:00. In the afternoon, several periods of ingestion and resting alternated until the last observable feeding phase in the evening hours from 18:00 onwards.

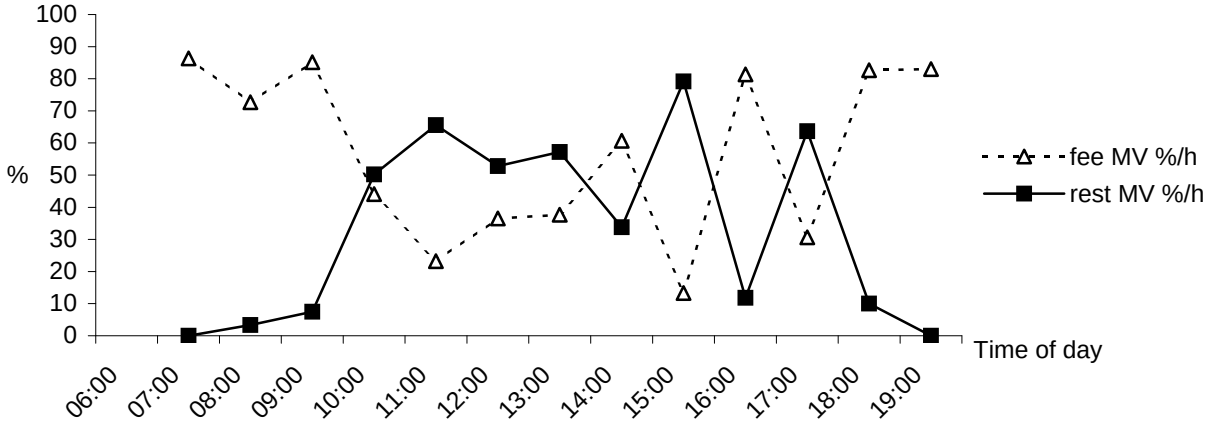

Figure 3.14: Daily activity rhythm of the Dybowski deer from September to November

During the winter season from December to February (Figure 3.15), alternating phases of feeding and resting behaviour occurred until 12:00, when a distinct feeding period was shown. After resting between 15:00 and 16:00, feeding followed for the rest of the daily observation period.

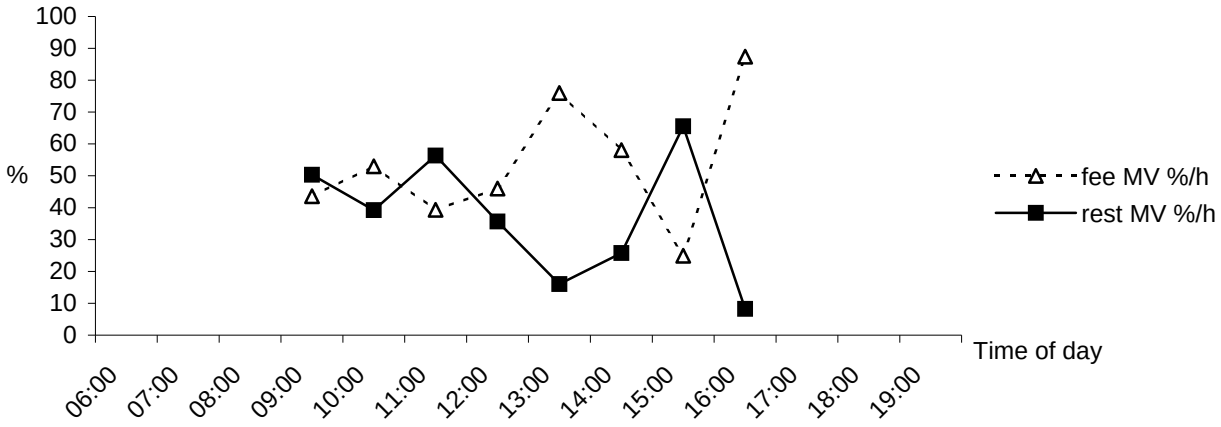

Figure 3.15: Daily activity rhythm of the Dybowski deer from December to February

3.2 Intra- and interspecific interactions

3.2.1 Intra- and interspecific interactions of the European bison

To display the results for the European bison's interactions, all contact between individuals was documented. This was done not only regarding interactions among the focus animals, but for all interactions in which they were involved. Most of the contact having only a very short duration, these are listed as single actions and evaluated according to the percentage of occurrence. All interactions were categorised into groups based on the age and gender of the interacting individuals. An extensive individual-interaction grid will be given below (Table 3.11).

3.2.1.1 Intra- and interspecific interactions of the European bison in general

The European bison's intra- and interspecific positive social contact is listed in Table 3.7. Most positive interactions occurred between the bull and adult cows (73.41% of all observed

interactions), followed by mother-calf interactions regarding their own calves (21.68%). Contact with other calves could only be documented twice over the complete investigation period. Also, there was only little contact between the bull and his offspring.

Table 3.7: Proportions of the European bison's intra- and interspecific positive social contact

	Cow - Cow	Cow - own Calf	Cow - other Calf	Calf - Calf	Bull - Cow	Bull - Calf	Europ. b. - Exm. p.	Europ. b. - Dyb. deer	Europ. b. - Visitor
Sum	0	75	2	8	254	7	0	0	0
%	0.00	21.68	0.58	2.31	73.41	2.02	0.00	0.00	0.00

Interactions between the calves occurred only seldom (2.31%). Positive social contact among the adult females or with the other species or visitors was not observed.

On the contrary, most agonistic contact occurred between the adult females (21.81%) and likewise between adult cows and other females' calves (21.50%) (Table 3.8). There was also regular agonistic behaviour of the bull towards his offspring (13.40%) as well as towards cows (12.15%). Agonistic interactions between calves occurred only seldom; agonistic behaviour of a cow towards her own calf only once. Interspecific agonistic contact appeared mostly between the European bison and the Exmoor ponies (13.40%), followed by interactions with visitors (7.79%) and the Dybowski deer (5.92%).

Table 3.8: Proportions of the European bison's intra- and interspecific agonistic social contact

	Cow - Cow	Cow - own Calf	Cow - other Calf	Calf - Calf	Bull - Cow	Bull - Calf	Europ. b. - Exm. p.	Europ. b. - Dyb. deer	Europ. b. - Visitor
Sum	70	1	69	12	39	43	43	19	25
%	21.81	0.31	21.50	3.74	12.15	13.40	13.40	5.92	7.79

3.2.1.2 Intra- and interspecific interactions of the European bison in different seasons

To analyse the appearance of social interactions in the seasonal context, the intra- and interspecific contact has been classified for the different seasons. Table 3.9 displays the distribution of the European bison's intra- and interspecific positive social contact over the different seasons.

Most of the positive contact happened in the summer and autumn months from June to November. Mother-calf interactions occurred mainly in June to August and regularly still in September to November. The highest interaction rate took place between the bull and adult cows, starting in June to August and reaching the top values in September to November.

Table 3.9: Proportions of the European bison's intra- and interspecific positive social contact in different seasons

		Cow - Cow	Cow - own Calf	Cow - other Calf	Calf - Calf	Bull - Cow	Bull - Calf	Europ. b. - Exm. p.	Europ. b. - Dyb. deer	Europ. b. - Visitor
March - May	Sum	0	3	1	1	1	0	0	0	0
	%	0.00	50.00	16.67	16.67	16.67	0.00	0.00	0.00	0.00
June - August	Sum	0	49	1	4	111	1	0	0	0
	%	0.00	29.52	0.60	2.41	66.87	0.60	0.00	0.00	0.00
September - November	Sum	0	22	0	3	135	6	0	0	0
	%	0.00	13.25	0.00	1.81	81.33	3.61	0.00	0.00	0.00
December - February	Sum	0	1	0	0	7	0	0	0	0
	%	0.00	12.50	0.00	0.00	87.50	0.00	0.00	0.00	0.00

Agonistic contact among the cows occurred over the whole observation period, although the frequency of contact was highest from June to November (Table 3.10). This was also the case for contact between the cows and the bull. Agonistic interactions between cows and other calves occurred almost consistently over the year. The bull also showed agonistic behaviour towards his offspring during the year, with the exception of the winter period from December to February.

Interspecific agonistic contact with the Exmoor ponies happened mostly from autumn to spring, whereas contact with the Dybowski deer was mainly limited to the winter season.

Agonistic contact with visitors could be observed almost exclusively from September to November.

Table 3.10: Proportions of the European bison's intra- and interspecific agonistic social contact in different seasons

		Cow - Cow	Cow - own Calf	Cow - other Calf	Calf - Calf	Bull - Cow	Bull - Calf	Europ. b. - Exm. p.	Europ. b. - Dyb. deer	Europ. b. - Visitor
March - May	Sum	6	0	18	4	2	14	7	0	0
	%	11.76	0.00	35.29	7.84	3.92	27.45	13.73	0.00	0.00
June - August	Sum	30	0	20	1	12	14	1	1	1
	%	37.50	0.00	25.00	1.25	15.00	17.50	1.25	1.25	1.25
September - November	Sum	27	1	21	6	20	14	13	0	24
	%	21.43	0.79	16.67	4.76	15.87	11.11	10.32	0.00	19.05
December - February	Sum	7	0	10	1	5	1	22	18	0
	%	10.94	0.00	15.63	1.56	7.81	1.56	34.38	28.13	0.00

3.2.1.3 Social interaction grids of the European bison

Table 3.11 displays the observed single positive interactions of the European bison, itemised for each individual. The focus animals are highlighted in grey. Six animals are highlighted here, as there was a change in the juvenile focus animal after "Zarella" was sold to another animal park during the observation period.

Table 3.11: Interaction grid of the European bison's intra- and interspecific positive social contact

soc + Contact to	from	Favorit	Zakka	Zaberta	Zakki	Zareta	Zareti	Zabra	Zabine	Zarana	Zakola	Zarella	Zaricco	Zabronzo	Zabasco	Zamoa	Zaziki	Zalando	Zandor	Exm. p.	Dyb. deer	Visitor
Favorit	am	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zakka	af	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zaberta	af	21	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Zakki	af	71	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zareta	af	43	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zareti	af	38	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zabra	af	77	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zabine	af	4	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0
Zarana	jf	7	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0
Zakola	jf	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0
Zarella	jf	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0
Zaricco	jm	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0
Zabronzo	jm	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0
Zabasco	jm	0	0	0	1	0	0	0	0	2	0	0	0	0	X	0	0	0	0	0	0	0
Zamoa	jm	0	0	0	16	0	0	0	0	1	0	0	0	0	0	X	0	0	0	0	0	0
Zaziki	jm	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	X	0	0	0	0	0
Zalando	jm	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	X	0	0	0	0
Zandor	jm	0	0	57	1	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0
Exm. p.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0
Dyb. deer		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0
Visitor		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X
Sum contact		261	0	57	18	0	0	0	0	4	0	4	0	0	0	0	0	0	2	0	0	0

am = adult male, af = adult female, jm = juvenile male, jf = juvenile female = Focus animal

The individual intra- and interspecific agonistic social interactions of the European bison are given in Table 3.12. The amounts of interactions displayed in Table 3.7 and Table 3.8 differ due to the fact that not all agonistic contact was listed in the interaction grids.

Agonistic behaviour can be categorised into direct and indirect contact (ALTMANN 1973, MARTIN & BATESON 2008). Direct contact is defined as one animal showing a behaviour towards another individual, which responds in any way to this behaviour. Indirect contact is defined as one animal causing another individual to react in any way without having shown a behaviour towards it. The most common situation for indirect interactions is one animal

actively avoiding another individual by stepping aside or walking away without any previous interaction or threatening behaviour.

This avoidance of direct contact was a major part of the intraspecific interactions, but would cause a false picture of the behaviour of the different animals to each other. For this reason, only the direct interactions are charted in the interaction grids of all species.

Table 3.12: Interaction grid of the European bison's intra- and interspecific agonistic social contact

soc - Contact	from / to	Favorit	Zakka	Zaberta	Zakki	Zareta	Zareti	Zabra	Zabine	Zarana	Zakola	Zarella	Zaricco	Zabronzo	Zabasco	Zamoa	Zaziki	Zalando	Zandor	Exm. p.	Dyb. deer	Visitor
Favorit	am	X	0	15	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zakka	af	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zaberta	af	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zakki	af	2	0	8	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zareta	af	2	0	5	5	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zareti	af	2	0	4	3	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zabra	af	1	0	6	1	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zabine	af	1	0	2	2	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0
Zarana	jf	3	0	4	3	2	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0
Zakola	jf	0	0	0	4	0	0	0	0	1	X	0	0	0	0	0	0	0	0	0	0	0
Zarella	jf	4	0	0	3	2	0	0	3	1	0	X	0	1	0	0	0	0	0	0	0	0
Zaricco	jm	2	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0
Zabronzo	jm	22	0	4	10	10	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0
Zabasco	jm	0	0	2	2	3	0	0	0	1	0	0	0	0	X	0	0	0	0	0	0	0
Zamoa	jm	3	0	2	0	1	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0
Zaziki	jm	1	0	0	1	4	0	0	0	0	0	0	0	0	0	0	X	0	0	0	1	0
Zalando	jm	2	0	0	2	1	0	0	0	0	0	2	0	0	0	0	0	X	0	0	0	0
Zandor	jm	2	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	X	0	0	0
Exm. p.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0
Dyb. deer		0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0
Visitor		11	0	8	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X
Sum contact		58	0	60	51	24	0	0	3	5	0	3	0	1	0	0	0	0	0	0	1	0

am = adult male, af = adult female, jm = juvenile male, jf = juvenile female = Focus animal

3.2.2 Intra- and interspecific interactions of the Exmoor ponies

3.2.2.1 Intra- and interspecific interactions of the Exmoor ponies in general

As with the European bison, the social interactions of the Exmoor ponies were categorised by positive and agonistic contact. Horses, however, regularly show mutual grooming behaviour (SCHÄFER 1993), which did not occur in the other investigated species. As mutual grooming always took between one and eight minutes, therefore lasting generally much longer than the other contact, it was regarded separately from the other positive social interactions.

Most of the Exmoor ponies' intra- and interspecific positive social contact occurred between the mares and their foals (Table 3.13). Of all interactions observed, 12.04% involved the stallion and his offspring, and 9.26% were between the stallion and the mares. Positive social contact between the foals took place for 6.94% of all observed interactions. Contact between mares was rarely observed, as was the mares' contact with other foals.

Intraspecific positive social interactions of the Exmoor ponies could not be observed with the European bison. Positive contact between the Exmoor ponies and the Dybowski deer stag "Ludwig", however, took place for 11.11% of all interactions. Contact with the visitors was limited to begging behaviour towards visitors ignoring the animal parks request not to feed the animals.

Table 3.13: Proportions of the Exmoor ponies' intra- and interspecific positive social contact (without mutual grooming)

	Mare - Mare	Mare - own Foal	Mare - other Foal	Foal - Foal	Stallion - Mare	Stallion - Foal	Exm. p. - Europ. b.	Exm. p. - Dyb. deer	Exm. p. - Visitor
Sum	5	105	4	15	20	26	0	24	17
%	2.31	48.61	1.85	6.94	9.26	12.04	0.00	11.11	7.87

Table 3.14 shows the proportions of the Exmoor ponies' intra- and interspecific agonistic social contact. Most of the agonistic behaviour among the Exmoor ponies arose between the mares and other foals, the stallion and the foals, and the stallion and the mares, all three comprising 10% of the overall interactions each.

Agonistic contact with the visitors could be observed only rarely. Intraspecific interactions with the European bison and the Dybowski deer arose to a larger extent.

Avoidance of direct contact comprised most of the intraspecific interactions. All 43 observed agonistic interactions between the Exmoor ponies and the European bison (Table 3.14) were avoiding behaviour of Exmoor ponies towards approaching European bison.
Also 25 (62.5%) of the observed agonistic interactions between the Exmoor ponies and the Dybowski deer were avoiding behaviours of the Exmoor ponies without any previous interaction.

Table 3.14: Proportions of the Exmoor ponies' intra- and interspecific agonistic social contact

	Mare - Mare	Mare - own Foal	Mare - other Foal	Foal - Foal	Stallion - Mare	Stallion - Foal	Exm. p. - Europ. b.	Exm. p. - Dyb. deer	Exm. p. - Visitor
Sum	6	3	18	8	15	16	43	40	5
%	3.90	1.95	11.69	5.19	9.74	10.39	27.92	25.97	3.25

3.2.2.2 Mutual grooming in general

The proportions of the Exmoor ponies' mutual grooming contacts are listed in Table 3.15.
The percentages are given for the sum of contact. Largest numbers of mutual grooming contact occurred between the foals (47.83%). The stallion was involved in mutual grooming with mares for 15.22%, and foals for 13.04% of all interactions. The mutual grooming contact between mares and foals counted for 8.70% for interactions with both their own and other mares' foals. Only rarely was mutual grooming between the mares.
Notable was one grooming interaction with the Dybowski deer stag "Ludwig" during the observation period.

Table 3.15: Proportions of the Exmoor ponies' mutual grooming contact

	Mare - Mare	Mare - own Foal	Mare - other Foal	Foal - Foal	Stallion - Mare	Stallion - Foal	Exm. p. - Europ. b.	Exm. p. - Dyb. deer
Sum Contact	2	4	4	22	6	7	0	1
Duration in minutes	4	10	7	49	13	10	0	2
Percentage %	4.35	8.70	8.70	47.83	13.04	15.22	0.00	2.17

3.2.2.3 Intra- and interspecific interactions of the Exmoor ponies in different seasons

The positive social interactions of the Exmoor ponies have also been classified for the different seasons. Most of the social contact between the mares and their foals occurred in summer and autumn from June to November (Table 3.16). Contact occurred mostly during this period, whereas in the winter and early spring from December to May fewer interactions arose. Most of the interspecific positive contact regarding the Dybowski deer also took place in the summer from June to August. Contact with the visitors occurred for the most part from September to November.

Table 3.16: Proportions of the Exmoor ponies' intra- and interspecific positive social contact in different seasons (without mutual grooming)

		Mare - Mare	Mare - own Foal	Mare - other Foal	Foal - Foal	Stallion - Mare	Stallion - Foal	Exm. p. - Europ. b.	Exm. p. - Dyb. deer	Exm. p. - Visitor
March - May	Sum	2	20	1	3	6	0	0	0	0
	%	6.25	62.50	3.13	9.38	18.75	0.00	0.00	0.00	0.00
June - August	Sum	2	35	3	10	10	12	0	22	3
	%	2.06	36.08	3.09	10.31	10.31	12.37	0.00	22.68	3.09
September - November	Sum	1	48	0	2	4	10	0	2	10
	%	1.30	62.34	0.00	2.60	5.19	12.99	0.00	2.60	12.99
December - February	Sum	0	2	0	0	0	4	0	0	4
	%	0.00	20.00	0.00	0.00	0.00	40.00	0.00	0.00	40.00

The proportions of the Exmoor ponies' intra- and interspecific agonistic social contact in different seasons are listed in Table 3.17. As with the positive intraspecific contact, most of the agonistic interactions took place from June to November. Regarding the interspecific agonistic contact of the Exmoor ponies, those with the European bison mainly occurred in autumn and especially winter. With the Dybowski deer, the agonistic contact remained restricted to the summer months from June to August.

Table 3.17: Proportions of the Exmoor ponies' intra- and interspecific agonistic social contact in different seasons

		Mare - Mare	Mare - own Foal	Mare - other Foal	Foal - Foal	Stallion - Mare	Stallion - Foal	Exm. p. - Europ. b.	Exm. p. - Dyb. deer	Exm. p. - Visitor
March - May	Sum	1	1	2	3	3	5	7	3	0
	%	4.00	4.00	8.00	12.00	12.00	20.00	28.00	12.00	0.00
June - August	Sum	5	2	13	4	6	4	1	0	5
	%	12.50	5.00	32.50	10.00	15.00	10.00	2.50	0.00	12.50
September - November	Sum	0	0	3	1	6	6	13	27	0
	%	0.00	0.00	5.36	1.79	10.71	10.71	23.21	48.21	0.00
December - February	Sum	0	0	0	0	0	1	22	10	0
	%	0.00	0.00	0.00	0.00	0.00	3.03	66.67	30.30	0.00

3.2.2.4 Social interaction grids and mutual grooming of the Exmoor ponies

The Exmoor ponies' intra- and interspecific positive social contact is listed as an interaction grid (Table 3.18). Since changes in the focus animals had to be made, more than five individuals are marked in the social interaction grid. As with the European bison, the juvenile focus animal ("Saba's Emily") was sold to another animal park during the observation period, so another individual ("Saba's Enya") had to be observed for the rest of the data collection. "Saba's Emma" and "Saba's Epona" were also sold during the investigation period, but not being focus animals this had no effect on the observation. Additionally, the stallion "Ernie" was relocated to another enclosure for breeding reasons and replaced by "Apollo", who also took Ernie's place as the adult male focus individual.

Table 3.18: Interaction grid of the Exmoor ponies' intra- and interspecific positive social contact

soc + Contact to	from	Apollo	Ernie	Gypsy	Saba's Calypso	Saba's Glücksburg	Saba's Hasselburg	Saba's Klosterburg	Saba's Emily	Saba's Emma	Saba's Enya	Saba's Epona	Saba's Fame	Saba's Fenya	Saba's Flora	Saba's Freya	Saba's Greta	Dyb. deer	Visitor
Apollo	am	X	X	0	0	0	0	0	0	X	0	X	0	0	0	0	0	0	0
Ernie	am	X	X	1	1	0	4	1	0	0	3	0	0	2	0	1	0	0	0
Gypsy	af	0	2	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saba's Calypso	af	0	8	0	X	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Saba's Glücksburg	af	0	0	0	0	X	0	0	1	0	0	0	0	0	0	0	0	0	0
Saba's Hasselburg	af	0	3	1	0	0	X	0	0	0	0	0	0	0	2	0	0	0	0
Saba's Klosterburg	af	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0
Saba's Emily	jf	0	2	0	0	0	0	0	X	0	0	0	0	0	1	1	0	1	0
Saba's Emma	jf	X	3	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0
Saba's Enya	jf	0	5	0	0	0	0	0	1	0	X	0	0	0	0	0	0	0	0
Saba's Epona	jf	X	5	0	0	0	2	0	6	0	0	X	0	0	0	0	0	0	0
Saba's Fame	jm	0	0	53	0	0	2	0	2	0	0	0	X	0	0	0	0	0	0
Saba's Fenya	jf	0	4	1	0	0	1	7	2	0	0	0	0	X	0	0	0	0	0
Saba's Flora	jf	0	0	0	0	0	22	0	1	0	0	0	0	0	X	0	0	0	0
Saba's Freya	jf	0	0	0	0	0	0	0	1	0	0	0	0	0	0	X	0	0	0
Saba's Greta	jf	0	0	0	0	0	0	18	1	0	0	0	0	0	0	0	X	0	0
Dyb. deer		0	0	0	0	0	0	0	9	9	0	4	0	0	2	0	0	X	0
Visitor		0	10	0	1	0	2	0	4	0	0	0	0	0	0	0	0	0	X
Sum contact		0	42	56	2	0	37	26	28	9	3	4	0	2	5	2	0	1	0

am = adult male, af = adult female, jm = juvenile male, jf = juvenile female = Focus animal

Table 3.19 shows the interaction grid of the Exmoor ponies' intra- and interspecific agonistic social contact.

The indirect agonistic interactions such as avoiding behaviour were not included (see Chapter 3.2.1.3 above).

Table 3.19: Interaction grid of the Exmoor ponies' intra- and interspecific agonistic social contact

soc - Contact to	from	Apollo	Ernie	Gypsy	Saba's Calypso	Saba's Glücksburg	Saba's Hasselburg	Saba's Klosterburg	Saba's Emily	Saba's Emma	Saba's Enya	Saba's Epona	Saba's Fame	Saba's Fenya	Saba's Flora	Saba's Freya	Saba's Greta	Dyb. deer	Visitor
Apollo	am	X	X	0	0	0	1	0	0	X	3	X	0	0	0	0	0	0	0
Ernie	am	X	X	0	1	0	4	1	3	0	1	0	0	1	0	0	0	1	0
Gypsy	af	0	0	X	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Saba's Calypso	af	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saba's Glücksburg	af	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0
Saba's Hasselburg	af	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	1	0
Saba's Klosterburg	af	0	1	0	0	0	0	X	0	0	0	0	0	0	0	0	0	3	0
Saba's Emily	jf	0	1	2	0	0	2	0	X	0	0	3	0	0	0	0	0	3	0
Saba's Emma	jf	X	0	3	0	0	3	0	0	X	0	0	0	0	0	0	0	0	0
Saba's Enya	jf	0	1	1	0	0	2	0	1	0	X	0	0	0	0	0	0	0	0
Saba's Epona	jf	X	2	1	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0
Saba's Fame	jm	0	1	0	0	0	0	1	0	0	1	0	X	0	0	0	0	0	0
Saba's Fenya	jf	0	0	0	0	0	0	0	0	0	1	0	0	X	0	0	0	0	0
Saba's Flora	jf	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0
Saba's Freya	jf	0	0	0	0	0	1	0	0	0	0	0	0	0	0	X	0	0	0
Saba's Greta	jf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0
Dyb. deer		0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0
Visitor		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X
Sum contact		0	6	9	1	1	13	2	4	0	6	3	0	1	0	0	0	9	0

am = adult male, af = adult female, jm = juvenile male, jf = juvenile female = Focus animal

In Table 3.20, all mutual grooming contact of the Exmoor ponies is displayed. Other than the positive and agonistic interactions, they are given in minutes.

Table 3.20: Interaction grid of the Exmoor ponies' intra- and interspecific mutual grooming contact

gro in minutes to	from	Apollo	Ernie	Gypsy	Saba's Calypso	Saba's Glücksburg	Saba's Hasselburg	Saba's Klosterburg	Saba's Emily	Saba's Emma	Saba's Enya	Saba's Epona	Saba's Fame	Saba's Fenya	Saba's Flora	Saba's Freya	Saba's Greta	Dyb. deer	Visitor
Apollo	am	X	X	0	0	0	0	0	0	X	0	X	0	0	0	0	0	0	0
Ernie	am	X	X	0	0	0	10	0	0	0	0	0	0	0	0	1	0	0	0
Gypsy	af	0	1	X	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0
Saba's Calypso	af	0	0	0	X	0	4	0	3	0	0	0	0	0	0	0	0	0	0
Saba's Glücksburg	af	0	0	0	0	X	0	0	4	0	0	0	0	0	0	0	0	0	0
Saba's Hasselburg	af	0	2	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0
Saba's Klosterburg	af	0	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0
Saba's Emily	jf	0	0	2	0	0	0	0	X	0	0	3	0	0	0	0	0	0	0
Saba's Emma	jf	X	5	0	0	0	0	0	1	X	0	0	0	0	0	0	0	0	0
Saba's Enya	jf	0	0	0	0	0	0	0	7	0	X	0	0	0	0	0	0	0	0
Saba's Epona	jf	X	4	1	0	0	0	0	28	0	0	X	0	0	0	0	0	0	0
Saba's Fame	jm	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0
Saba's Fenya	jf	0	0	0	0	0	0	0	9	0	0	0	0	X	0	0	0	0	0
Saba's Flora	jf	0	0	0	0	0	3	0	0	0	0	0	0	0	X	0	0	0	0
Saba's Freya	jf	0	0	0	0	0	0	0	2	0	0	0	0	0	0	X	0	0	0
Saba's Greta	jf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0
Dyb. deer		0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	X	0
Visitor		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X
Sum minutes		0	12	3	0	0	17	0	56	0	3	4	0	0	0	1	0	0	0

am = adult male, af = adult female, jm = juvenile male, jf = juvenile female = Focus animal

3.2.2.5 Mutual grooming in different seasons

As with the intra- and interspecific positive or agonistic social interactions, the grooming contact of the Exmoor ponies was analysed in the seasonal context (Table 3.21).
Most grooming occurred in spring from March to May. The only exception to this trend was the mutual grooming contact of the foals, which interacted mainly in summer and autumn from June to November.

Table 3.21: Proportions of the Exmoor ponies' mutual grooming contact in different seasons

		Mare - Mare	Mare - own Foal	Mare - other Foal	Foal - Foal	Stallion - Mare	Stallion - Foal	Exm. p. - Europ. b.	Exm. p. - Dyb. deer
March - May	Sum Contact	1	2	2	4	3	1	0	0
	Duration in minutes	2	6	3	7	7	1	0	0
June - August	Sum Contact	1	1	1	6	1	5	0	1
	Duration in minutes	2	3	3	19	2	9	0	2
September - November	Sum Contact	0	1	1	10	2	0	0	0
	Duration in minutes	0	1	1	21	4	0	0	0
December - February	Sum Contact	0	0	0	1	0	0	0	0
	Duration in minutes	0	0	0	2	0	0	0	0

3.2.3 Intra- and interspecific interactions of the Dybowski deer

3.2.3.1 Intra- and interspecific interactions of the Dybowski deer in general

The proportions of the Dybowski deer's intra- and interspecific positive social contact are listed in Table 3.22. Most of the interactions occurred between the hinds and their own deer calves, counting for 44.74% of all observed positive social contact. Stag-hind interactions arose for 16.45%, and positive contact among the hinds for 7.24%. Deer calves' interactions could not be observed, for there was only one surviving calf in the investigation period.

Like with the Exmoor ponies, intraspecific positive social contact occurred with the visitors exclusively as begging behaviour, counting for 9.21% of all contact in total. The Dybowski deer's contact with the Exmoor ponies made up 15.79% of the positive social interactions.

Table 3.22: Proportions of the Dybowski deer's intra- and interspecific positive social contact

	Hind - Hind	Hind - own Deer calf	Hind - other Deer calf	Deer calf - Deer calf	Stag - Hind	Stag - Deer calf	Dyb. deer - Europ. b.	Dyb. deer - Exm. p.	Dyb. deer - Visitor
Sum	11	68	6	0	25	4	0	24	14
%	7.24	44.74	3.95	0.00	16.45	2.63	0.00	15.79	9.21

Agonistic social contact between the hinds occurred for 30.11%, and between the stag and the hinds for 21.51% (Table 3.23). Contact with the visitors counted to 9.21% of all agonistic interactions, but was limited to indirect contact (see Chapter 3.2.1.3 above) by the avoiding behaviour of the Dybowski deer. A similar trend appeared, although less distinctive, with the agonistic interactions with the European bison and the Exmoor ponies. Although this contact counted for 10.22% and 21.51% respectively, about half of each of these interactions were again avoiding behaviour.

Table 3.23: Proportions of the Dybowski deer's intra- and interspecific agonistic social contact

	Hind - Hind	Hind - own Deer calf	Hind - other Deer calf	Deer calf - Deer calf	Stag - Hind	Stag - Deer calf	Dyb. deer - Europ. b.	Dyb. deer - Exm. p.	Dyb. deer - Visitor
Sum	56	0	0	0	40	4	19	40	27
%	30.11	0.00	0.00	0.00	21.51	2.15	10.22	21.51	14.52

3.2.3.2 Intra- and interspecific interactions of the Dybowski deer in different seasons

Table 3.24 shows the proportions of the Dybowski deer's intra- and interspecific positive social contact in different seasons. As with the other species, most interactions took place in summer and autumn from June to November. In winter from December to February fewer interactions took place, whereas in spring from March to May nearly no contact occurred.

Table 3.24: Proportions of the Dybowski deer's intra- and interspecific positive social contact in different seasons

		Hind - Hind	Hind - own Deer calf	Hind - other Deer calf	Deer calf - Deer calf	Stag - Hind	Stag - Deer calf	Dyb. deer - Europ. b.	Dyb. deer - Exm. p.	Dyb. deer - Visitor
March - May	Sum	1	0	0	0	0	0	0	0	0
	%	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
June - August	Sum	5	45	6	0	10	0	0	22	3
	%	5.49	49.45	6.59	0.00	10.99	0.00	0.00	24.18	3.30
September - November	Sum	3	11	0	0	13	2	0	2	7
	%	7.89	28.95	0.00	0.00	34.21	5.26	0.00	5.26	18.42
December - February	Sum	2	12	0	0	2	2			4
	%	9.09	54.55	0.00	0.00	9.09	9.09	0.00	0.00	18.18

Agonistic interactions between the hinds arose mostly in summer from June to August. Contact between the stag and the hinds occurred mostly in autumn from September to November (Table 3.25), as did the intraspecific agonistic interactions with the Exmoor ponies. The interactions with the European bison happened mostly in winter from December to February, and interactions with the visitors in summer from June to August.

Table 3.25: Proportions of the Dybowski deer's intra- and interspecific agonistic social contact in different seasons

		Hind - Hind	Hind - own Deer calf	Hind - other Deer calf	Deer calf - Deer calf	Stag - Hind	Stag - Deer calf	Dyb. deer - Europ. b.	Dyb. deer - Exm. p.	Dyb. deer - Visitor
March - May	Sum	7	0	0	0	0	0	0	3	0
	%	70.00	0.00	0.00	0.00	0.00	0.00	0.00	30.00	0.00
June - August	Sum	36	0	0	0	0	0	1	0	25
	%	58.06	0.00	0.00	0.00	0.00	0.00	1.61	0.00	40.32
September - November	Sum	10	0	0	0	35	4	0	27	0
	%	13.16	0.00	0.00	0.00	46.05	5.26	0.00	35.53	0.00
December - February	Sum	3	0	0	0	5	0	18	10	2
	%	7.89	0.00	0.00	0.00	13.16	0.00	47.37	26.32	5.26

3.2.3.3 Social interaction grids of the Dybowski deer

Table 3.26: Interaction grid of the Dybowski deer's intra- and interspecific positive social contact

soc + Contact to	from	Ludwig	Luise	Lisbeth	Lotte	Lisa	Lutz	Europ. b.	Exm. p.	Visitor
Ludwig	am	X	0	0	0	0	2	0	24	0
Luise	af	11	X	0	0	0	0	0	0	0
Lisbeth	af	9	0	X	0	0	2	0	0	0
Lotte	af	4	1	2	X	0	0	0	0	0
Lisa	af	4	0	1	6	X	7	0	0	0
Lutz	jm	3	0	3	1	62	X	0	0	0
Europ. b.		0	0	0	0	0	0	X	0	0
Exm. p.		3	0	0	0	0	0	0	X	0
Visitor		11	1	1	1	0	0	0	0	X
Sum contact		45	2	7	8	62	11	0	24	0

am = adult male, af = adult female, jm = juvenile male

= Focus animal

The interaction grid of the Dybowski deer's intra- and interspecific positive social contact is displayed in Table 3.26.

All agonistic intra- and interspecific social contact of the Dybowski deer are listed in Table 3.27. As with the other species, the indirect agonistic interactions such as avoiding behaviour were not included in the interaction grid (see Chapter 3.2.1.3 above).

Table 3.27: Interaction grid of the Dybowski deer's intra- and interspecific agonistic social contact

soc - Contact to	from	Ludwig	Luise	Lisbeth	Lotte	Lisa	Lutz	Europ. b.	Exm. p.	Visitor
Ludwig	am	X	0	0	0	0	0	2	0	0
Luise	af	0	X	0	0	0	0	0	0	3
Lisbeth	af	2	3	X	0	0	0	2	0	7
Lotte	af	1	0	0	X	0	0	2	0	6
Lisa	af	1	11	6	6	X	0	2	0	5
Lutz	jm	1	0	0	0	0	X	2	0	0
Europ. b.		0	0	0	0	0	0	X	0	0
Exm. p.		0	0	9	0	0	0	0	X	0
Visitor		0	0	0	0	0	0	0	0	X
Sum contact		5	14	15	6	0	0	10	0	21

am = adult male, af = adult female, jm = juvenile male

= Focus animal

3.3 Habitat use

The habitat use was documented by noting the actual position of every focus animal on a grid map of the enclosure every ten minutes of the observation period. An exemplar map with full legend is given in Figure 11.1 (Appendix). The frequency of the used enclosure quadrants was plotted in increments of 10%, based on the highest value.

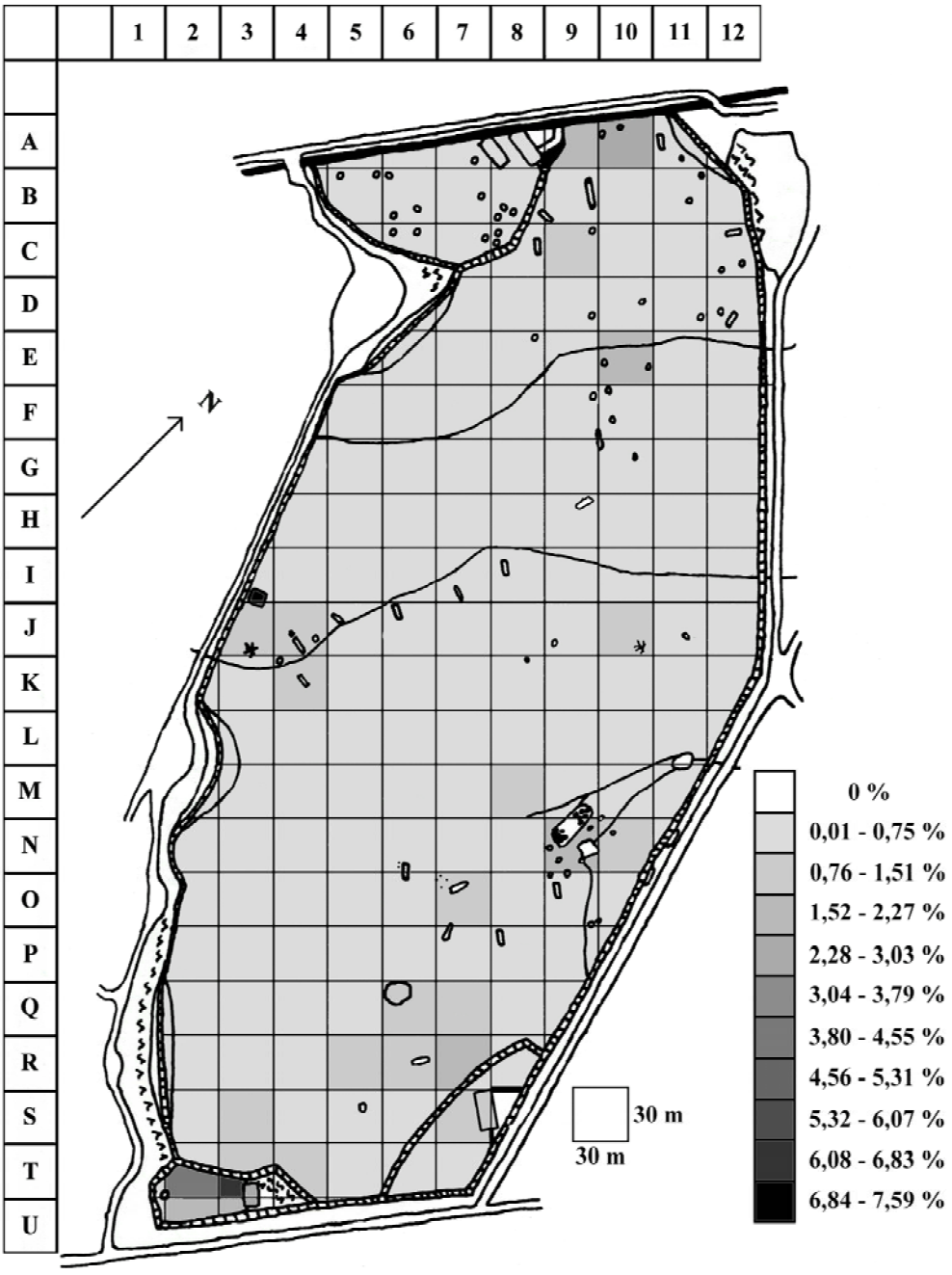

Figure 3.16: Habitat use of all species over the complete observation period

Figure 3.16 displays the habitat use of all three observed species over the complete investigation period. As shown on this grid, all areas of the 14ha enclosure were used by the

animals, albeit to different extents. The area used the most was the hay rack (I3) with 7.59%, and increased values were also recorded for parts of the Dybowski deer's separating enclosure.

3.3.1 Habitat use in general

3.3.1.1 European bison

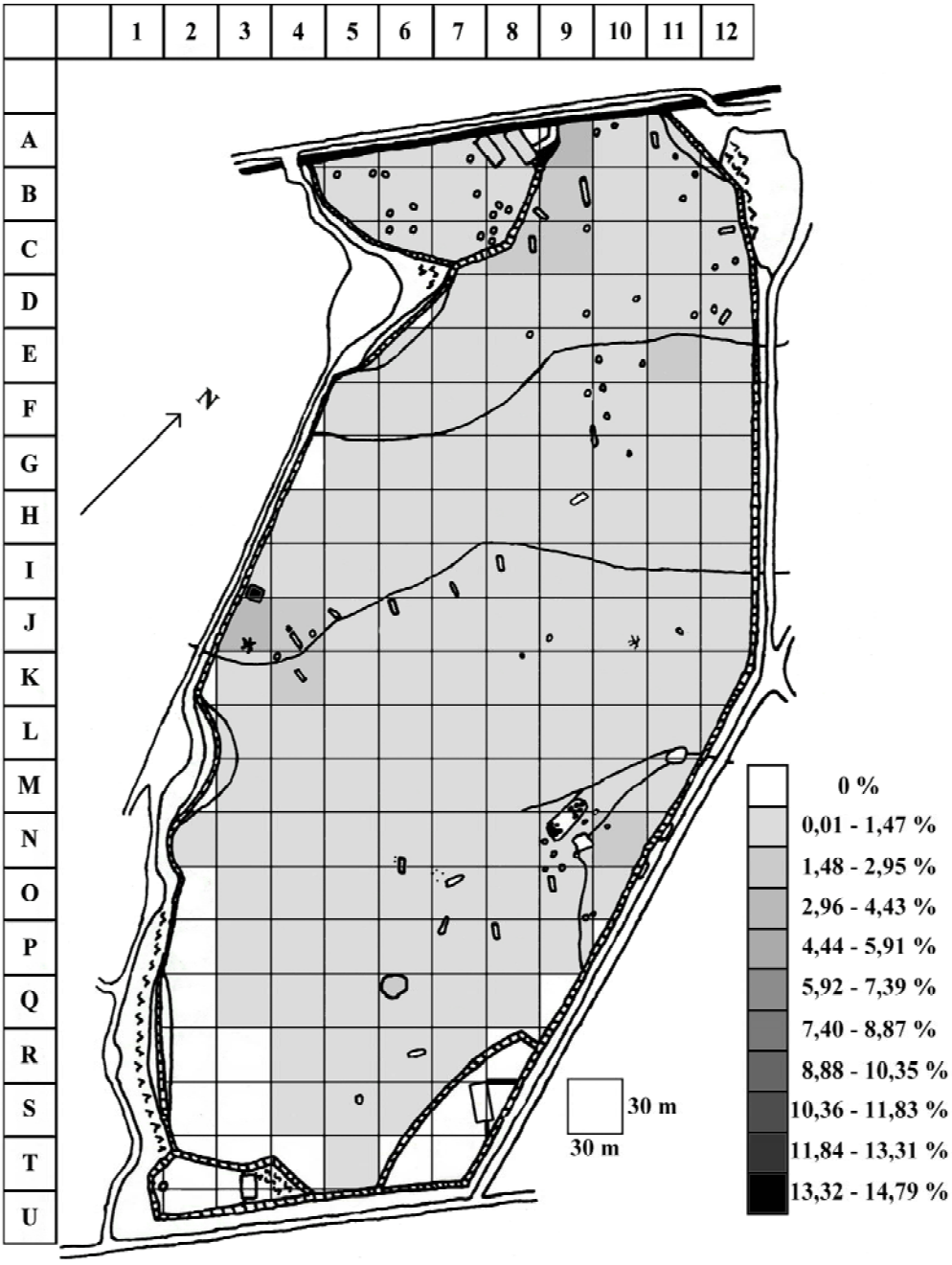

Figure 3.17: Habitat use of the European bison over the complete observation period

Over the complete observation period, the European bison's use of the hay rack (in I3) had the highest proportion with 14.79% (Figure 3.17). They used most parts of the enclosure quite regularly, with the exception of the area close to the Dybowski deer's separation enclosure. Both the Exmoor ponies' and the Dybowski deer's separation enclosures were generally not accessible for the European bison. Slightly more frequented than most open parts of the enclosure were the shady quadrants under the trees of E11, K4 and N10, as well as the areas in proximity to the European bison's separation enclosure (A8 and A,B,C9).

3.3.1.2 Exmoor ponies

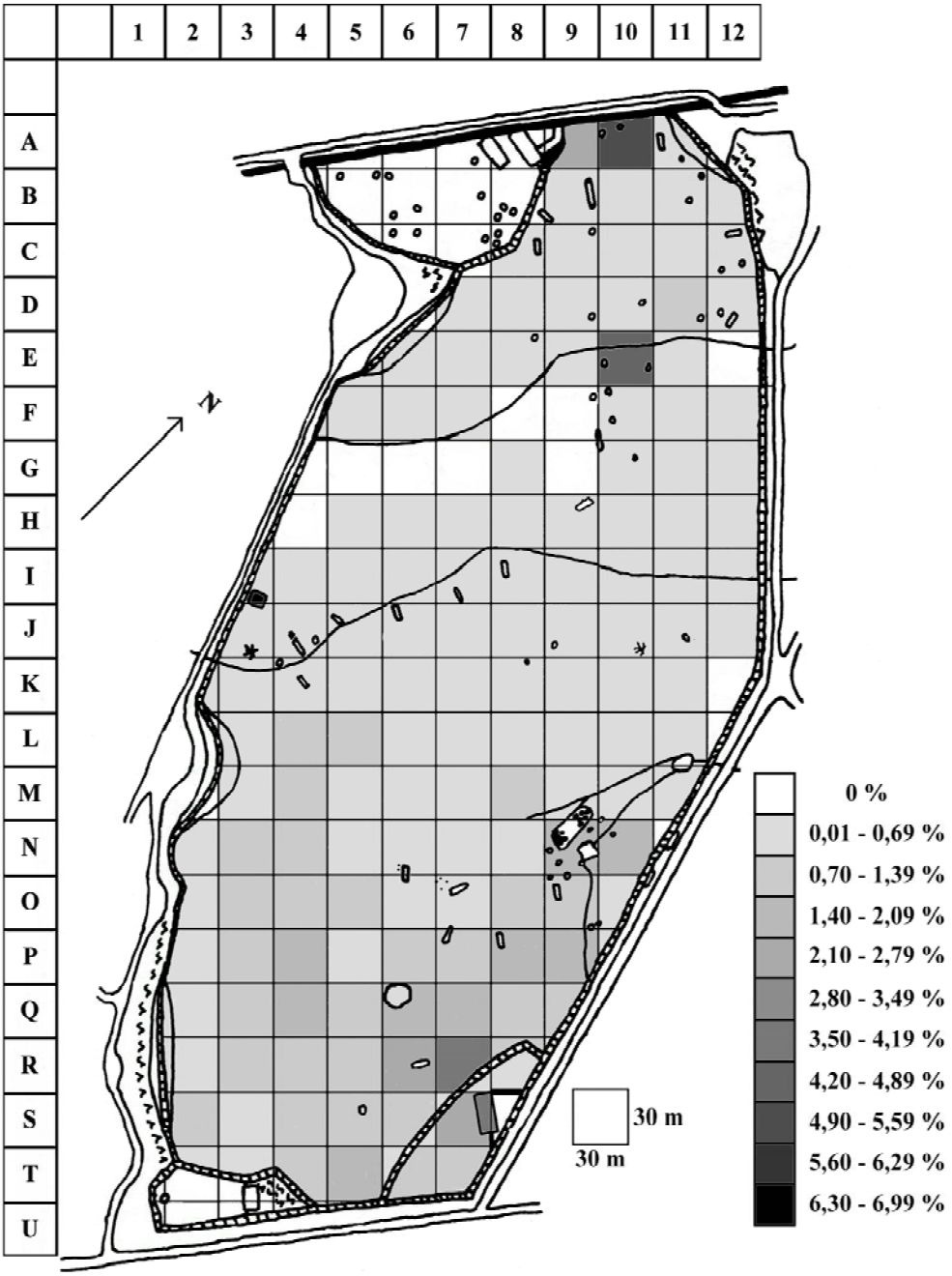

Figure 3.18: Habitat use of the Exmoor ponies over the complete observation period

The habitat use of the Exmoor ponies over the complete observation period is shown in Figure 3.18. As with the European bison, the most frequented quadrant was the hay rack (in I3), but other areas like A and E10 were also used prevalently. Overall, a tendency to roam in proximity to their separation enclosure is shown here for the Exmoor ponies. Nevertheless, most of the compound was used regularly, with the exception of the banks of the northern rivulet crossing the enclosure and the area near one of the major alley crosses (K and L12).

3.3.1.3 Dybowski deer

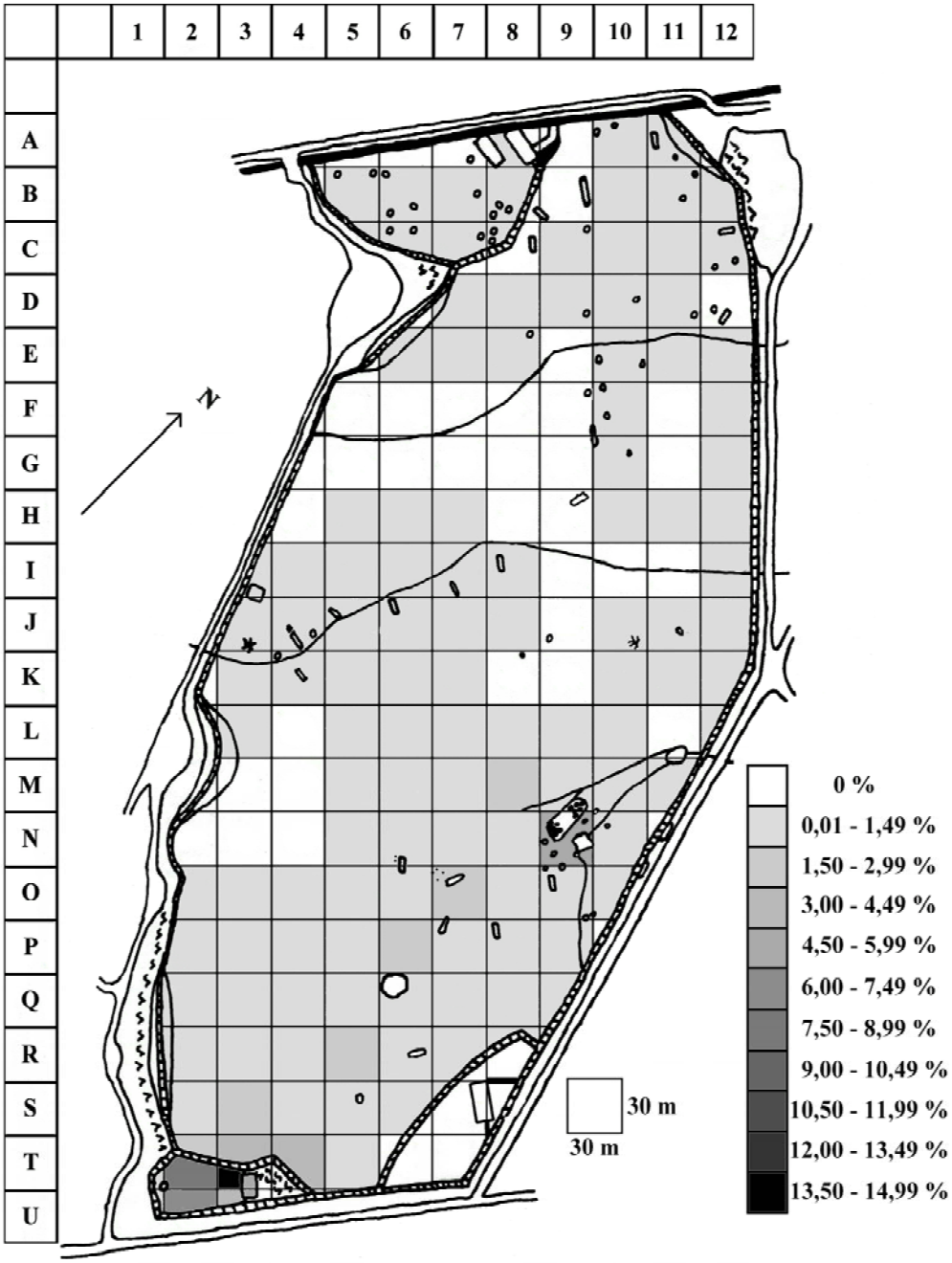

Figure 3.19: Habitat use of the Dybowski deer over the complete observation period

Over the complete observation period, the Dybowski deer spent most of the time in the separation enclosure and its surrounding areas (Figure 3.19). However, large parts of the 14ha-wide compound were used regularly, although some of the particularly exposed areas were avoided. The Dybowski deer used the European bison's separation enclosure whenever the gate was not closed and the European bison were in distant areas.

3.3.2 Habitat use in different seasons

3.3.2.1 European bison

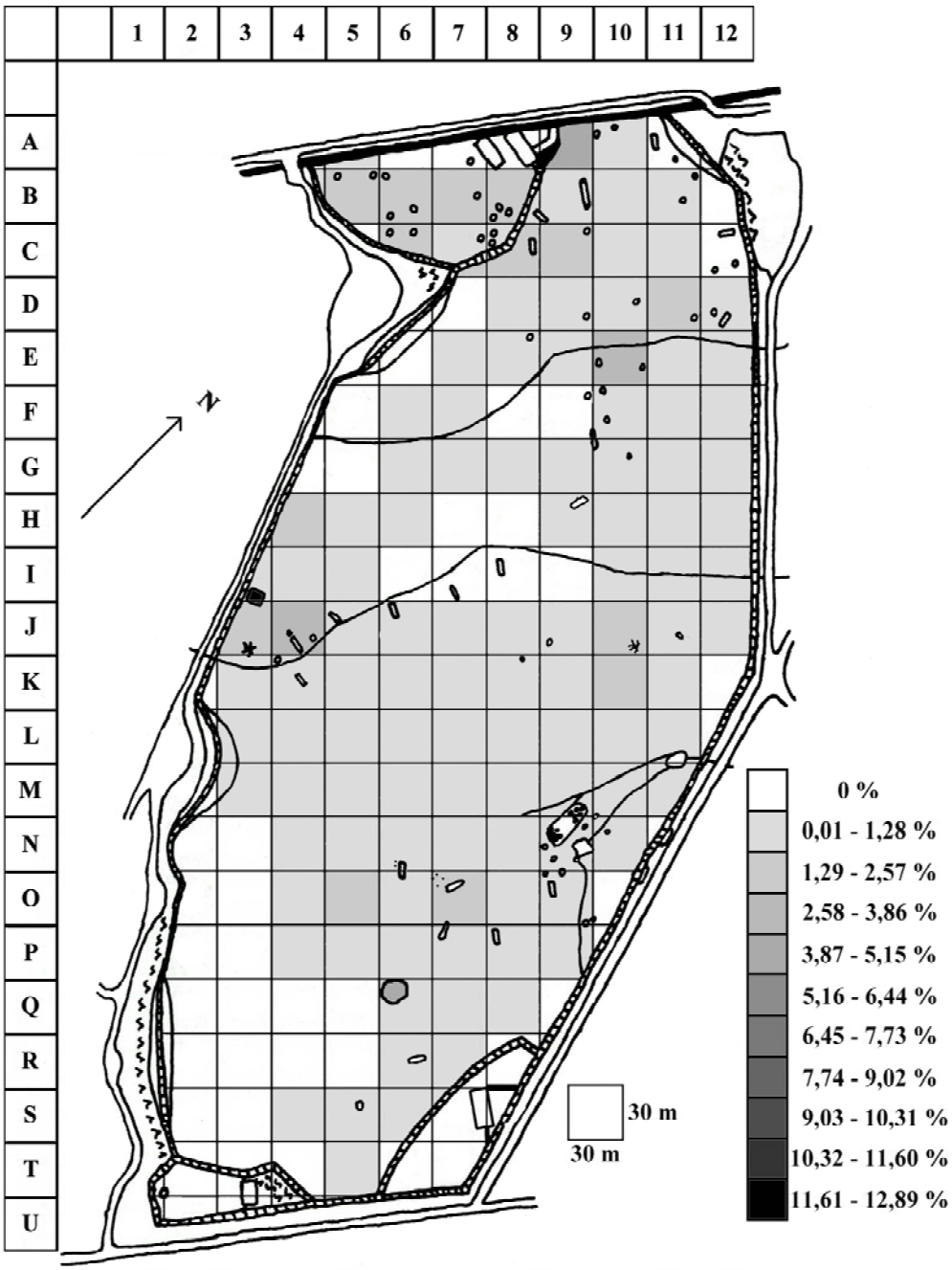

Figure 3.20: Habitat use of the European bison from March to May

From March to May, the European bison used the hay rack for 12.89% of the observation period (Figure 3.20). The sand bathing area (in Q6) was also frequented regularly, as were the areas near the European bison's separation enclosure. Not all areas of the compound were used during this season.

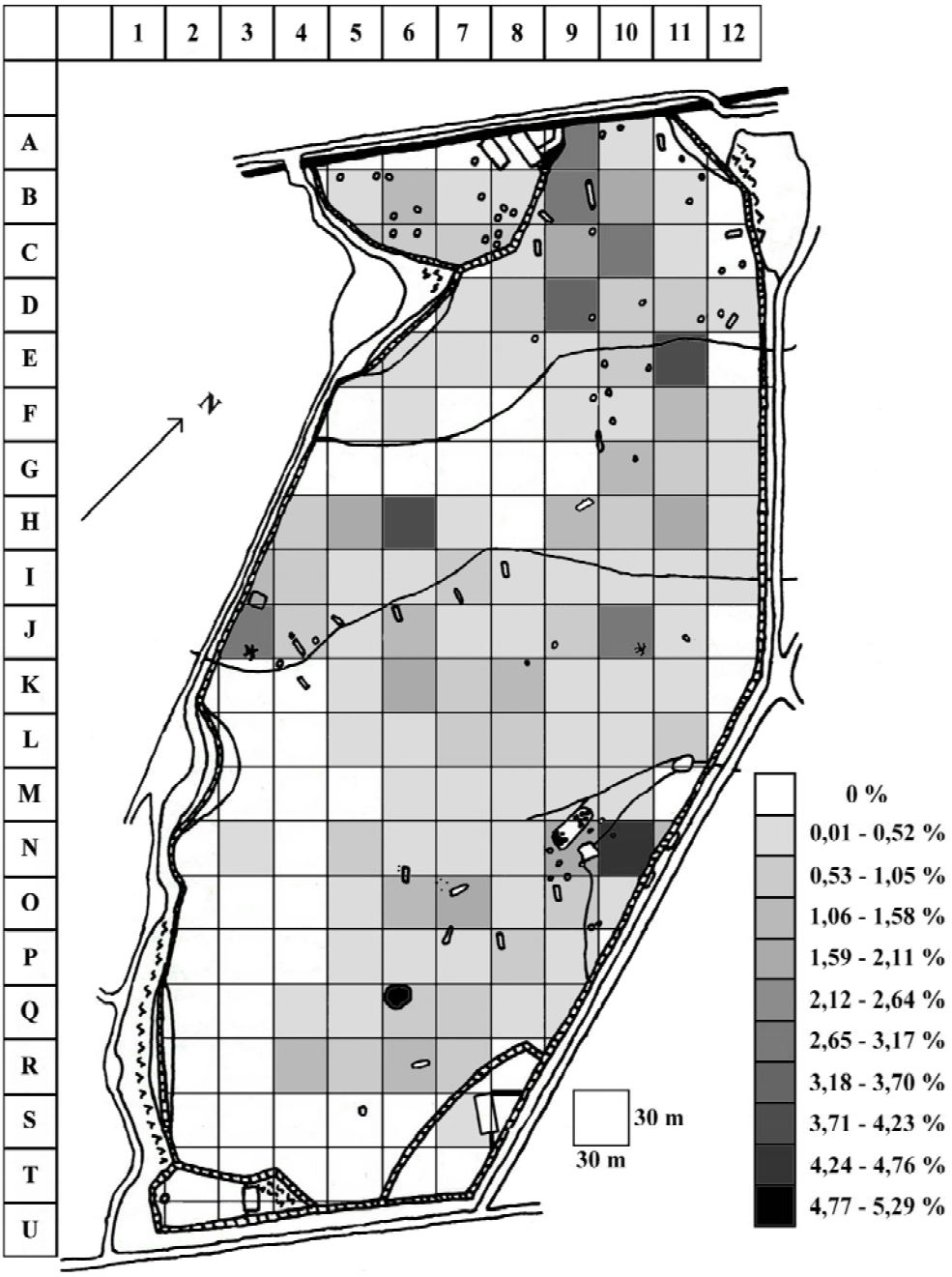

Figure 3.21: Habitat use of the European bison from June to August

From June to August, the sand bath (in Q6) became the most frequented area of the compound for the European bison (Figure 3.21). The areas close to the separation enclosure and the quadrants E11, H6 and N10 were also used regularly. The overall area was used to a smaller extent in summer than in spring. Summer was the only season where the hay rack (in I3) was not frequented as much by the European bison as in the rest of the year.

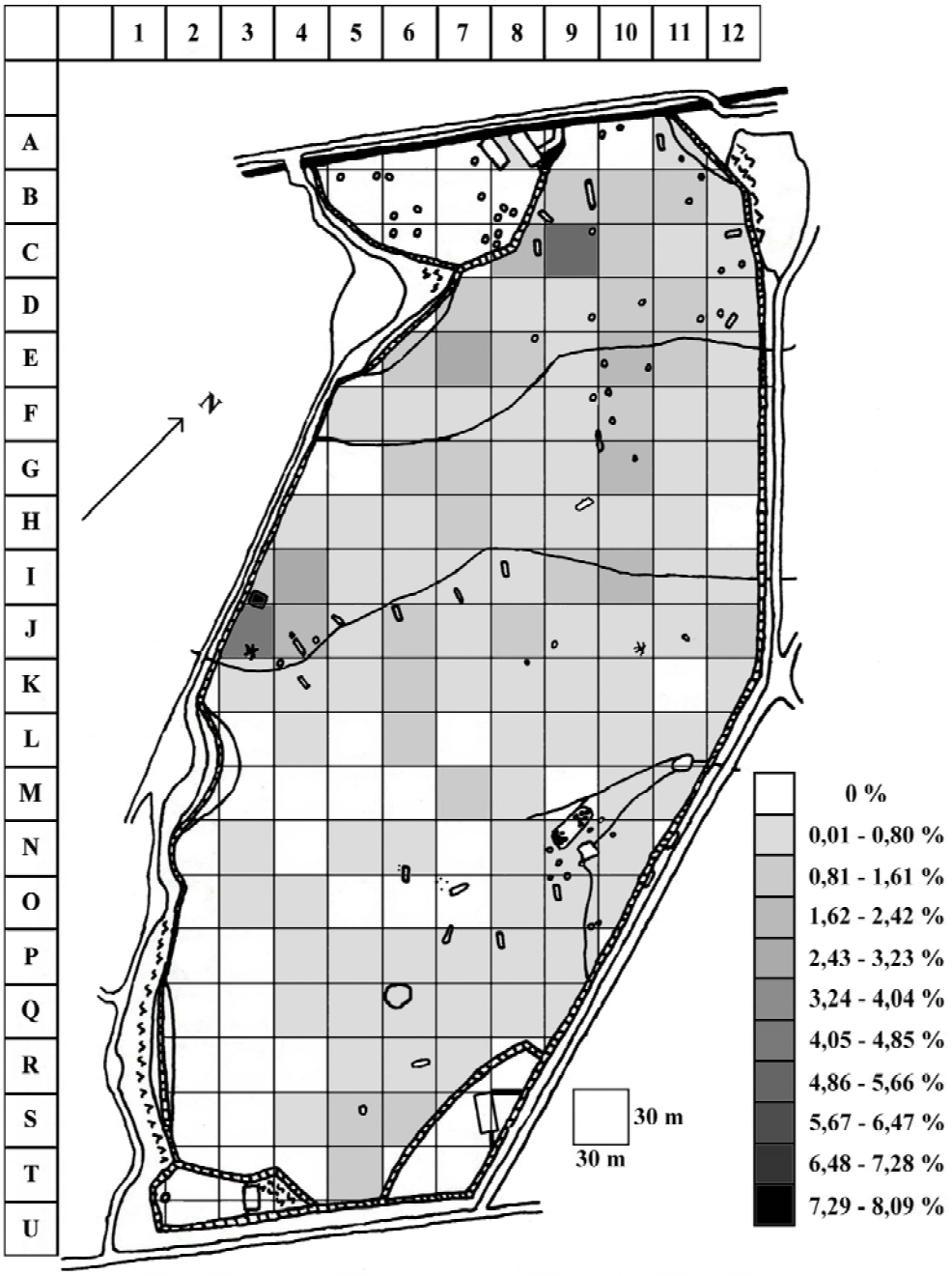

Figure 3.22: Habitat use of the European bison from September to November

The habitat use of the European bison from September to November is displayed in Figure 3.22. Here, the most frequented areas were again the hay rack and its surrounding quadrants, as was the sheltered area C9. The other parts of the enclosure were used more than in summer, but areas in proximity to the Dybowski deer's separation enclosure were still avoided.

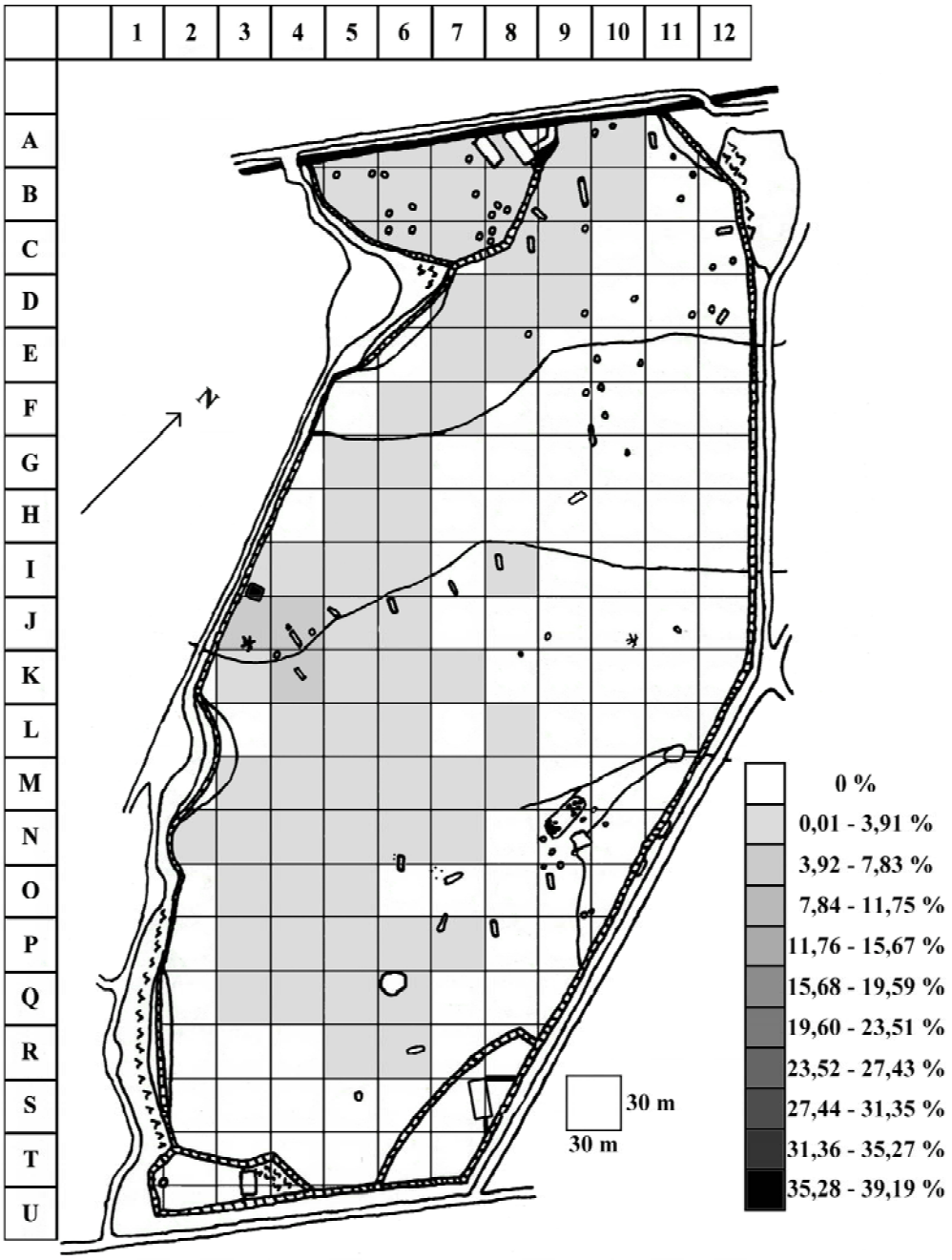

Figure 3.23: Habitat use of the European bison from December to February

From December to February, the European bison reduced their roaming range to the western and northern parts of the compound, including their separation enclosure (Figure 3.23). Of the total observation time, 39.19% was spent at the hay rack (in I3) and in its close vicinity.

3.3.2.2 Exmoor ponies

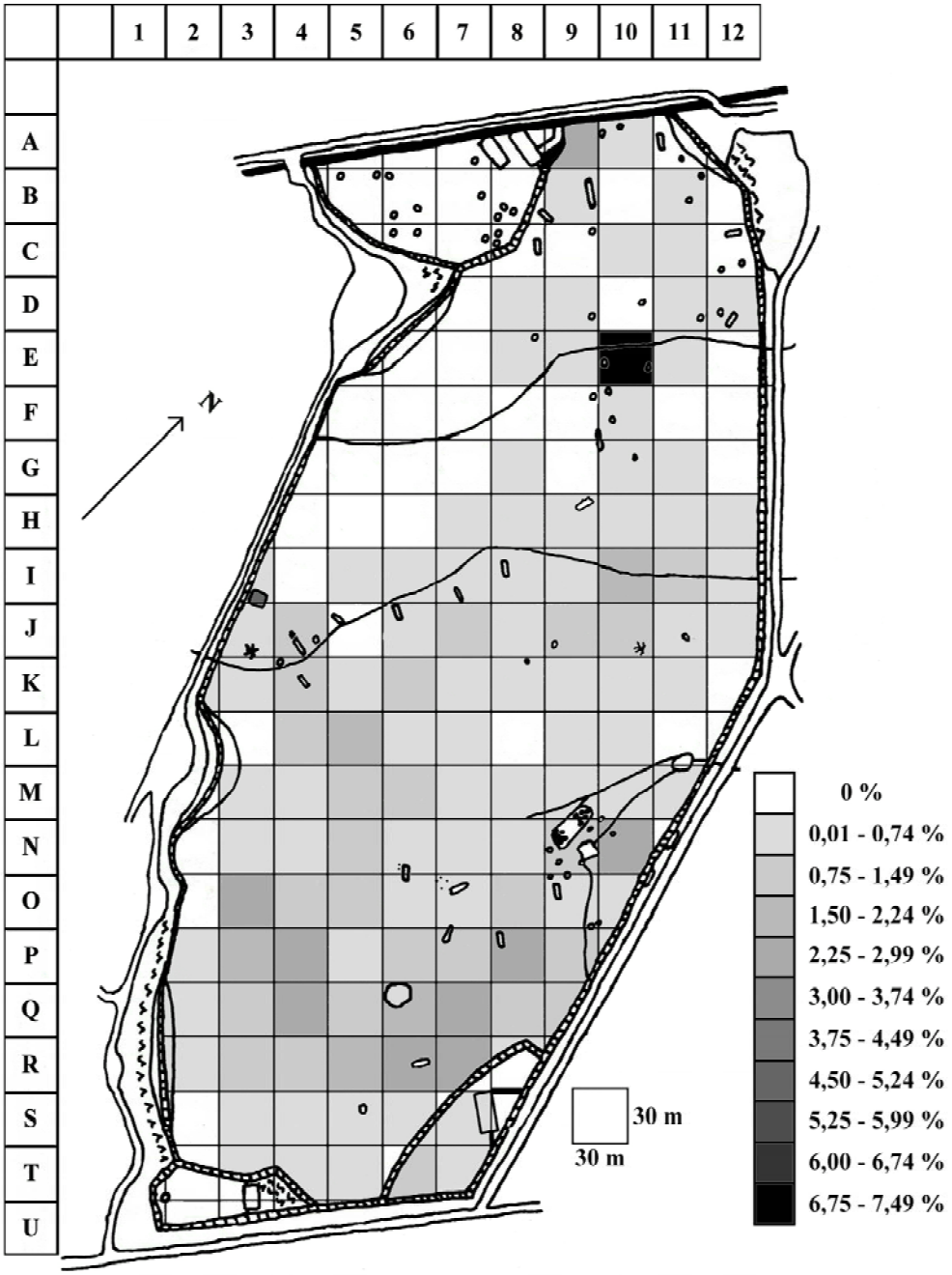

Figure 3.24: Habitat use of the Exmoor ponies from March to May

Figure 3.24 shows the habitat use of the Exmoor ponies from March to May. Generally using mainly the southern areas of the enclosure, the place where the Exmoor ponies spent most of the time in this season was at E10. The hay rack was also sought out regularly, as was the feed yard of the European bison (A9).

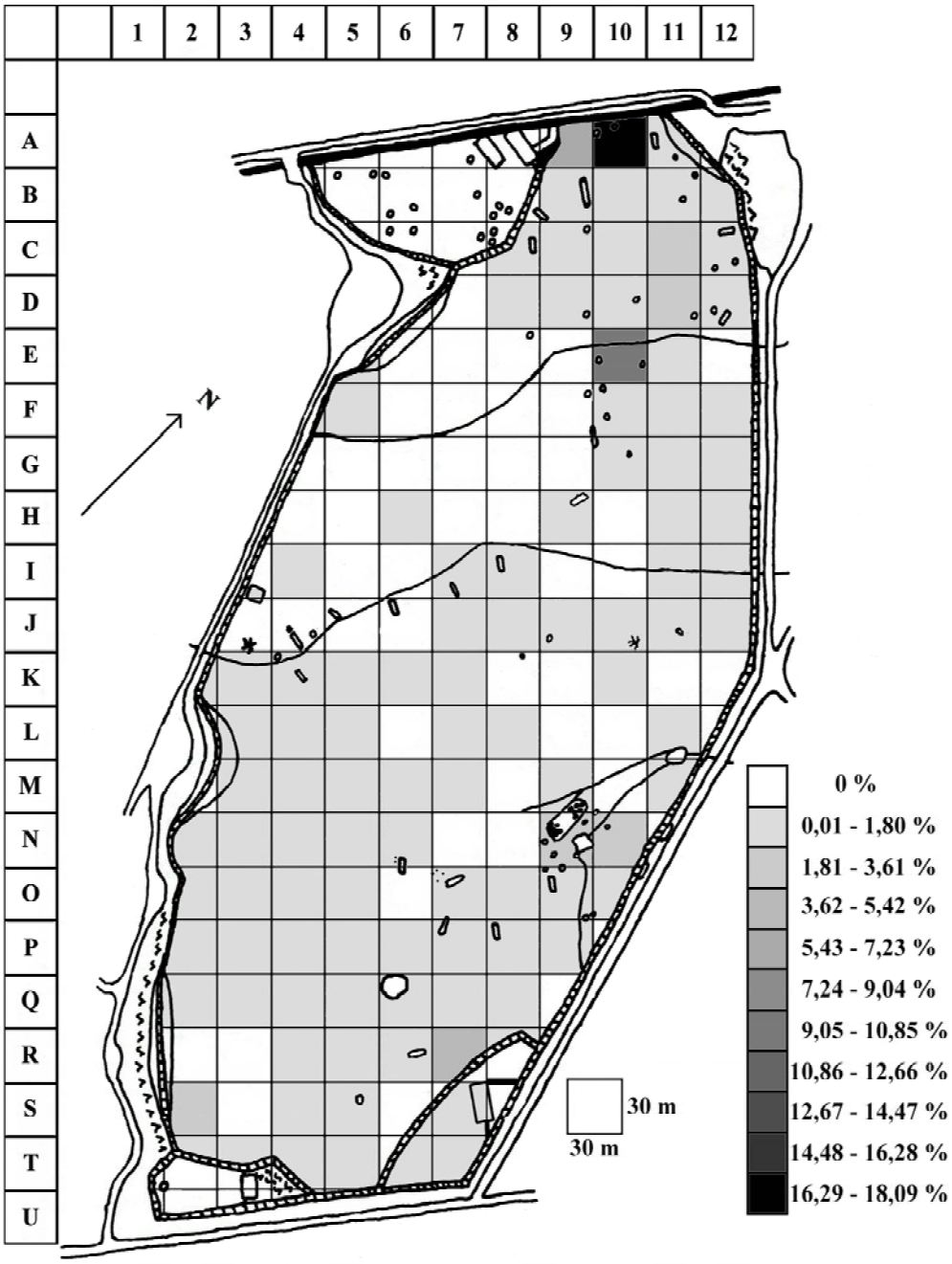

Figure 3.25: Habitat use of the Exmoor ponies from June to August

In the summer season from June to August, the overall use of the compound was more restricted than in spring (Figure 3.25). An average 18.09% of the day was spent on A10, and 10.54% on E10.

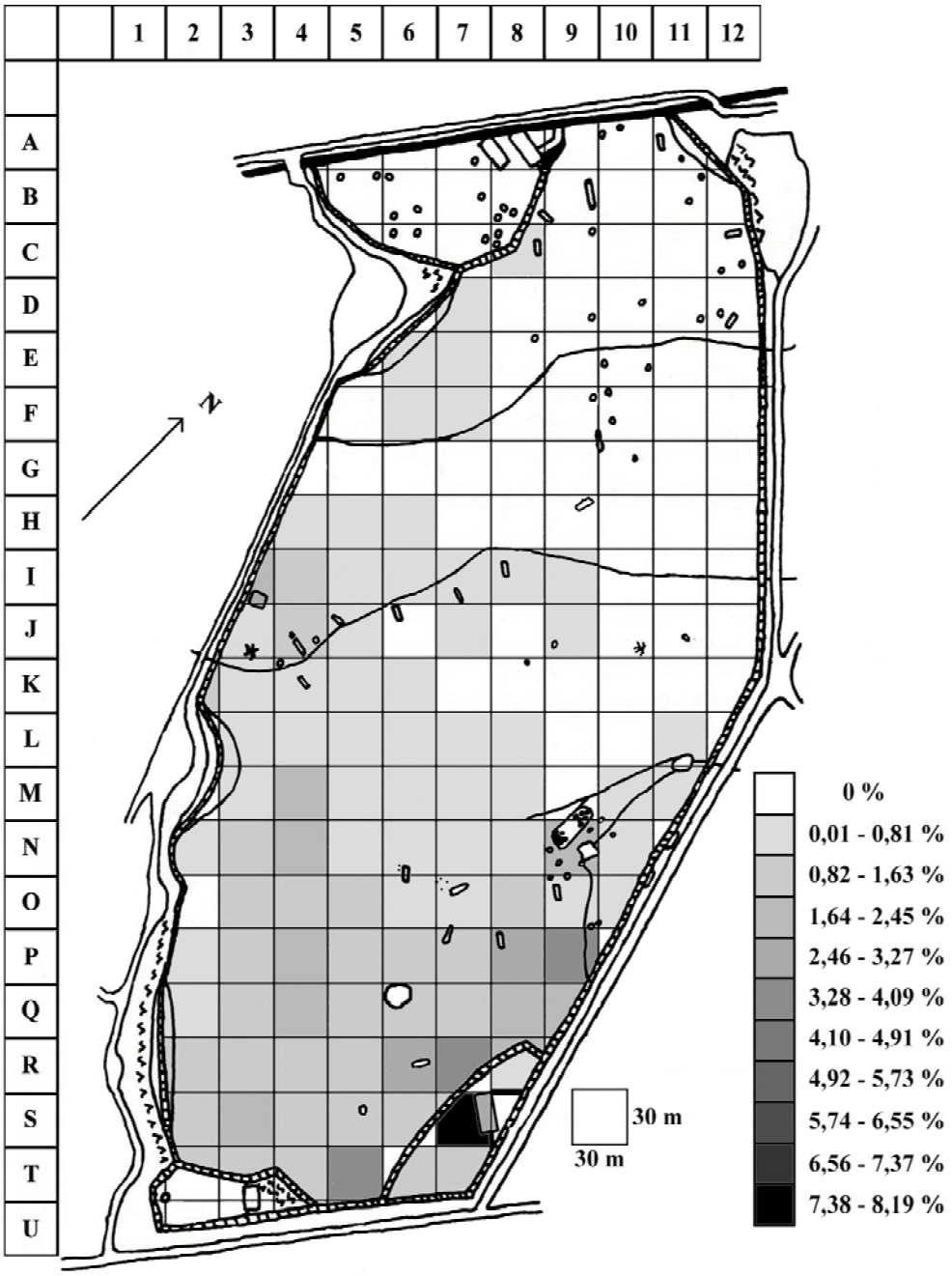

Figure 3.26: Habitat use of the Exmoor ponies from September to November

The habitat use of the Exmoor ponies from September to November shows a centring of the Exmoor ponies' activities towards the southern parts of the enclosure (Figure 3.26). During this season, most of the time was spent in the separation enclosure and its vicinity. The northern parts of the compound, contrary to in spring, were not used at all during summer.

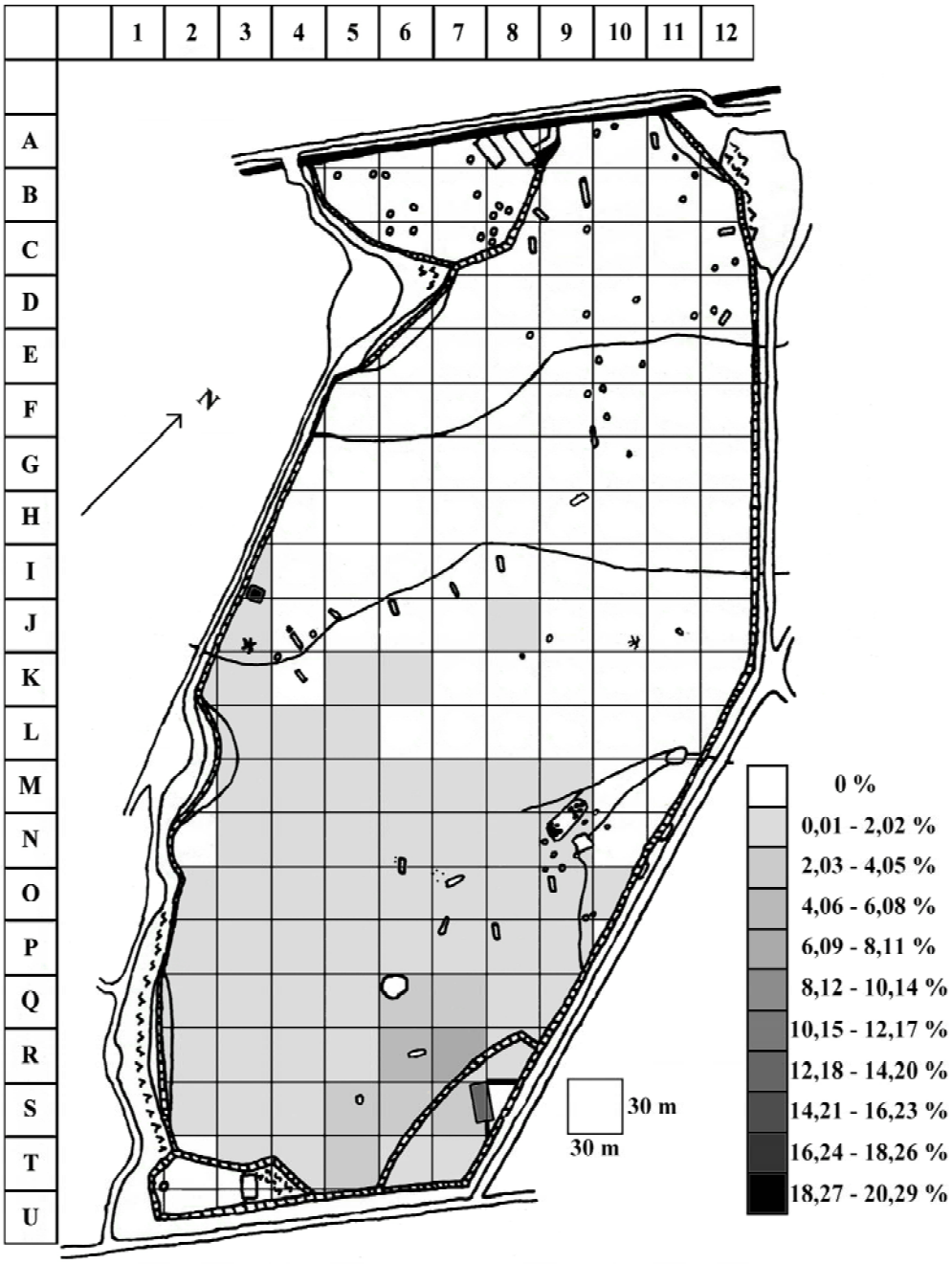

Figure 3.27: Habitat use of the Exmoor ponies from December to February

In winter from December to February the Exmoor ponies' activity range was even more restricted towards the southern areas (Figure 3.27). Still showing high percentages of use for the separation enclosure, most of the time was now spent at the hay rack (in I3).

3.3.2.3 Dybowski deer

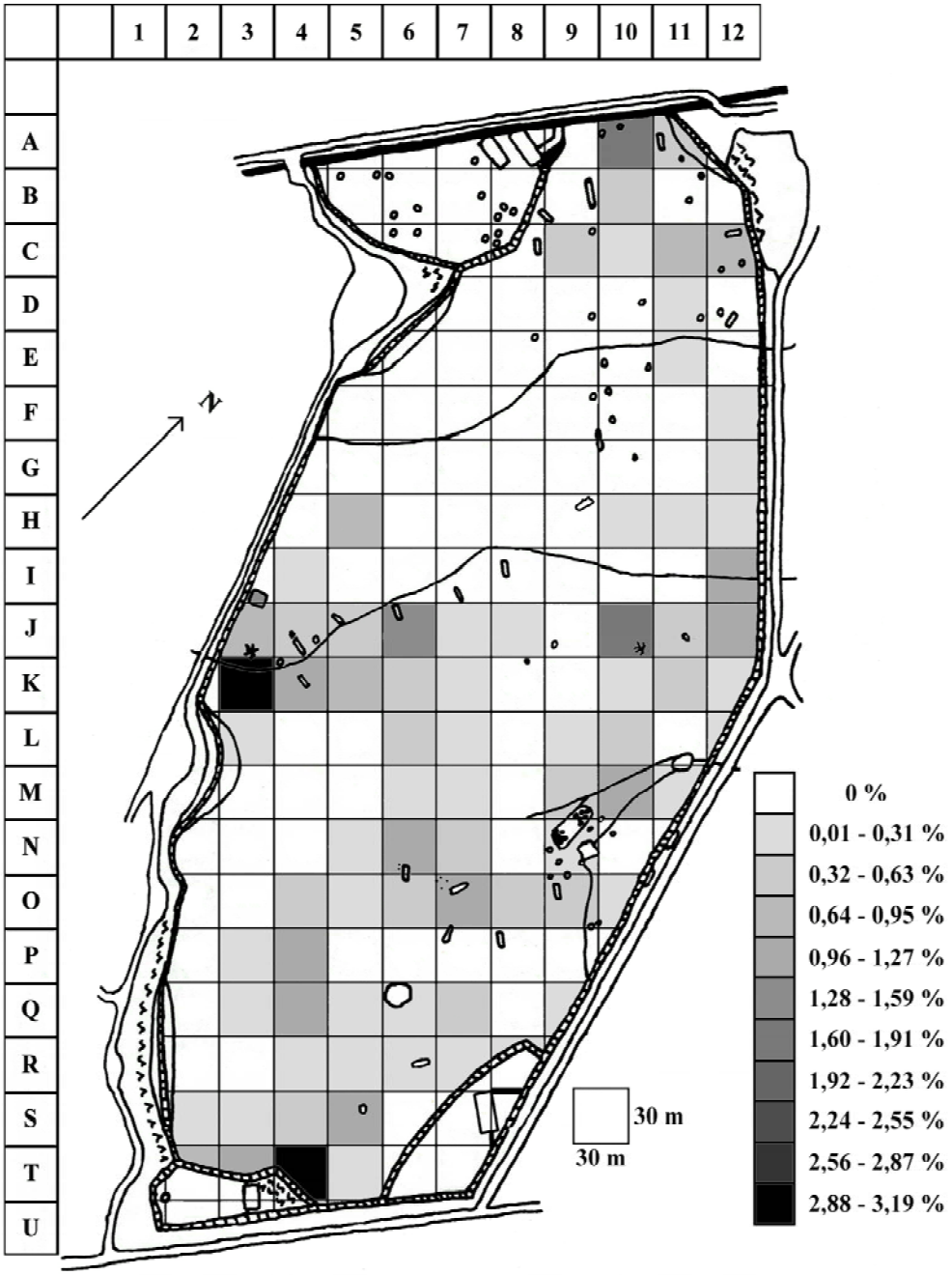

Figure 3.28: Habitat use of the Dybowski deer from March to May

Figure 3.28 displays the Dybowski deer's habitat use in spring from March to May. The Dybowski deer used the enclosure in a patchy way, avoiding all open areas where possible. Most of the time was spent with 3.04% and 3.19% at K3 and T4 respectively.

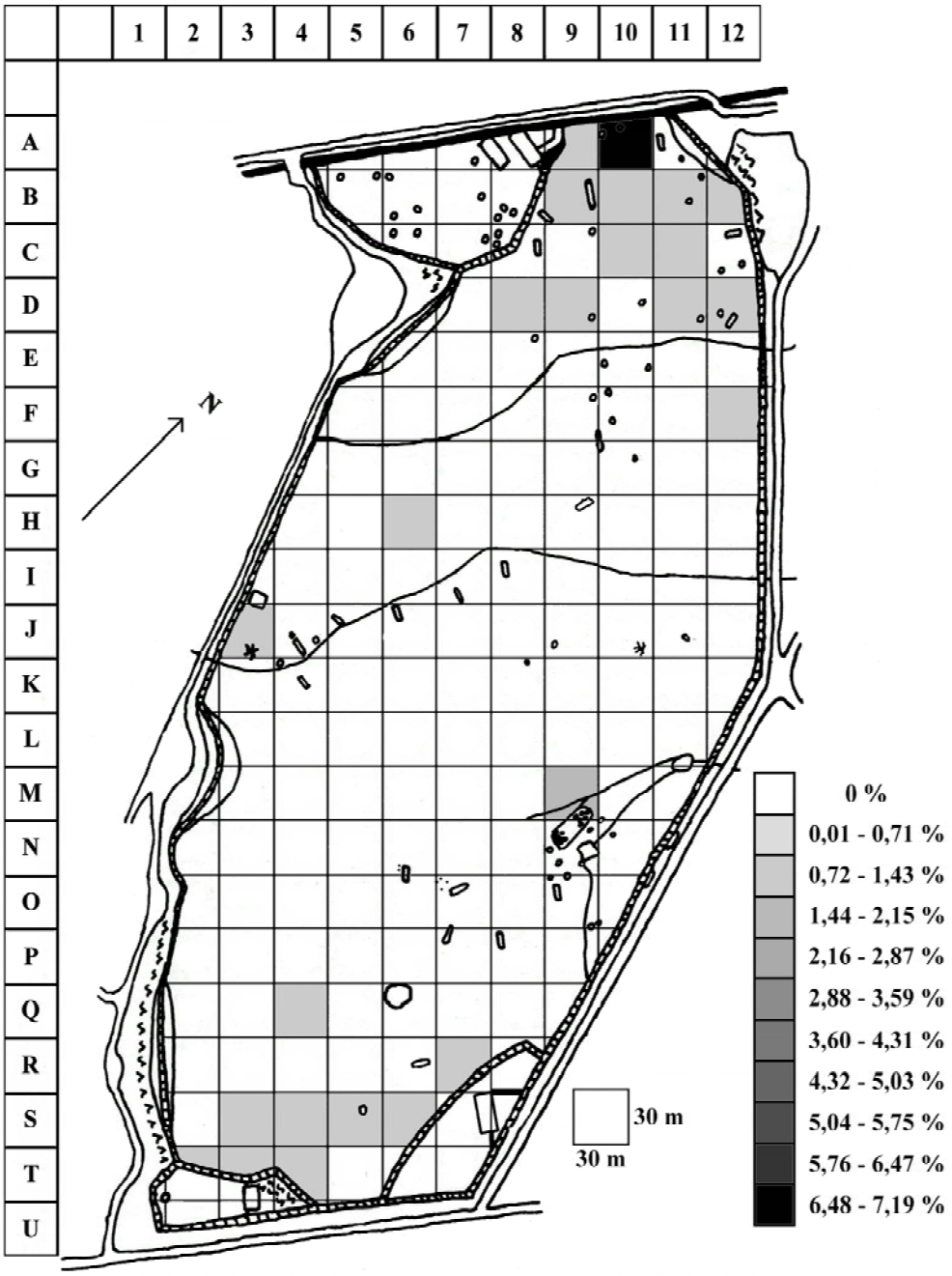

Figure 3.29: Habitat use of the Dybowski deer from June to August

From June to August, the hinds were locked in the separation enclosure for giving birth under controlled conditions. For this reason the proportions for the separation enclosure are not included and the values for the large compound are solely based on the stags' habitat use (Figure 3.29). The stag used the enclosure in a split way, either staying in proximity of the separation enclosure and the hinds or staying with the Exmoor ponies at A10, which he did for most of his time.

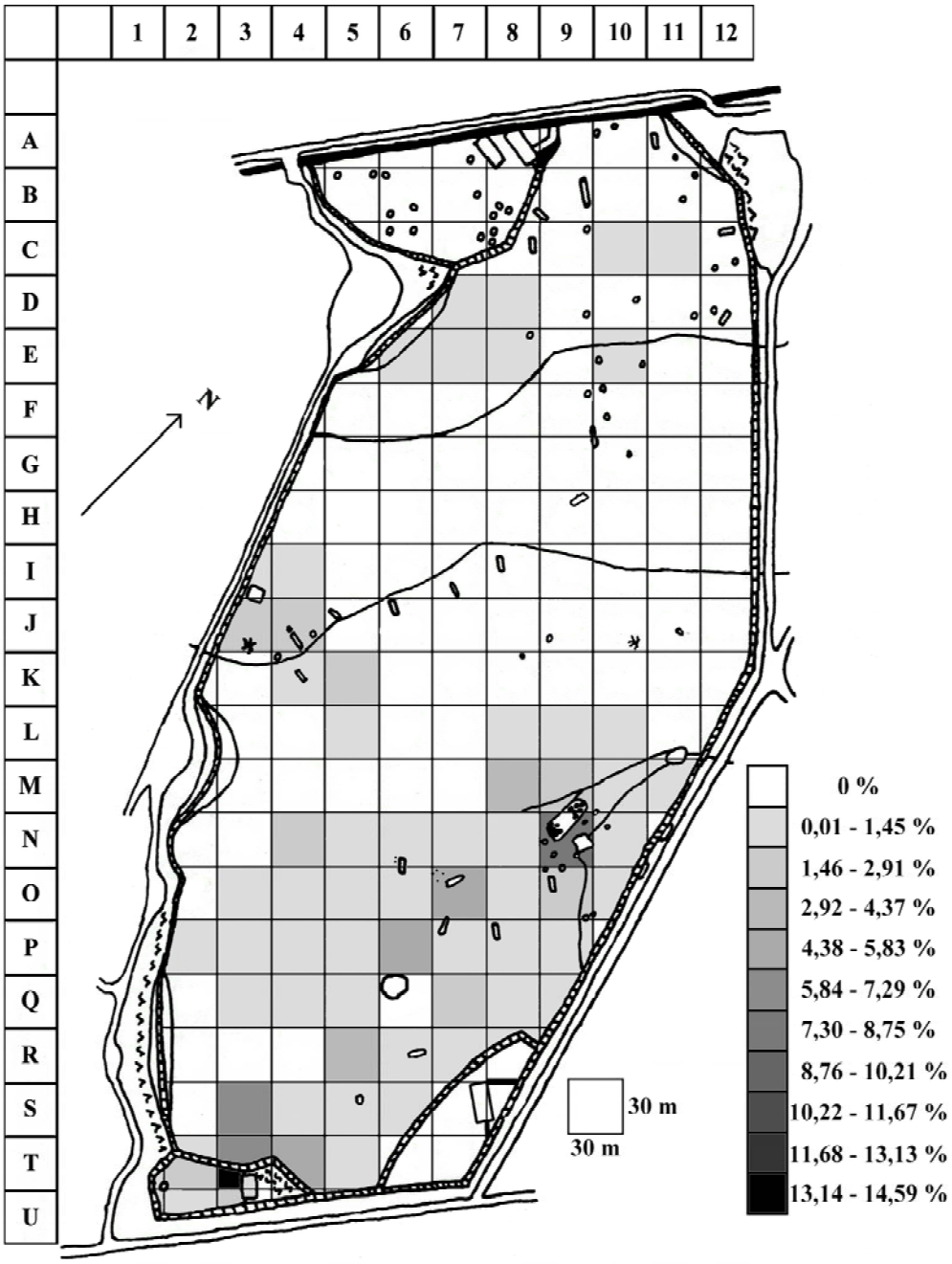

Figure 3.30: Habitat use of the Dybowski deer from September to November

Although having the opportunity again to roam free on the large compound, the Dybowski deer stayed in the separation enclosure for most of the time during autumn from September to November (Figure 3.30). Like the Exmoor ponies, they mostly used the southern parts of the enclosure, staying in more or less covered areas like N9, O7 or S4 and T4.

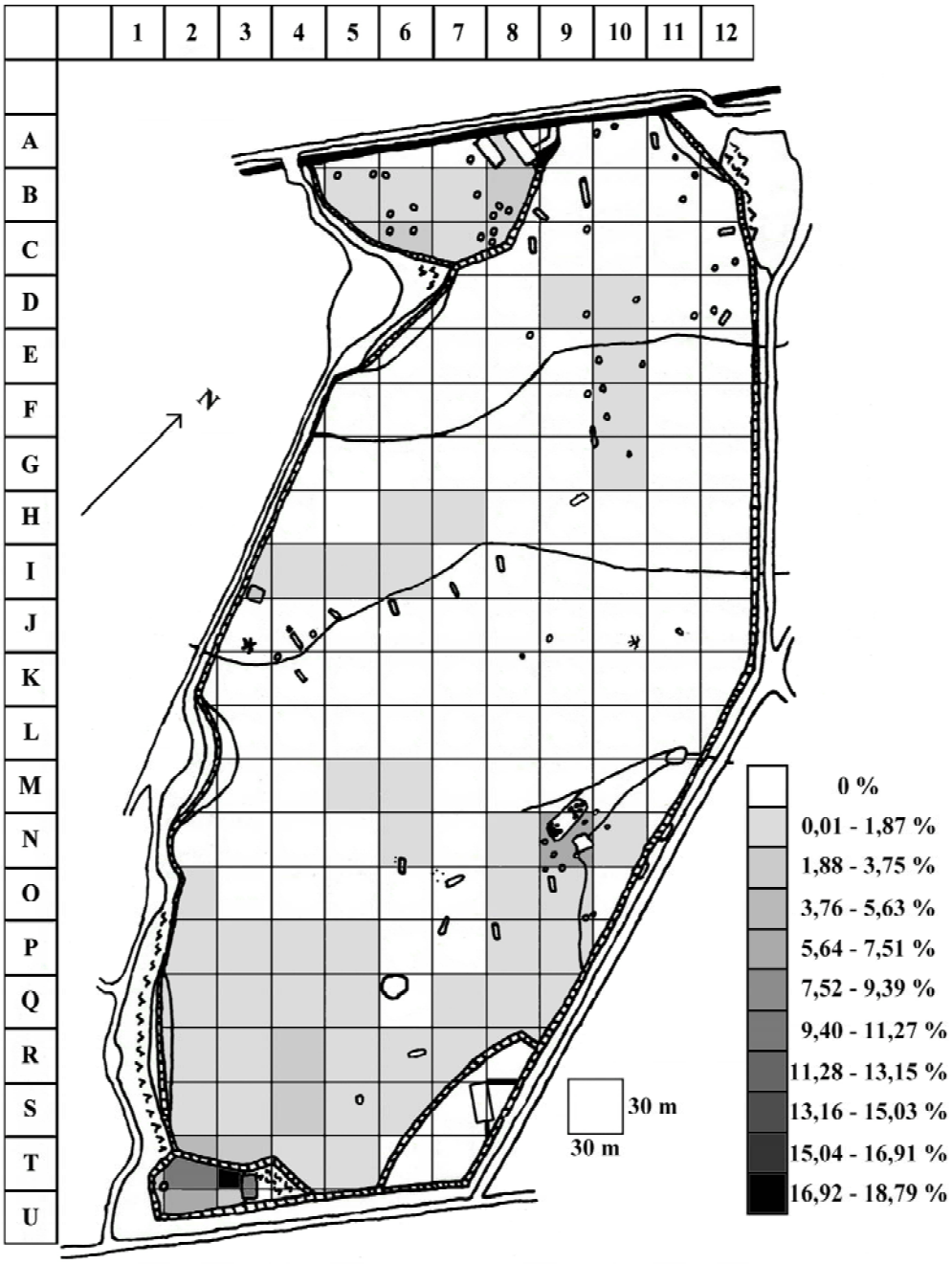

Figure 3.31: Habitat use of the Dybowski deer from December to February

In winter from December to February, the Dybowski deer's habitat use resembled that of September to November (Figure 3.31). Most of the time was again spent in the separation enclosure and its vicinity, the roaming range even more restricted than in autumn.

Instead, the Dybowski deer used the hay rack, if only seldom, and took the opportunity to remain in the European bison's separation enclosure when the gate was open and the bison were in other parts of the area.

4 Discussion

4.1 Behaviour

4.1.1 European bison

The European bison at Tierpark Sababurg fed for a mean 47.73% (11.45 hours) and rested for 43.05% (10.33 hours) of the day over the complete observation period (Table 3.1). SCHMITZ (2012) found for semi-free European bison in the Rothaargebirge near the town of Bad Berleburg (North Rhine-Westphalia, Germany) an average of 36.84% of the day was spent on feeding and 44.90% resting. CABOŃ-RACZYŃSKA et al. (1983, 1987) found a mean 45% for each feeding and resting behaviour in free-roaming European bison of Białowieża Forest National Park (Poland) over the whole year. POETTINGER (2011) examined the behaviour of European bison in an enclosure with regular supplementary feeding and observed 28% of the day spent feeding and 44% resting. For different cattle breeds under semi-natural conditions, SCHRADER et al. (2006) and HOUPT (1998) found averages of 8–12 hours of daily ingestion and 7–12 hours of resting behaviour.

All these results display a range of roughly equal parts of the main behaviours of European bison over the year, with a tendency towards a higher amount of daily resting behaviour.

Cattle ruminate when resting and the daily time devoted to ruminating is approximately three-quarters of that spent on grazing (TRIBE 1955). Thus, the daily energy intake for self-preservation is reached, although with larger amounts of time spent resting in regard to daily feeding behaviour.

European bison's movements are connected mainly with feeding activity to ensure the best possible use of food supply and therefore vary between the seasons (KRASIŃSKA et al. 1987, KRASIŃSKI & KRASIŃSKA 1992). As an average over the year, locomotion accounted for 6.79% of the day for the Tierpark Sababurg's European bison (Table 3.1). SCHMITZ (2012) documented 7.26%, nearly the same amount of time spent on locomotion for semi-free European bison, and UZAL & UGURLU (2010) observed 9.9% of the day dedicated to movement in cattle.

MITLÖHNER et al. (2001) found 6.80% of the day used for locomotion and POETTINGER (2011) documented 6.00% of daily moving behaviour for European bison.

Comforting behaviour was examined only rarely in other studies. Occurring only 1.68% of the day in the European bison of Tierpark Sababurg (Table 3.1), this value seems to be in line with the findings of SCHMITZ (2012) and POETTINGER (2011), who could document an average of 2.30% and 1.0% respectively.

Overall, the main behaviours of the observed European bison at Tierpark Sababurg seem to be consistent with those of free-ranging European bison or ones under semi-natural conditions.

The given daily percentages of the main behaviours are means over the complete observation period. However, there are seasonal variations in the behaviour of wild animals in the course of the year, and this occurred in the European bison at Tierpark Sababurg (Table 3.4). The seasonal variation in feeding behaviour with low values for winter and summer in contrast to extended food intake in spring and autumn was documented in exactly the same manner by POETTINGER (2011) for captive European bison at the Umweltbildungsstätte Donaumoos (Bavaria, Germany). CABOŃ-RACZYŃSKA et al. (1983) also found a decreased amount of feeding behaviour in winter, counting for only 30% of the day for free-living European bison in Białowieża Forest National Park (Poland). They could also prove about 60% of the European bison's day was dedicated to feeding in spring and about 64% for autumn, which is in line with the findings of the present study.

For semi-free European bison in the Rothaargebirge (North Rhine-Westphalia, Germany), SCHMITZ (2012) found similar results, observing the highest daily amount of time spent on feeding for spring and autumn, while feeding occurred much less during the summer and winter seasons.

Resting as the second main behaviour in animals varied in the opposite way to feeding behaviour (Table 3.4). With high amounts of daily feeding, the time spent resting decreased and vice versa. This is again in accordance with the findings of the cited studies above (CABOŃ-RACZYŃSKA et al. 1983, POETTINGER 2011, SCHMITZ 2012).

Locomotion of the European bison at Tierpark Sababurg varied only slightly between the different seasons (Table 3.4). This is in line with the findings of studies on European bison with supplementary feeding. For European bison, movements are connected mainly with feeding activity to ensure optimum use of food supply (KRASIŃSKA et al. 1987, KRASIŃSKI & KRASIŃSKA 1992); the animals with supplementary feeding are not forced to walk long distances to gain the daily amount of energy for self-preservation in the season with low food availability.

Comforting behaviour is generally low in wild and domestic cattle (WAßMUTH 2002, ZÄHNER et al. 2004) and was observed in only a few studies regarding different seasons. UZAL &

UGURLU (2010) found the main occurrences of comforting behaviour in cattle in summer, as did CABOŃ-RACZYŃSKA et al. (1987) and POETTINGER (2011) with European bison. The main behaviour shown in this season was wallowing in dusty places or sand baths, which was also the case with the European bison at Tierpark Sababurg. Additionally, rubbing occurred regularly, mostly during the moulting season in spring.
The social behaviour of the European bison will be discussed in detail separately (4.3.1 below).

4.1.2 Exmoor ponies

The Exmoor ponies at Tierpark Sababurg dedicated a mean 58.62% of the day to feeding behaviour over the complete observation period (Table 3.2). This corresponds to 14.07 hours per day, which matches the results of numerous other studies on wild horses. Amongst others, DUNCAN (1980) found for free-roaming Camargue horses a mean daily time spent feeding of 14–15 hours. One year of observation of Liebenthal horses by WOLLENWEBER (2007) showed horses feeding for 14.6 hours per day. MIELKE (1999) found Przewalski horses in the reservation area Schorfheide (Brandenburg, Germany) spent 14 hours of the day on ingestion behaviour. For domestic horses, SCHÄFER (1993) states 12 hours per day being used for food intake.
In addition to feeding, resting behaviour took up the largest proportion of wild horses' days (SCHÄFER 1993). IHLE (1984) and SCHÄFER (1993) both described resting behaviour in horses to last for 7–9 hours per day. MIELKE (1999) documented 6 hours of resting behaviour for Przewalski horses. DUNCAN (1985) and BOYD (1998) both found resting behaviour in horses to last between 5 and 7.5 hours per day. The investigated Exmoor ponies at Tierpark Sababurg spent an average of 34.54% per day on resting, the equivalent of 8.29 hours (Table 3.2). That proves the Exmoor ponies' behaviour being in the normal range found in other studies.
Locomotive behaviours occurred for 0.93 hours (or 56 minutes) per day on average over the complete investigation period (Table 3.2). Only little results are known from other studies for this behaviour. DUNCAN (1985) and BOYD (1988) found 1.5–2 hours per day spent on locomotion and LAMOOT & HOFFMANN (2004) documented a range of 1.1–2.2 hours of locomotive behaviour per day. Regarding the differences in size and habitat structure of the roaming areas, reduced values for the Exmoor ponies in the 14ha-wide compound of Tierpark

Sababurg seem logical in contrast to the results of DUNCAN (1985) and BOYD (1988) for free-roaming horses in the Camargue region (France).

The Exmoor ponies at Tierpark Sababurg used on average about 19 minutes or 1.37% of the day for comforting behaviour. WOLLENWEBER (2007) could observe about 14 minutes of daily autogrooming. MIELKE (1999) documented 33 minutes of comforting behaviour per day, but only for the summer months, and BOYD (1988b) found about 28 minutes of daily autogrooming for Camargue horses.

The social contact will be discussed with the inter- and intraspecific interactions (4.3.2 below).

Those results represent the mean values of the Exmoor ponies' behaviour over the complete investigation period. However, as with free-roaming wild horses, there were seasonal variations in the proportions of the shown behaviours in the course of the year (see 3.1.3.2 above). The daily amount of time spent on food intake is highest in spring from March to May, and in autumn from September to November, and lowest in summer from June to August. During winter, the feeding time decreased only slightly in comparison to the mean value for the whole year (Table 3.5).

Seasonal adjustment of the main behaviours is normal in wild animals. For free-roaming wild horses in the Camargue region (France), DUNCAN (1992) and MENARD et al. (2002) found an increase of up to two hours of daily foraging in winter and a reduced feeding time in summer. Przewalski horses also showed an increase in the daily time spent feeding during winter (SCHEIBE et al. 1998a) with a decreased amount of feeding in summer, as same as RIEDIGER (1995) proved for Exmoor ponies in their natural habitat.

Regarding the results of the current study on Exmoor ponies at Tierpark Sababurg, the decrease in feeding behaviour during summer is clearly distinct. An increase for the winter months did not take place, as the daily feeding time had already increased in autumn. For horses under controlled conditions with feed ad libitum, the seasonal variations showed by free-ranging animals are regularly proved to be slightly altered or reduced (e.g. PIRKELMANN 1991, MEYER & COENEN 2002).

At Tierpark Sababurg, supplementary feeding in the form of hay is provided ad libitum over the whole year. More or less ignoring it in summer (Figure 3.25), the ponies spent about 20% of their time at the hay rack during winter (Figure 3.27). As MOSLEY (1999), AVENT (2002) and HU et al. (2002), amongst others, could prove, social dominance within herds and between different species of wild animals both influence habitat selection and feeding behaviour. The European bison being the largest and dominant species in the compound, they

are generally avoided by the Exmoor ponies and Dybowski deer. As the European bison stayed at the hay rack and in its vicinity for about 40% of the day (Figure 3.23), the Exmoor ponies only had the chance to feed on hay when the European bison remained in other parts of the enclosure.

Wild and domestic ungulates are able to recognise other individuals and establish and maintain consistent dominance hierarchies (VAN KREVELD 1970). This may be the reason why the Exmoor ponies increased the time spent feeding in autumn. Being kept together with the European bison for years, they are used to a restricted access to hay in winter and compensate for this shortage by increasing their food intake in autumn to build up reserves for the season with limited vegetation.

Corresponding to feeding behaviour, the daily amount of time spent resting is altered in the opposite way, being highest in summer and lowest in spring and autumn (Table 3.5). In line with DUNCAN (1992) and LAMOOT & HOFFMANN (2004), the percentages of feeding and resting behaviour are correlated with the availability and quality of feed. If there is enough feed with sufficient nutritional value, the time needed to reach the daily level of physical preservation is shorter than with nutrient-poor feed. In summer with lots of qualitative biomass, the required amount of daily feed is reached earlier than in the seasons with limited vegetation. This extents the animals' time for other activities, and could be observed regularly in feral horses (SALTER & HUDSON 1979, KEIPER et al. 1980, DUNCAN 1985, VAN DIERENDONCK et al. 1996, BERGER A. et al. 1999, COSYNS et al. 2001 and MENARD et al. 2002).

The proportions of feeding and resting behaviour are reflected in the daily locomotion of the Exmoor ponies. Although most of the daily feeding in horses takes place as grazing while slowly pacing an area (PIOTROWSKI 1983, SCHÄFER 1993, ZEITLER-FEICHT 2008), locomotive behaviour was defined as directed movement from one place to another for any reason, without further behaviours involved (MCDONNELL 2003) (Table 11.1). Locomotion corresponded to the activity behaviour of the Exmoor ponies, moving most with high daily amounts of feeding and least with high proportions of daily resting. Having to search for suitable food patches in autumn, the animals have to roam the area long-range and thus increase their daily locomotion, in contrast to the summer with extent resting periods.

This relationship is also shown in the daily proportions of comforting behaviour and the social interactions. Comforting behaviour took place mostly in spring and summer, decreasing towards the winter season (Table 3.5).

Several authors described similar findings, stating mainly two reasons for this trend. Increased proportions of comforting behaviour in spring are attributed to changing the winter coat (SCHÄFER 1993, MIELKE 1999, WOLLENWEBER 2007), whereas autogrooming in summer is mostly due to irritations by insects (TYLER 1972, BOYD 1988b, SCHÄFER 1993). This would also explain the behaviour in winter, where stinging insects are absent and only little comforting behaviour is shown, which corresponds to findings of other studies (EBHARDT 1954, TYLER 1972, SCHÄFER 1993, LAMOOT & HOFFMANN 2004, DELLING 2009).

Social interactions mainly occurred in summer and autumn, with only small amounts in spring and seldom during winter. In spring, most interactions took place between mares and their foals. In summer, the interactions were distributed more evenly across the individuals. Like the locomotive and comforting behaviours, the social interactions are strongly related to the main daily activities of feeding and resting. Physical proximity is the premise for an occurrence of direct interactions (e.g. POPP 1984, POPP & BUNKFELDT-POPP 1986, DALESZCZYK 2004, 2005, MALEK 2009). This proximity is lowest while grazing and highest in resting periods, especially in summer while resting huddled in the shade (TYLER 1972, POPP 1984, POPP & BUNKFELDT-POPP 1986).

Regarding the results for the summer season, the Exmoor ponies not only had the time for social contact, but also their closer proximity during extended resting periods favoured more positive as well as agonistic social contact than in winter (TYLER 1972, KIMURA 1998). The social interactions themselves will be discussed below (4.3.2 below).

4.1.3 Dybowski deer

Reference values are rare for the behaviour of Dybowski deer. Belonging to a threatened subspecies (IUCN 2012), there are only a few free-living populations. Even fewer herds are kept in zoological institutions (UECKERMANN 1992, MCCULLOUGH et al. 2009), so data are difficult to obtain. More studies were conducted regarding other Sika deer subspecies, whose data can be used for evaluation of the Dybowski deer's behaviour. Additionally, the general deer behaviour is comparable in different species, if the variations due to habitat and environmental conditions are considered (BASKIN & DANELL 2003).

The Dybowski deer at Tierpark Sababurg fed on average for 47.22% of the day (Table 3.3). Sika and Sambar deer (*Cervus unicolor*) were observed at Kunming Zoo (Yunnan Province, China) by HU et al. (2002) to feed for 26.93% and 29.72% respectively from March to April. The study of AVENT (2008) on a mixed-species deer exhibit at ZSL Whipsnade Zoo

(Bedfordshire, England) found 29.26% of the day spent on feeding behaviour by Sika deer. However, it should be mentioned that in both studies the feeding behaviour was mostly restricted to intake of supplementary feed. For free-roaming Sichuan Sika deer (*C. n. sichuanicus*), GUO (2003) found a mean daily feeding activity of 52.07%. For semi-free Sika deer studied in Pingshan Wildlife Experimental Farm (Heilongjiang Province, China) during early summer, LIU et al. (1999) found an average of 67.47% spent on feeding. Being a Wildlife farm producing venison, the deer are fed supplementary to the natural food resources of the compounds, resulting in higher daily feeding proportions.

Resting behaviour occurred for a daily mean of 43.64% for the Dybowski deer at Tierpark Sababurg (Table 3.3). GUO (2003) observed 46.79% of daily resting behaviour for free-roaming Sichuan Sika deer. Resting took up 45.21% of the Sambar deer's day and 34.07% of the Sika deer's day, in line with HU et al. (2002).

These results for the main daily behaviours of wild animals show a general analogy between the observed Dybowski deer's behaviour and the findings of other studies.

Regarding locomotive behaviour, LIU et al. (2004) found free-roaming Sichuan sika deer in the Tiebu Nature Reserve (Sichuan Province, China) moved for 15.20% of the day. Under enclosure conditions at Kunming Zoo (Yunnan Province, China), the Sika deer's locomotive behaviour took up 8.42% of the day, whereas Sambar deer spent 2.99% on moving each day (HU et al. 2002). For the Tierpark Sababurg's Dybowski deer, 4.55% of daily behaviour was locomotive. No comparable data were found on comforting behaviour in deer, so the average daily value of 2.44% of the Dybowski deer remains undiscussed.

The Dybowski deer showed seasonal variations in the proportions of the behaviours in the course of the year (see 3.1.3.3 above). Feeding took the smallest amount of time with 41.85% of the day in summer, while a maximum of 52.98% was reached in winter (Table 3.6). In spring and autumn, 48.19% and 49.78% respectively of the daily time was spent on feeding.

Long-term observation and thus seasonal results for free-ranging Sika deer are rare, but GUO (2003) found 55.29% of the day was spent feeding in spring, 46.42% in summer, 48.21% in autumn, and 47.75% in winter. The data of studies on other deer species show similar results with an increase of the daily amount of time spent feeding towards winter. Red deer (*Cervus elaphus*) are known to feed for 36% of the day in summer and for 44% in winter (BERGER A 1999). CLUTTON-BROCK et al. (1982) also found differences from 44% to 53% of daily feeding from summer to winter for Red deer. For White-tailed deer (*Odocoileus virginianus*), HELLICKSON (2002) found 34.9% of feeding per day in summer and 41.2% in winter.

As in the present study, the daily amount of time spent resting varied in the opposite way to the feeding behaviour in the specified studies above.

The Dybowski deer showed locomotion behaviour in varying ways during the seasons (Table 3.6). The daily percentages of locomotion increased in the course of the year from 2.39% in spring to 6.86% in winter. This is in line with the findings of HU et al. (2002), who observed 2.99% of daily motion in spring for Sika deer. For the summer season, HELLICKSON (2002) found 3–4% of locomotive behaviour per day and CLUTTON-BROCK et al. (1982) could prove 6.8% per day accounting for movement during winter. SAKURAGI et al. (2002) also found similar patterns for free-ranging Sika deer. GILBERT et al. (1970) surmised that ungulate species of the northern hemisphere generally are influenced by the winter season due to reduced food availability and snow cover. Especially deep snow reduces access for foraging and increases the cost of locomotion (PARKER et al. 1984, FANCY & WHITE 1987), which leads to higher proportions of daily locomotive and feeding behaviour during the winter season.

No comparable data was found regarding comforting behaviour of deer. Being only rarely observable and having mostly only very short durations, many researchers only focus on the main behaviours (BUBENIK 1962). However, regarding the proportions of behaviour in the different seasons (Table 3.6), showing most comforting activities during summer and least in winter, one can assume the same reasons as for the other species (4.1.2 above). Several authors described stinging insects being the cause for most autogrooming behaviours in summer (EBHARDT 1954, TYLER 1972, SCHÄFER 1993, LAMOOT & HOFFMANN 2004). The absence of those in winter thus expresses in smaller amounts of autogrooming during winter TYLER 1972, BOYD 1988b, SCHÄFER 1993, DELLING 2009).

Behavioural interactions in cervids are typically low (VANKOVA et al. 1999, BARTOŠ et al. 2002) and will be discussed separately (4.3.3 below).

4.2 Daily activity rhythms

4.2.1 European bison

European bison's daily activity rhythm is polyphase and thus typical of other ruminants; phases of foraging alternate with resting spent mostly on rumination (TRIBE 1955, CABOŃ-RACZYŃSKA et al. 1983, 1987). Over the complete observation period, this becomes partially visible for the European bison at Tierpark Sababurg (Figure 3.1). Here, feeding occurred

mainly in the early morning, before noon and during the evening hours, whereas resting dominated the noon and afternoon. This pattern is due to the displayed results being based on the mean values for all seasons. The high proportions of resting behaviour in winter (see below) influence the diagram of the daily activity rhythm over the year, so the alternating phases of ingestion and resting visible for most of the seasons are overlaid (Figure 3.4 to Figure 3.7).

The overall tendency to feed extensively in the morning and evening hours is present and well known for wild and domestic cattle, as proven by CABOŃ-RACZYŃSKA et al. (1983, 1987), LEFCOURT & SCHMIDTMANN (1989), SCHRADER et al. (2006), POETTINGER (2011) and SCHMITZ (2012), among others.

In the different seasons, the daily rhythm of the European bison is altered due to environmental changes (KRASIŃSKI 1967, 1978, CABOŃ-RACZYŃSKA et al. 1983, 1987, KRASIŃSKI & KRASIŃSKA 1992).

In spring, five peaks of feeding behaviour occurred with the European bison at Tierpark Sababurg (Figure 3.4). CABOŃ-RACZYŃSKA et al. (1987) describe four feeding periods in spring for free-living European bison in Białowieża Forest (Poland), as also proven by SCHMITZ (2012) for European bison in the Rothaargebirge (North Rhine-Westphalia, Germany).

During summer, the feeding periods are the most distinct (Figure 3.5). This is due to the main phases of European bison's daily activity rhythms being highly synchronised in the herd during this season (CABOŃ-RACZYŃSKA et al. 1983, 1987, LEFCOURT & SCHMIDTMANN 1989, ROUYS 2003). The result of four feeding periods for the Tierpark Sababurg's European bison matches the findings of KRASIŃSKA & KRASIŃSKI (2008) and SCHMITZ (2012).

During autumn, three main peaks of activity took place (Figure 3.6), occurring mainly in the morning and evening hours. This is in line with the results of WRÓBLEWSKI (1927), POPP (1999) and ROUYS et al. (2001), who also found a similar pattern for European bison under different environmental conditions.

The distinctiveness in activity rhythms for spring and autumn in regard to the summer season is caused by displaying the mean values of five focus animals. As the behaviour is synchronised in summer and during most parts of winter, the periods of food concurrence in spring and autumn cause the animals to each maintain their own, individual daily activity rhythm (CABOŃ-RACZYŃSKA et al. 1983, 1987, LEFCOURT & SCHMIDTMANN 1989, ROUYS 2003). Especially during grazing in seasons with scarce vegetation, SATO (1982) found the active movement of high-ranking animals influencing the low-ranking animals to accomplish

an independent activity pattern. Particularly young, aging and weak cattle will thus often graze away from the herd or use the resting phases of the dominant individuals to roam on preferred food patches (MANNING & STAMP-DAWKINS 1998). This individuality in the focus animals leads to a decreased distinctiveness in the daily activity rhythms.
In winter, the daily activity rhythm is again more or less synchronised in that most of the time was spent resting at the hay rack (Figure 3.7). Feeding now occurred in the morning hours and in an irregular pattern towards the evening. As also found by POETTINGER (2011), the morning feeding period is mostly dedicated to feeding on supplementary feed at the stables, whereas the afternoon and evening feeding remains restricted to hay and grazing.
In general, the European bison at Tierpark Sababurg seem to maintain a daily activity rhythm very similar to those under semi-free and free-roaming conditions. Although influenced by management and supplementary feeding, which is still also conducted for the free-living populations (PUCEK 2004, SIPKO 2011 pers. comm.), the animals' behaviour remains in a typical polyphase rhythm throughout the year and can thus be regarded as in the normal range for wild animals.

4.2.2 Exmoor ponies

Feeding and resting behaviour take up the largest amount of horses' time and thus determine their daily routine. The results of numerous studies vary in the daily percentages of those main behaviours due to differences in observation, season, group size and husbandry conditions, but a daily activity rhythm of distinct alternating feeding and resting periods could be observed in nearly every investigation.
ISENBÜGEL (1999) found two main feeding periods in summer, lasting about 5–6 hours each, divided by inserted resting phases. WOLLENWEBER (2007) observed three periods of feeding alternating with two resting phases in Liebenthal horses, as did SCHÄFER (1993) for Fjord horses.
VAN DIERENDONCK (1996) described Przewalski horses' alternating feeding and resting periods in changed characteristics for different seasons, and RIEDIGER (1995) could prove the same varying activity rhythm in free-ranging Exmoor ponies.
Regarding the results of the present study, the Exmoor ponies showed a clear daily activity rhythm with two extended feeding periods in the morning and evening hours as well as a third, shorter one between two resting periods before noon and in the early afternoon (Figure

3.2). This matches the findings of the other researchers and proves the Exmoor ponies' behaviour at Tierpark Sababurg is generally in the normal range for wild horses.

Those activity rhythms are known to vary across seasons due to behavioural changes in the daily amount of time spent on feeding and resting (3.1.4.2 above).

Feeding for 68.08% of the day in spring (Table 3.5) was divided into four peaks with three intersecting resting periods (Figure 3.8). Those resting periods not exceeding the values of the feeding proportions are mainly due to working with mean values of five focus animals. During summer, horses show synchronised herd behaviour, whereas this pattern is indistinctive from late autumn to spring (TYLER 1972, VON GOLDSCHMIDT-ROTHSCHILD & TSCHANZ 1978, SCHÄFER 1993, DELLING 2009). During this time, all individuals show their own daily activity rhythms, indeed oriented around a general pattern, but with individual variations. This staggered asynchrony leads to decreased mean proportions for the behaviours (TYLER 1972, VON GOLDSCHMIDT-ROTHSCHILD & TSCHANZ 1978, SCHÄFER 1993, DELLING 2009). However, the tendencies of the daily activity pattern remain distinct.

During summer from June to August, the daily resting periods are extended for about 4.5 hours per day at the expense of feeding behaviour (Table 3.5). Here, feeding mostly occurred in the early morning and the evening hours, with two short ingestion periods at 11:00 and 16:00 (Figure 3.9). These findings are similar to those of other studies on wild horses, who also found an increase of several hours for the daily time spent resting in the summer months (SAMBRAUS 1978, CROWELL-DAVIS et al. 1985, 1994, BOYD et al. 1988).

In autumn, the daily amount of time spent on feeding was the highest in the course of the year (Table 3.5), which is also shown in the daily activity pattern (Figure 3.10). Three main peaks of feeding periods dominate the Exmoor ponies' day, interrupted only by three indicated resting phases. The high proportions of feeding in this season are probably caused by the feeding concurrence with and dominance of the European bison in winter (see 4.1.2 above).

From December to February, the Exmoor ponies' activities were more or less split into two main phases (Figure 3.11). Resting until about 14:00, the ponies started feeding in early afternoon and dedicated the rest of the observable daytime to ingestion behaviour. Some, but not all, Exmoor ponies used the hours before noon from about 09:00 to 11:00 to feed on the hay rack, while the European bison were fed at their separation enclosure so they could be controlled by the keepers (Figure 3.7). The same happened in the afternoon hours from 13:00 to 14:00 and 15:00 to 16:00. Parts of the European bison herd were roaming and feeding elsewhere at the compound during this time, so the Exmoor ponies had the chance to use the hay rack during this period.

4.2.3 Dybowski deer

As with the other species, the daily activity pattern of the Dybowski deer varied in the different seasons. In spring, there were three observable periods of feeding behaviour per day, separated by two resting phases (Figure 3.12). This is in line with the findings of LIU et al. (2002), who could prove three grazing peaks for semi-free Sika deer at Pingshan Wildlife Experimental Farm (Heilongjiang Province, China). This pattern did not vary much during summer, the feeding periods starting only earlier. Additionally, the activity phases are more distinct in summer due to an increased synchrony of the Dybowski deer's behaviour (Figure 3.13). LIU et al. (1999) found a similar daily activity pattern in the Sika deer of China for the summer months.

In autumn from September to November, the Dybowski deer extended their daily feeding activity rhythm by an additional feeding period toward the evening and elongated the feeding period in the morning (Figure 3.14). GUO (2003) found a similar trend for free ranging Sichuan sika deer (*C. n. sichuanicus*). HELLICKSON (2002) also proved this for White-tailed deer (*Odocoileus virginianus*) until the start of the rut. For the winter season from December to February, again three feeding periods occurred with the Dybowski deer at Tierpark Sababurg, though with the main proportions in the afternoon and evening hours (Figure 3.15). This activity pattern could also be proved by VAN ACKEN (1972) for Fallow deer (*Dama dama*) and GUO (2003) for Sichuan sika deer (*C. n. sichuanicus*).

Overall, the Dybowski deer's daily activity behaviour at Tierpark Sababurg seems to be in accordance with those of free-ranging individuals and the findings of other deer species.

4.3 Intra- and interspecific interactions

4.3.1 European bison

4.3.1.1 Intraspecific interactions of the European bison

Social interactions are generally low in wild and domestic cattle (WAßMUTH 2002, ZÄHNER et al. 2004, POETTINGER 2011). Despite their distinctive herd behaviour, the animals normally

keep to a distance of about 1.5 to 3 metres apart. This is only reduced for rarer social interactions (KONDO & HURNIK 1990). The well-defined hierarchical structure of the herd is built within 24 to 72 hours after regrouping or changes in herd composition due to deaths or births (BALČIAUSKAS 1999). Once the dominance relationship of any pair of animals is learned, it eliminates the need for further combat and minimises social interactions (BEILHARZ & ZEEB 1982).

Interactions between cows could not be observed, which matches the findings of POETTINGER (2011), who could also prove no positive social interactions among adult females in European bison. Positive social interactions remained mostly restricted to mother-calf relationships and bull-cow interactions during the rutting season (Table 3.9).

The mother-calf relationship in bovines is thought to be typal (CABOŃ-RACZYŃSKA et al. 1987) and characterised by an extremely close bond, especially during the first postnatal week (DALESZCZYK 2004). The distance between mother and calf is generally no more than 3 metres during this period (KRASIŃSKA & KRASIŃSKI 2008), in which numerous mother-calf interactions – especially licking of the calf – occur frequently (HINZ 2002).

This could also be observed for the Tierpark Sababurg's European bison (Table 3.11). "Zakki" – the mother of "Zamoa", and "Zaberta", the mother of "Zandor" – showed most of the positive social interactions in the adult females, and those interactions were almost exclusively directed to her own calves.

The rut caused most of the rest of the social interaction in the Tierpark Sababurg's European bison and started at the end of August, lasting until mid-October (Table 3.9).

This matches the findings from studies on free-ranging European bison. JAROCKI (1830) and KARKOV (1903) reported the start of the rut at the end of July to the end of September. WRÓBLEWSKI (1927) documented August to October as the main rutting period, and CABOŃ-RACZYŃSKA et al. (1987) and PUCEK (1986, 2004) could prove the same, although individual cows have been reported to come into oestrus as early as July or as late as November or December.

The high proportions of social interactions during this time are due to the characteristic rutting behaviour of European bison. The cows are seasonal polyoestrous and are in heat for about 1–3 days (POETTINGER 2011). During this period, the dominant bull follows the cow and engages her regularly, which leads to increased proportions of social interactions for this season (POETTINGER 2011), as could also be proven for the observed herd. As shown on the social interaction grid (Table 3.11), the adult cows were the main recipients of the bulls'

positive behaviours, whereas the younger females and the offspring only rarely had interactions with the dominant male.

Increased aggressive bull behaviour towards calves and younger herd members during the rut, as described by KRASIŃSKI & RACZYŃSKI (1967) and KRASIŃSKA & KRASIŃSKI (2008), could not be documented at Tierpark Sababurg (Table 3.10). The only individual threatened regularly was "Zabronzo", not only by "Favorit", the dominant male, but also by some of the adult females (Table 3.12). European bison bulls becoming sexually mature at around two years (MOHR 1952, JACZEWSKI 1958). "Zabronzo", born early in 2009, presumably reached pubescence in autumn 2010. Thus, he approached oestrus cows and the following dominant male regularly. As with free-ranging European bison, he was either chased off by "Favorit" or his approaches towards adult females in the absence of the dominant male were responded to with agonistic behaviour by the cows themselves (CABOŃ-RACZYŃSKA et al. 1987, KRASIŃSKA & KRASIŃSKI 2008).

Agonistic interactions between adult cows were mostly short, threatening gestures due to calf-guarding behaviour and concurrence about preferred food patches or resting sites. BEILHARZ & ZEEB (1982) described agonistic behaviour in wild and domestic cattle to be ritualised and occur in sequence: approach, threat, physical contact or fighting, only rarely exceeding the level of threatening. Once the dominance relationship of any pair of animals is learned, it eliminates the need for further combat. This should be the case for the Tierpark Sababurg's European bison, being a grown herd of more or less related animals, and would explain the low agonistic behaviour among the individuals.

4.3.1.2 Interspecific interactions of the European bison

Interspecific behaviour in European bison is poor. Intraspecific positive social interactions in European bison already being low, no positive interactions with other species has been documented so far. This was also the case in the current study; no positive interaction with the Exmoor ponies or Dybowski deer could be observed.

Agonistic interactions with other species are, however, documented in a few cases. JAROCKI (1830), KARKOV (1903), WRÓBLEWSKI (1927) and POETTINGER (2011) described aggressive behaviour towards domestic horses and approaching dogs, mostly by young bulls or calf-guarding females. NIGGE & SCHULZE-HAGEN (2004) could document a fatal attack of a female European bison towards a wild boar (*Sus scrofa*), and RIEDL (2005) observed an European bison attacking a domestic sheep. Those are the only cases to be found in the

literature on European bison regarding aggressive behaviour towards other species. Generally, larger animals tend to accept and do not dominate smaller animals, in the wild as well as in mixed species enclosures (KLEIMAN et al. 1996, THOMAS & MARUSKA 1996). In an exchange between two animals where one is clearly larger, healthier, stronger and/or older than the other, it may take only a mere movement, gesture or threat to make the smaller animal submit or yield space (ALBRIGHT & ARAVE 1997). The subordinate animal retreats from the dominant at the slightest and even indirect threat, and physical contact is of minor importance as long as the animals can see each other's posture (BEILHARZ & ZEEB 1982). This results in relatively low agonistic encounters, especially in species of ungulates which have been held together for long periods of time. These form and maintain stable structures of species dominance hierarchy (MOSLEY 1999).

Being used to each others' presence, the three species kept together at Tierpark Sababurg have evolved individual home-ranges and time-adjusted habitat uses to minimise encounters (4.4 below), which results in low agonistic interactions. Thus, the Exmoor ponies and Dybowski deer at Tierpark Sababurg avoided the European bison, mostly without any threatening or displacing behaviour shown. The simple approach of the European bison by walking in the other species' direction normally caused the Exmoor ponies and Dybowski deer to give way. Those indirect interactions happened at most during the rut in autumn, when the European bison deviated from their regular habitat use, and in winter (Table 3.10). During this season, the European bison spent most of the time at the hay rack and the other species only had the chance to use it during the absence of the European bison. When the bison returned from roaming, the ponies and deer eluded them. This repeating pattern was characteristic for the winter season and resulted in the highest proportion for interspecific interactions. Direct interspecific agonistic contact only occurred between one female European bison ("Zakki") and the Dybowski deer, which were chased of from the hay rack having not noticed the approaching European bison.

Towards humans, no aggressive behaviour is known for free-ranging European bison (GRACZYK 1987, BALČIAUSKAS 1999, LINDNER et al. 2006). For captive European bison, aggressive behaviour towards visitors and/or keepers has been reported irregularly, but especially for small enclosures with only little possibilities for retreat (GRACZYK 1987, BALČIAUSKAS 1999, LINDNER et al. 2006). In large enclosures, the behaviour of European bison trends toward wild (BALČIAUSKAS 1999). This seems also to be the case at Tierpark Sababurg. Threatening behaviour towards visitors was only to be observed in cows guarding their calves and the dominant male during the rut (Table 3.10), when visitors left the paths

and approached the fences when the European bison were close. However, no advancing or attacking behaviour towards visitors has been documented so far at Tierpark Sababurg.

4.3.2 Exmoor ponies

4.3.2.1 Intraspecific interactions of the Exmoor ponies

Living in socially organised herds is characteristic in feral horses, wherein two different forms are distinguished (KLINGEL 1972, 1974a 1974b, 1974c, 1975, 1977, 1980, SCHÄFER 1993). The common form, which is applicable for the Exmoor ponies, is the non-territorial organisation in herds of mostly related adult females, of different ages, with their offspring and one dominant stallion (KLINGEL 1968, JOUBERT 1972, TYLER 1972). Those harems remain stable for long times and maintain a relatively clear and consistent hierarchy (FEIST & MCCULLOUGH 1976, BERGER J 1986, RUBENSTEIN 1981, HOUPT & KEIPER 1982, HOFFMANN 1983, KEIPER & SAMBRAUS 1986, KEIPER 1988, SCHÄFER 1993), although this is not necessarily linear but can be built of complex triangulated relationships (GRZIMEK 1944, MONTGOMERY 1957, TYLER 1972).

To maintain this hierarchy, intraspecific social behaviour in feral horses is relatively complex. Positive social interactions at Tierpark Sababurg were highest among mares and their foals. In contrast to the normal development of slowly increasing the distance between mare and foal and thus decreasing the social contact with the growing of the foals in the course of the year (TYLER 1972, SCHÄFER 1993), the Exmoor ponies at Tierpark Sababurg showed a differing pattern (Table 3.16). This was due to one of the focus mares ("Gypsy") giving birth to her foal ("Fame") unusually late (29 August) in 2010. This increased the means for mare-foal interactions for autumn in particular as Gypsy was a very caring mother, keeping strong contact to her offspring (Table 3.18), hence the unusual behavioural pattern. The general pattern described by TYLER (1972), however, remained observable for the other Exmoor ponies despite this. Positive interactions between the foals and with the stallion occurred regularly, mainly in the summer months, whereas interactions among the adult mares remained rare throughout the year ((Table 3.16). Those findings are consistent with the results of TYLER (1972), KIMURA (1998), LAMOOT (2004) and LAMOOT & HOFFMANN (2004), who described seasonal variances in social interactions for horses. They propose those variances were caused by increased individual distances during foraging in the seasons with lower food availability during winter versus increased and synchronised resting behaviour with short individual distances during summer. As physical proximity is necessary for direct social

interactions, the probability of social contact is thus highest during phases of resting huddled, as is common in horses during the summer season (DOBRORUKA 1961, TYLER 1972, GATES 1979, CARSON & WOOD-GUSH 1983, SCHÄFER 1993). This applies not only for the positive, but also for the negative social interactions in horses. Concurrence for the best places in the shade or preferred food patches leads to increased agonistic interactions during the summer season, although those interactions are on a very low agonistic level (KIMURA 1998, LAMOOT & HOFFMANN 2004). The main purpose of interspecific agonistic behaviour is to maintain the hierarchy of the herd, not to injure another herd member. Therefore, these interactions are mainly restricted to short threatening gestures (HEINTZELMANN-GRÖNGRÖFT 1984). This pattern could also be proven for the Exmoor ponies at Tierpark Sababurg. Those agonistic interactions not related to concurrence behaviour over resting spots or food patches occurred as mares guarding their newly born foals from other herd members or the stallion chasing off foals from mares in heat (Table 3.17), both of which are common behaviours in feral horses (JOUBERT 1972, DUNCAN 1980, 1982, FEH 1988, SCHÄFER 1993, BAKER 1993, 2008).

4.3.2.2 Mutual grooming

Having particular weight amongst the behaviours of horses and normally lasting much longer than all other social interactions (SCHÄFER 1993), the Exmoor ponies' mutual grooming contact was analysed separately (Table 3.21). Mutual grooming in adult mares occurred only seldom, whereas the stallion, and especially the juveniles, displayed regular grooming contact. As with the other social interactions, the mutual grooming contact varied during the seasons. It could be observed regularly in spring and summer, declining in autumn and hardly occurring in winter.

In line with the other social interactions, the increased proportions are thought to be correlated with the diminished individual distances during summer and also influenced by the presence of irritating stinging insects (DOBRORUKA 1961, TYLER 1972, KIMURA 1998, LAMOOT & HOFFMANN 2004). Those are also proposed to be influencing the increased proportions of mutual grooming in spring, alongside irritations due to fur change (TYLER 1972, DUNCAN 1980, 1985, KIMURA 1998, LAMOOT & HOFFMANN 2004).

Because horses are known to carefully choose their mutual grooming partners (CLUTTON-BROCK et al. 1976, SCHÄFER 1993), the interaction grid of the mutual grooming contact shows the preferences and friendships of the focus animals (Table 3.20). The foals in particular showed increased time spent on this social behaviour, probably building up intensified

relationships already in this early age to last for years in most cases, facilitating the formation of a stable hierarchy as adult individuals (FEIST & MCCULLOUGH 1976, CLUTTON-BROCK et al. 1976).

4.3.2.3 Interspecific interactions of the Exmoor ponies

Horses' interspecific interactions are low, but known from several studies as they are regularly kept together with cattle or sheep (BAERSELMAN & VERA 1995, CORNELISSEN & VULINK 1995, SCHEIBE et al. 1998a, 1998b, SCHARF 2000, BUNZEL-DRÜKE 2001, BUNZEL-DRÜKE & SCHARF 2004). Interactions between semi-free or free-ranging feral horses and other wild animal species are also known to occur, for example with Roe deer (*Capreolus capreolus*) or Red deer (*Cervus elaphus*) (TYLER 1972, CLUTTON-BROCK et al. 1976, GATES 1979, 1980, BAKER 1993, 2008, BERGER A 1999).

Horses generally are dominant over cattle, even if the cattle is the larger and heavier breed (BUNZEL-DRÜKE et al. 2008). Direct or physical interactions are only documented in a few cases, however (BUNZEL-DRÜKE et al. 2008). The only exception are European bison, which dominate horses in enclosures as in the wild (WRÓBLEWSKI 1927, BUNZEL-DRÜKE et al. 2008, POETTINGER 2011). With deer and smaller domestic ungulate species such as sheep, horses are normally compatible, more or less ignoring these animals (BAKER 1993, 2008, SCHARF 2000, BUNZEL-DRÜKE et al. 2008).

These findings of other studies are consistent with the current results for the Exmoor ponies at Tierpark Sababurg (Table 3.16 and Table 3.17). Positive social interactions with the European bison did not occur. Instead, the Exmoor ponies avoided proximity with the European bison, although no direct contact or attacks have been observed. Positive social interactions towards the Dybowski deer were restricted to the stag "Ludwig", but occurred regularly during the summer season. During this time the hinds were kept in the separation enclosure for giving birth and the stag looked to the Exmoor ponies for herd contact (4.3.3.2 below). Visitors trying to feed the Exmoor ponies caused begging behaviour, especially in the stallion ("Ernie") and a juvenile mare ("Saba's Emily") (Table 3.18).

Agonistic interspecific behaviour between the Exmoor ponies and the European bison only occurred when the Exmoor ponies avoided approaching European bison (4.3.1.2 above).

Direct agonistic interactions with the Dybowski deer were dependent on the individuals. Even though the leading hind ("Lisbeth") chased the Exmoor ponies off several times (Table 3.27), they were generally avoided by the Dybowski deer (Table 3.17), with the exception of the

stag. Agonistic behaviour in regard to visitors was only observed once as fleeing behaviour due to being frightened by a sudden umbrella opening during resting at the fence.

4.3.3 Dybowski deer

4.3.3.1 Intraspecific interactions of the Dybowski deer

Behavioural interactions in cervid species are typically low, both within and between species (VANKOVA et al. 1999, BARTOŠ et al. 2002, AVENT 2008). Positive social interactions occur only seldom within adult animals and are mostly restricted to hind-calf relationships and the rutting season (MCGHEE & BACCUS 2006).

This is also apparent from the observed Dybowski deer at Tierpark Sababurg in terms of their positive social interactions in the different seasons (Table 3.24), as well as the social interaction grid for these animals (Table 3.26). Most of the positive social interactions occurred between hind and deer calf ("Lisa" and "Lutz"), reaching the highest rates shortly after birth.

Interactions between the stag ("Ludwig") and the hinds mainly occurred during the rut from August to November. This long period of rutting activity with low expression in comparison to other deer species is typical for Sika deer (BENNETSEN 1977, MCCULLOUGH et al. 2009).

Large variation in rutting activity for Sika deer has been reported across Europe and also within very small areas (MCCULLOUGH et al. 2009). According to BENNETSEN (1977) the rutting season varies considerably even from one herd to another. MATUSZEWSKI (1988) reported the start of the rut in mid-September for the south and in mid-October for the north of Poland. In the Czech Republic, Weserbergland and Möhnesee (Germany), Forêt de la Harth (France) and in the areas of origin in Northern Asia, Sika deer rutting usually starts in mid-October and often persists until December (CAILMAIL 1988, HAKE 1988, BASKIN & DANELL 2003). An extended period of rut resulting in late births may be a good indication of adaptability of the species in the given conditions (MCCULLOUGH et al. 2009). Keeping only one stag in the compound, the natural variability of rutting behaviour could be carried out due to the lack of male concurrence, thus causing the Dybowski deer at Tierpark Sababurg to mate according to their individual rhythm, although the main rut takes place from August to the end of September.

The fawning and rutting seasons being the times of the year where positive social interactions mainly take place, they are also the periods where most agonistic interactions occur (Table 3.25).

Female patterns of interspecific dominance in deer species are generally less obvious than dominance in males (CLUTTON-BROCK et al. 1979, 1982, MCGHEE & BACCUS 2006, AVENT 2008). However, female aggression occurs in different deer species to a different extent throughout the year (CHAPMAN & CHAPMAN 1997). As birthing occurs mainly in early summer, an increased aggression between hinds could be proven with increasing deer calf numbers in the herd for Fallow deer (*Dama dama*), White-tailed deer (*Odocoileus virginianus*) and Red deer (*Cervus elaphus*) (CHAPMAN & CHAPMAN 1997, MCGHEE & BACCUS 2006, BARTOŠ et al. 2002). This pattern is thought to be an adaptation for those temperate zone species to increase nutrient intake for winter, with increased weights improving fawning success (LANGBEIN & PUTMAN 1992).

For Axis deer (*Axis axis*) and Fallow deer (*Dama dama*) under conditions with sufficient food availability, MCGHEE & BACCUS (2006) found a contrary pattern with declining aggression with rising deer calf numbers towards autumn. This matches the results of the Dybowski deer at Tierpark Sababurg. Although the deer calf numbers did not rise, agonistic behaviour decreased towards autumn (Table 3.25). Assuming the aggression was caused by food concurrence, the ample food supply for the animals may probably relate to this decrease.

4.3.3.2 Interspecific interactions of the Dybowski deer

Interspecific Sika behaviour is rather flexible (MCCULLOUGH et al. 2009). Some authors reported pacific co-existence of free-roaming Sika deer with other species (GUO 2000, SAKURAGI et al. 2003), although positive social interactions with other wild animals have not been documented so far. Others in turn could prove intolerance by Sika deer towards other species (BARTOŠ & ŽIROVNICKÝ 1982). DANILKIN (1996) cited instances of Sika deer chasing Roe deer (*Capreolus capreolus*) from feeding sites, and described Sika deer appearing as an aggressive and successful competitor with Fallow deer (*Dama dama*) in the Czech Republic.

The current study is the first to prove regular positive interspecific social interactions for Dybowski deer. Interactions with visitors occurred seldom and irregularly, with exception of spring, over the year (Table 3.24). Visitors ignoring the Tierpark Sababurg's request not to feed the animals approached the enclosure and tried to offer feed to the Dybowski deer, which was usually taken, mostly by the stag. This is not unusual for Sika deer, which are known to

become very tame when kept in animal interaction areas and/or allowed to be fed. This is common in several wild animal parks in Germany (DWV 2012). The stag, originating from such an enclosure, was used to visitors before being relocated to Tierpark Sababurg, whereas the hinds are not inured to being fed.

Positive social interactions with the European bison did not take place during the observation period, whereas interspecific social behaviour was regularly observed between the Dybowski deer and the Exmoor ponies (Table 3.24). This positive contact was restricted to the stag ("Ludwig") and the younger Exmoor ponies (Table 3.26 and Table 3.18). The interactions between those species mainly occurred in the summer season, when the hinds were locked in the separation enclosure for giving birth under controlled conditions. During this period, the stag stayed with the Exmoor ponies for most of the time (3.3.2.3 and 3.3.2.2 above) and was included in the herd behaviour as an accepted member. As Sika deer tend to have small, stable group sizes in the wild (THE BRITISH DEER SOCIETY 2008), the lack of direct contact to conspecifics may have caused the Dybowski deer stag to look for this proximity to the other animals. Being held together for long periods of time or even being born into this animal society, the animals know each other individually. Stable structures of dominance hierarchy have evolved, allowing even unusual animal relationships to develop (MOSLEY 1999). Although most of the interactions were initiated by the Exmoor ponies, "Ludwig" did not avoid physical contact and sometimes even responded to mutual grooming, as long as the Exmoor ponies did not touch his velvet antlers. Antlers are extremely sensitive during accretion in deer (MCGHEE & BACCUS 2006), and the stag responded with avoiding behaviour when touched here.

The stag's proximity and contact with the Exmoor ponies diminished after the hinds and deer calves were released from the separation enclosure in August (Table 3.24). Nevertheless, unlike the rest of the deer, the stag showed no avoiding behaviour or timidness towards the Exmoor ponies during the rest of the year.

Agonistic behaviour towards the other species on the compound could be observed only rarely for the Dybowski deer at Tierpark Sababurg. ENQUIST & LEIMAR (1983, 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 form stable structures of dominance hierarchy as a mechanism to avoid high levels of aggression. Both is the case at Tierpark Sababurg, as sufficient feed is provided regularly and most of the animals were born and raised on the compound and so are used to the presence of the other species.

Regarding the social interaction grid for the agonistic contact of the Dybowski deer (Table 3.27), it is clear that only one hind ("Lisbeth") showed aggressive behaviour towards the Exmoor ponies. Curious Exmoor pony foals approached the Dybowski deer going below the normal individual distance and were chased off by the leading hind. Adult Exmoor ponies were avoided by the Dybowski deer, as were the European bison.
Visitors approaching close to the fences were also avoided by the hinds in most cases, whereas the stag normally tried to beg for feed (see above).

4.4 Habitat use

4.4.1 European bison

Analysing the habitat use of the European bison at Tierpark Sababurg over the complete observation period (Figure 3.17), it becomes apparent that most parts of the enclosure were used quite regularly, with the exception of the area by the Dybowski deer's separation enclosure. The hay rack had the highest proportion of use due to being the main whereabouts of the European bison during the winter season (Figure 3.23), causing the mean values to be increased for the complete observation period. Slightly more frequented than most open parts of the enclosure were the shady quadrants under the trees, as well as the areas in the vicinity of the European bison' separation enclosure.
Under free-living conditions, European bison movements are connected mainly with feeding activity to ensure optimum use of food supply (KRASIŃSKA et al. 2000). KRASIŃSKA et al. (1987) found habitat utilisation depended on group size and structure, habitat preferences and rotational exploitation of the environment to prevent overgrazing. Several other studies reported European bison using their territory in a rotation system, foraging in a continuous slow movement and returning every few days to the same site (PUCEK et al. 2003, DALESZCZYK et al. 2007). In seasons and regions with sufficient food availability, European bison are regularly reported to become very attached to their stands, not leaving them without important reasons (WRÓBLEWSKI 1927, BALČIAUSKAS 1999, PUCEK et al. 2004, POETTINGER 2011). However, occasional migrations from twenty to several hundred kilometres can sometimes occur, especially by older bulls (KRASIŃSKA et al. 2000).
Those findings would explain the regular use of the European bison's compound at Tierpark Sababurg over the complete observation period. Grazing all areas with appropriate vegetation

in a regular and rotational pattern leads to a more or less uniform use of the area, with preferred places for different behaviours under special conditions.

At the beginning of spring, only little vegetation was available on the compound and the European bison thus spent most of the time at the hay rack (Figure 3.20). With the start of the vegetation period, the animals began to roam the compound searching for the first sprouting grasses, foliage and herbs. The first warm days towards the coming summer season were spent either at the sand bath or in the shade. The same result was found by POPP (1999) and POETTINGER (2011), both documenting an increase of home range size with the vegetational season, and sand baths as preferred resting sites in spring. Several authors also studied free-living European bisons in Białowieża Forest. They found that, especially in spring and autumn, the open, grassy areas are positively selected due to being a nutritiously rich source of forage when the forest habitat cannot provide sufficient food (KRASIŃSKA et al. 1997a, 1997b, DALESZCZYK et al. 2007).

In summer, most time was spent in the shade of trees or at the sand bath (Figure 3.21). Feeding occurred mostly in the morning and evening hours (3.1.4.1 above) and took place at more selective patches of vegetation. Several authors stated seasonal preferences of feeding for different seasons (GRACZYK 1987, BOROWSKI & KOSSAK 1972, DALESZCZYK et al. 2007). Although European bison are extremely flexible in foraging habits, they tend to search for preferred plants in summer, for enough nutritiously rich food is available and allows the animals to select the plant species to forage on (GRACZYK 1987, BOROWSKI & KOSSAK 1972, DALESZCZYK et al. 2007). The same seems to be the case for European bison in enclosures. This was observed at Tierpark Sababurg, in semi-free European bison in the Rothaargebirge (North Rhine-Westphalia, Germany) (LINDNER et al. 2006) and for captive European bison at the Umweltbildungsstätte Donaumoos (Bavaria, Germany) (POETTINGER 2011).

The habitat use of the Tierpark Sababurg's European bison in autumn is also on a wider scale than in summer or winter (Figure 3.22). The reason is probably the nutritious advantage of the grassy areas with the decreasing herb and leaf abundance in comparison to the summer season, as discussed above. Additionally, the more sheltered areas in proximity to the European bison' separation enclosure are used regularly, especially during harsh weather in this season. The influence of climatic conditions on the behaviour and habitat use will be discussed separately (4.5.1 below). The hay rack is again used more frequently towards the

end of autumn, which matches the findings of KRASIŃSKI (1967), CABOŃ-RACZYŃSKA (1987), BALČIAUSKAS (1999), DALESZCZYK et al. 2007 and POETTINGER (2011). All found European bison tending to gather around the feeders, whether at game feeders in Białowieża Forest or at those in enclosures, at the end of autumn.

At the latest in winter, the majority even of free-living European bison gather around feeding sites and stay in their vicinity for most of the day (KRASIŃSKI 1967, PUCEK et al. 2003, 2004, DALESZCZYK et al. 2007). The European bison at Tierpark Sababurg spent about 40% of the observed time at the hay rack. Roaming occurred mostly in the surrounding areas, especially in the early morning and evening hours (Figure 3.23). Similar patterns were described by POETTINGER (2011) and SCHMITZ (2012), so the results from the present study seem to represent a normal behaviour for the European bison.

4.4.2 Exmoor ponies

The habitat use as displayed in Figure 3.18 for the complete observation period shows that the Exmoor ponies used nearly all accessible areas of the 14ha-wide compound, although to different extents.
The hay rack was used most in winter, not only for feeding but also for resting behaviour. In summer mostly the shady areas under the trees of A and E10 were used. Overall, a tendency to roam in the vicinity of the separation enclosure can be seen.
These inconstancies in habitat use are normal in horses and other wild animals. Several authors stated not all areas of a home range being coequal, but some places being used more often than others (HAFEZ et al. 1967, SUFFLING 1988, DUNCAN 1992, GUDMUNDSSON & DYRMUNDSSON 1994, BOUMAN 1998, KUHNE 2003, KUBALEK 2005, ARNOLD et al. 2006, KUNTZ et al. 2006a, 2006b). KEIPER & BERGER (1982) and BERGER J (1986) believe the areas of activity to be caused by the horses' use of particular places for specific behaviours. Horses' activity ranges are determined by the availability of feed, shelter and mating possibilities (SCHÄFER 1993). The availability of feed particularly is correlated with the home range size of horses (WARING 2003), in which the quantity as well as quality of the nutrition strongly affects the seasonal variations in the activity ranges (MCCORT 1984).
Seasonal variations in habitat use were also seen with the Tierpark Sababurg's Exmoor ponies.

In spring from March to May, the Exmoor ponies roamed large parts of the compound with a higher utilisation of the southern areas (Figure 3.24). There are no extreme differences in food availability on the meadows of the compound in the vegetation period, so this may not be the cause for the Exmoor ponies' preference of the southern areas for feeding. For resting, the Exmoor ponies mainly used the higher-lying northern parts, especially the shade of old woodland-pasture trees (E10). This may be due to increased wind and thus decreased appearance of stinging insects. It became obvious that the Exmoor ponies did only use their preferred resting place when the European bison were roaming other parts of the compound. The bison generally preferred the northern parts of the enclosure, and this could explain the tendency of the Exmoor ponies and Dybowski deer to concentrate on the opposite, southern areas. Being held together for many years, it is likely that stable structures of dominance hierarchy have formed as a mechanism to avoid high levels of aggressive encounters. This is known for many other species in mixed-species exhibits, and also in the wild (THOMAS & MARUSKA 1996, MOSLEY 1999, AVENT 2008). Thus, the partitioning of the compound into different, albeit overlapping, home ranges may be the main cause for the habitat use of the animals in this enclosure.

As in spring, the Exmoor ponies mainly used the southern part for grazing during summer (Figure 3.25), whereas the European bison preferred the northern areas (Figure 3.21). For resting behaviour, this trend reversed. The Exmoor ponies spent most of the time resting in the shade of the Tierpark Sababurg's surrounding wall (A10) and also again under the trees of E10, while the European bison mainly used the sand bath for resting behaviour. The Exmoor ponies' habitat use, like the daily activity rhythm, thus matches that of the European bison (Figure 3.9 and Figure 3.5 respectively). The daily activities of both species seem to be phased in some way, dividing the compound between each other with as little direct contact as possible.

From September to November, the Exmoor ponies confined their activity range in regard to the spring and summer season (Figure 3.26). Here, the main proportion of time was spent in the separation enclosure and its vicinity. The climatic conditions being very windy and wet from northern directions, the Exmoor ponies were given the opportunity to search for shelter in the half-open stable. If it weren't for the European bison's preference for the more sheltered northern areas at the Tierpark Sababurg's surrounding wall (Figure 3.22), the Exmoor ponies would have had little opportunity to avoid the weather. The general influence

of the weather on behaviour and habitat use of the animals will be discussed separately (4.5.2 below).
Having sufficient feed and shelter in close proximity, the Exmoor ponies were not forced to roam on a large scale, although extended parts of the compound were still used over this season. The hay rack in particular was frequented more often with reduced vegetation cover. Access to the hay rack was again mainly dependent on the European bison' movements and thus restricted to the morning and evening hours, when the bison were roaming the compound for feeding (Figure 3.10 and Figure 3.6).

In winter from December to February, the Exmoor ponies' ranging area was even more restricted towards the southern parts of the compound, but they used the hay rack to a larger extent (Figure 3.27).
This behaviour is probably due to the same reasons as those in autumn. Although being in the season with lowest food availability on the meadows, the daily amount of time spent on ingestion is not as high as in free-ranging horses (4.1.2 above). At Tierpark Sababurg, supplementary feeding of hay ad libitum is necessary to sustain the number of animals in this enclosure without a negative impact on the natural vegetation cover by excessive utilisation in winter. This reduces the daily amount of time dedicated to feeding for the Exmoor ponies and thus limits the needed home range to find sufficient feed (PIRKELMANN 1991, SCHÄFER 1993, MEYER & COENEN 2002).

4.4.3 Dybowski deer

As Figure 3.19 shows, the Dybowski deer spent most of the observation period in the separation enclosure and its surrounding areas, although large parts of the compound were used regularly. Only the particularly exposed areas were avoided by the Dybowski deer.
Originating from the border of Russia and China, this subspecies prefers woodlands and forest with dense understorey, but forages in open grassy areas (SMITH & XIE 2008). Sika deer generally are highly adaptable to different environmental conditions and show a broad variety of behavioural differentiations, especially in habitat use (HARRIS 2008). Several authors described small, migrating populations in mountainous regions (WANG et al. 2007) and large Sika aggregations in lowland forests and plains (XU et al. 1998). Others found populations of open forests and grasslands of valley bottoms and foothills below 300m (HSU et al. 1997), as

well as primarily sedentary populations, although those also showed some seasonal movement depending on water availability (DANG et al. 1990).
Large variations in behaviour and habitat use have been reported even across the introduced European Sika deer populations and also within very small areas (MATUSZEWSKI 1988, MCCULLOUGH et al. 2009), so comparison of data is difficult.

At Tierpark Sababurg, the Dybowski deer used the compound in a patchy way during spring from March to May, avoiding the open areas (Figure 3.28). The deer's habitat use could also have been influenced by that of the European bison and Exmoor ponies (Figure 3.20 and Figure 3.24 respectively), which roamed large scales of the area during this season rich on vegetation. Being the smallest animals in this mixed-species enclosure, the Dybowski deer were generally the weakest in competition, although there were exceptions with individuals (4.3.3.2 above). Often being displaced by the larger species from the preferred food patches, this could have caused the Dybowski deer to use the compound in such an irregular way.
Sika deer are, unlike most other deer species, extremely unspecific in food preferences. GUO (2003) found the deer mainly feeding on shrubs and brushes. SMITH & XIE (2008) reported them to forage primarily on open grassy areas. DANG et al. (1990) observed them feeding mainly on browse and fruit, and Sika deer in Tiebu Nature Reserve (Sichuan Province, China) fed generally on a wide variety of plant species without defined preferences (HARRIS 2008). Due to these findings, it seems unlikely that food patchiness and distribution causes the patchiness in the Dybowski deer's habitat use, as would be the cause in browsing deer species such as Roe deer (*Capreolus capreolus*) (BUBENIK 1962), Moose (*Alces alces*) (HAMILTON et al. 1980), Mule deer (*Odocoileus hemionus*) or Elk (*Cervus elaphus nelsoni*) (PARKER et al. 1984).

From June to August, the hinds were held in the separation enclosure for giving birth under more controlled conditions than on the large compound. Figure 3.29 thus only shows the habitat use of the stag. He used the enclosure in a split way, either staying in proximity to the separation enclosure and the hinds or mixing with the Exmoor ponies at A10 (Figure 3.25), which he did most of his time.
Sika deer in the wild mostly live in small herds that generally consist of harems with dominant males (GUO 2000, GUO & ZHENG 2000), although some males are even reported to live solitary (THE BRITISH DEER SOCIETY 2008).

This could explain the habitat use of the stag in summer. Seeking the proximity to his harem in the separation enclosure on the one hand, and, when lacking direct contact, seeking the herd security with the Exmoor ponies on the other. High-value feed was available in sufficient amount on each area of the compound, so a widespread use of the area was not necessary during this season and the habitat use was mostly restricted to the locations in proximity to the resting places.

In autumn from September to November, all Dybowski deer again had free access to the large compound, using mainly the southern parts (Figure 3.30). As in spring, the open areas were avoided, but only little time was spent in the northern areas. This again was probably caused by the presence of the European bison, who spent larger proportions of the day in the vicinity of their own separation enclosure (Figure 3.22).
The Dybowski deer mostly roamed in proximity to the Exmoor ponies during this season, regularly retreating to their separation enclosure for resting behaviour. The climatic conditions being quite harsh during parts of autumn and this part of the compound being well sheltered by large trees may be another reason for the increased use of this area.

This proportion of use is raised even more from December to February (Figure 3.31). Although the deer sometimes roamed the northern parts of the compound as well, most of the Dybowski deer's time was spent in the separation enclosure. This area is partially grown with coniferous trees, mainly spruce (*Picea spec.*) and pine (*Pinus spec.*). Interestingly, several studies have shown a positive correlation between the habitat selection of Sika deer with coniferous and mixed forests in winter (TAKATSUKI 1989, 1992a, 1992b, KAJI et al. 1995). These forests are important winter habitats for Sika deer to access food resources. Many studies indicate the importance of mature coniferous forest to Sika deer during winter. Old-growth forests have been shown to provide protection from deep snow and severe climatic conditions, vegetation cover for rest sites, access to nutritional forage, protection and/or refuge from predators and human activities. They are an essential winter habitat for deer (GILBERT et al. 1970, HAMILTON et al. 1980, TAKATSUKI 1989, 1992b, SAKURAGI et al. 2003).
It remains to be seen whether their natural preference for forest habitats or the refuge of the separation enclosure from the other species causes the Dybowski deer to reduce their range to this in winter. As the Dybowski deer, like the other species, are given supplementary feed throughout the whole year, perhaps this also has an impact on reducing the foraging need and thus activity range for the animals.

4.5 Influence of different weather conditions on behaviour and habitat use

4.5.1 European bison

Bovines have a broad range of tolerance regarding temperatures and other climatic factors. The influence of weather conditions on animals adjusted to being kept outside all year is thus generally low (ZEEB 1978, WAßMUTH 2002, ZÄHNER et al. 2004). POPP (2010) found no significant effect of weather conditions not related to seasonal adjustment for domestic cattle in grazing projects in the Thuringian Rhoen and the South Black Forest (Thuringia and Baden-Wuerttemberg, Germany). KOROČKINA (1972, 1973), PUCEK (1986), KRASIŃSKA et al. (1987, 2000), DZIĘCIOŁOWSKI (1991) and DALESZCZYK et al. (2007) found climatic factors not influencing exclusively free-ranging European bison' behaviour or habitat use. Only extreme snow cover caused the European bison to limit their roaming during winter (KRASIŃSKA et al. 2000). For the present study, the maximum snow cover was 35cm on the open area (as a mean from measurements at three different reference points) and did not influence the European bison' behaviour or habitat use. The effects of snow cover for free-ranging bison have been documented for over 1m of snow cover (KRASIŃSKA et al. 2000), so the difference is probably due to the disparity in the thickness of snow.

Additionally, extreme heat caused the European bison at Tierpark Sababurg to spent most of their time resting, especially at the sand bath. This matches the results of POPP (1999), ROUYS (2003) and POETTINGER (2011), who found the same pattern for different European bison in enclosures as well as for free-ranging populations.

Generally, the European bison at Tierpark Sababurg did not alter their behaviour or daily routine due to weather changes. Even strong rainfall or rising storms had no effect on the behaviour of the animals, as also described by HERRIG & HAUGEN (1969), KOROČKINA (1969) and PUCEK (2004) for free-ranging European bison.

4.5.2 Exmoor ponies

Wild horses are evolutionarily well adapted to the climatic conditions of their natural habitat in the course of the year (SCHÄFER 1993). Thus, the behaviour and habitat use of these animals changes due to season and the connected changes in the general climatic and environmental conditions, and short-term weather has a minor influence (DUNCAN 1980, 1985, MAYES & DUNCAN 1986).

This could be also proven for the Exmoor ponies at Tierpark Sababurg, which did not show distinct behavioural changes due to temporary weather changes not related to season. Only severe conditions influenced the Exmoor ponies behaviour and habitat use. Even strong rainfall alone thus had no effect on the animals, but rainfall in combination with strong winds and unusually low temperatures, especially during summer, caused the Exmoor ponies to search for shelter. This was also found by TYLER (1972), PRATT et al. (1986), KUHNE (2003), WOLLENWEBER (2007) and BAKER (2008). Temperature changes alone had no obvious influence on the Exmoor ponies, although extreme heat in summer redounded to extended resting behaviour during daytime, which is normal in feral horses (TYLER 1972, PRATT et al. 1986, WOLLENWEBER 2007). Interestingly, there seems to be a tendency to increased resting behaviour at the expense of feeding with rising atmospheric pressure, but further study would be required to prove the positive influence, as the obtained data are insufficient using just one measurement at one location per hour for the whole compound.

4.5.3 Dybowski deer

For Sika deer, behaviour is generally rather flexible and the species is known to be highly adaptable to different conditions (PUTMAN & MANN 1990, PUTMAN 2000, 2008, MCCULLOUGH et al. 2009). Comparison of the behaviour among different groups under different conditions is difficult. LIU (2002, 2004) found semi-free Sika deer to minimise food intake in hot and sunny weather and during rainfall, which would match the results of the current study. However, GUO (2003) reported no obvious influence of climatic factors not related to season for free-ranging Sika at Tiebu Nature Reserve (Sichuan Province, China). Other researchers stated several changes in behaviour occurring irregularly and probably being only partly influenced by short-term weather conditions (MANN & PUTMAN 1989, CHADWICK et al. 1996, STAINES 1998, IGOTA et al. 2004).

The habitat use of Sika deer also varies strongly between the different populations (MCCULLOUGH et al. 2009). From seasonal migrations to very local distributions, numerous kinds of variations have been described (e.g. TAKATSUKI 1989, 1992a, 1992b, KAJI et al. 1995, GUO 2003, SAKURAGI et al. 2003, MCCULLOUGH et al. 2009). Consequently, the results on habitat use due to weather influence also differ greatly among the studies.

For the Dybowski deer at Tierpark Sababurg, there seems to be the tendency to avoid strong rainfall by retreating into more sheltered areas, whereas surprisingly strong winds seem to cause an increase in feeding behaviour on the open areas. This could be due to the noise made

by rustling foliage, which would drown out approaching predators and thus cause the Dybowski deer instinctively to search for open areas for a better view as compensation, as proposed for Roe deer (*Capreolus capreolus*) (DANILKIN 1996) or White-tailed deer (*Odocoileus virginianus*) (HELLICKSON 2002).

4.6 Influence of visitor attendance on behaviour and habitat use

4.6.1 European bison

The normal reaction of free-ranging European bison to approaching humans is escaping behaviour, with flight distances of about 70–200m (GRACZYK 1987, BALČIAUSKAS 1999, LINDNER et al. 2006, KRASIŃSKA & KRASIŃSKI 2007, SCHNEIDER 2010). However, European bison in enclosures normally get used to humans and change their behaviour, not being perturbed by the presence of visitors or keepers (BALČIAUSKAS 1999, POPP 1999, LINDNER et al. 2006, POETTINGER 2011). Only adult females with newly born calves showed an increased guarding behaviour, not only towards visitors but also towards the other animals on the compound. This is quite normal for European bison (DALESZCZYK 2004, 2005). As the 14ha-wide enclosure at Tierpark Sababurg offers enough room for retreat, the European bison do not seem to be influenced even by large visitor numbers, especially on event days. However, there seems to be the tendency to avoid the areas close to the fence and to roam the more central parts of the compound on those days. It was stated by REINHARDT et al. (1978) and GRANDIN (1989) that cattle will avoid sources of noise and disturbance and choose non-habitual resting sites if the preferred ones are close to the noise or disturbance. This could also be true for the European bison, and their reason for roaming in the central parts of the compound on days with large visitor attendance.

4.6.2 Exmoor ponies

Horses do show a broad range of behavioural responses in regard to the presence of humans, governed by breed, age, gender and individual character (SCHÄFER 1993). Free-ranging horses in Shackleford Banks, Cape Lookout National Seashore (North Carolina, USA) are known to chase off visitors approaching within a certain distance (PRIOLI & TAYLOR 2007). Captive Przewalski horses (*Equus ferus przewalskii*) in zoo environments are reported to become

regularly disturbed in their natural behaviour by large visitor attendances (KOLTER & ZIMMERMANN 1988), or being affected only by especially loud sounds from passing visitors (BOYD 1988). For semi-free Exmoor ponies on Langeland (Denmark), DELLING (2008, 2009) documented only little avoiding behaviour of animals towards the presence of visitors, as CORNELISSEN & VULINK (1995) and VERA (1997, 1998) also proved for Konik horses (*Equus caballus*) in the nature reserve Oostvaardersplassen (Netherlands). As the enclosure at Tierpark Sababurg is not accessible for visitors, no larger influence of different visitor attendances was observable in the Exmoor ponies. Although some interactions with vistitors took place (4.3.2.3 above), the animals did not alter their behaviour due to visitor numbers or events. Being used to the presence of humans and having the ability to remain at a certain distance to the fence, the Exmoor ponies did not avoid the areas close to the visitors, but used the compound in a manner unaffected by their presence.

4.6.3 Dybowski deer

Sika deer are rather flexible in their behaviour and adaptation to different environmental influences (MCCULLOUGH et al. 2009). This is also true for their behaviour towards humans, which is extremely variable and differs strongly among various studies. For free-ranging Sika populations, GUO (2003) and LUI et al. (2004) found the animals to generally flee human approaches at different flight distances. HAMILTON et al. (1980) and TAKATSUKI (1989, 1992b) described avoidance behaviour occurring especially in winter. Semi-free Sika deer are proven to be able to habituate to the presence of humans (LIU et al. 1999, 2002). Captive Sika are even known to become tame (HU et al. 2002, DWV 2012) and are thus often kept in animal interaction areas and/or are allowed to be fed in several wild animal parks in Germany (DWV 2012). No observable influence of different visitor attendances on the Dybowski deer at Tierpark Sababurg could be proven in the present study. Therefore, it can be proposed that this is due to their adaptation to the zoo environment. The only cases when the deer paid attention to visitors was with approaching groups and visitors with dogs when roaming close to the fence. At a greater distance, even those were individually more or less ignored.

4.7 Study limitations

The present study analysed the behaviour, inter- and intraspecific interactions, as well as the habitat use of European bison, Exmoor ponies and Dybowski deer in a large-scale mixed-species enclosure at Tierpark Sababurg.

Despite all effort for objectivity, observation of behaviour by human observers can always cause minor mistakes in noticing, recognising and documenting behaviours in the observed animals, particularly short ones. The large amount of data during the long observation period and the continuous, experienced data collection can, however, provide a very clear picture of the animals' behaviour (ALTMANN 1973, MARTIN & BATESON 2008). Furthermore, this special study had the advantage of the animals knowing the observer personally for years and being generally used to visitors, so the influence of the observers' presence on the behaviour was minimised in comparison to other studies.

The daily observation time was limited to the hours of daylight, as the 14ha-wide compound offers no chance for the use of a night-vision observation. This could be considered a weak point in the method, but regarding the results of 24h-observations of animals under controlled conditions or GPS activity data (e.g. DUNCAN 1982, SAKURAGI et al. 2003, SCHMITZ 2012), this is of minor importance for wild animals' behaviour, and daily activity rhythms are relatively consistent.

The representativeness of this method is thus reasonable and was used in multitudinous studies, which also alleviates comparison of data. Being easily reproducible, the personal observation is one of the most widely used methods, and despite possible minor inaccuracies probably the most suitable method of analysing the behaviour of animals.

Documenting the positions of the animals in the compound was conducted in the same way as MARTIN & BATESON (2008) and MALEK (2009). Noting the exact positions on a grid map of the enclosure is a matter of practice, which was done before data collection commenced. Estimating the exact position of an animal on a 14ha-wide compound may also lead to minor misjudgements, especially at grid borders. But by using trees, smaller bushes, fence posts, rivulets or other enclosure characteristics as reference points, and also by knowing the enclosure well from the inside due to working at Tierpark Sababurg for several years, the observer was always able to recognise the anent grid plots containing the observed animals.

5 Conclusions, future research and management recommendations

The results of the current study provide the first insight into the behaviour, intra- and interspecific interactions, as well at the habitat use of three large mammal species in cohabitation of a large-scale, near-natural enclosure. Tierpark Sababurg is the only zoological institution which keeps European bison, Exmoor ponies and Dybowski deer together and thus offers the unique opportunity to examine this species combination with regard to future use for grazing projects in nature conservation areas.

As could be proven, all three species behave in a very natural way comparable to free-ranging populations, with all seasonal variations and only minor adaptations to living in an enclosure. The animals maintain their individual daily activity rhythms, wanderings and social behaviours in disregard to the environmental influence of having a restricted range and living in a wild animal park managed by humans. Interactions between the species do occur regularly, but due to an established hierarchy they are restricted to positive or only indirect agonistic contact, as is also common in free-living individuals. The compound is used in an attuned way by all species. The European bison are the dominant species, and the Exmoor ponies and the Dybowski deer have adjusted to their movements. However, no concurrence was observable for most of the year, as the 14ha-wide compound provides enough food, sheltered areas and habitat structure to avoid conflicts over resources. Only in winter do the European bison dominate the hay rack for most of the day. In any case, due to perpetuation of daily activity rhythms and an organised management, the other species get the opportunity to use this feed.

Generally the intra- as much as the interspecific social organisation of all three species is highly coordinated and well established. Even changes in herd composition due to breeding management did not influence the relationships between the European bison, Exmoor ponies and Dybowski deer. Although the added animals were not used to the presence of the other species, they quickly adapted to the hierarchy.

The presence of visitors is only of minor importance, for the 14ha-wide compound offers enough room for the animals to retreat and avoid the approaching visitors. Even though in a few cases individuals of the Exmoor ponies and Dybowski deer took feed from visitors ignoring the animal parks request not to feed the animals, the general behaviour of all species towards visitors was to remain aloof.

Although further studies and closer examinations of different patterns are still necessary, the current results can already prove the wild species combination of European bison, Exmoor

ponies and Dybowski deer is effective and without problems. Furthermore, it could be shown that they behave in a natural way when managed in enclosed areas which are large enough to ensure the possibility of avoiding direct contact. These findings offer a unique possibility to improve the already common use of large herbivores for nature conservation. Until now, mostly domesticated breeds are used in grazing projects. The examined animals as wild species, however, have a far more natural feeding ecology and roaming behaviour, and could thus much better simulate the impact of the large herbivores that dominated our landscapes in ancient times.

This form of nature conservation management is already well known to promote the number of available ecological niches, mainly through the creation of a heterogeneous landscape. A higher structural diversity in a given area leads to a larger number of plant species finding suitable conditions for survival, which in turn allows the establishment of complex biological communities. The use of natural wild species could thus implement scientifically sound and successful nature conservation more effectively, especially on larger areas or on those being difficult to access. Additionally, the use of European bison, Exmoor ponies and Dybowski deer would result in an increase of population numbers of these endangered species. This would help to promote their survival. And not least, wild species in natural landscapes have been proven to be an enormous opportunity for visitor education in environmental issues and ecology, which is one of the major aims of modern institutions of nature conservation.

Collaboration with different projects including European bison and wild horses have already been established, and future research is planned to realise large-scale areas grazed by wild animals once roaming free in Central Europe.

Nevertheless, the established keepings of different European wild ungulate species have also to be observed and examined going forward. Zoo-based research still provides the best opportunities to study behavioural and demographic issues, reproductive physiology, evolutionary genetics and lots of other topics in detail, which is not possible or very difficult to cover in free-roaming animals. In particular, if different species of ungulates are kept together in mixed-species exhibits, close attention should be paid to interspecific dominance and its subsequent effects.

For the well-being of animals in captivity, effective management is extremely important, especially in regard to captive breeding programmes of threatened species where the maintenance of optimum fitness is vital and the implications of management failure can be severe. For the actual management of the European bison, Exmoor ponies and Dybowski deer at Tierpark Sababurg, a few recommendations are to be made from a scientific point of view.

Many studies proved European bison to feed on a large variety of plant and herb species. Thereby, one important part of the diet consists of bark and foliage (BOROWSKI & KOSSAK 1972, GĘBCZYŃSKA & KRASIŃSKA 1972, KOROČKINA 1972, 1973, CABOŃ-RACZYŃSKA et al. 1983, 1987, KRASIŃSKA et al. 1987, KRASIŃSKI & KRASIŃSKA 1992, POPP 1999, KRASIŃSKA et al. 2000, PUCEK 2004, DALESZCZYK 2007, JAROSEVICZ & PIROZNIKOW 2008, SCHMITZ 2012). It is therefore recommended that the feeding of branches, which up to now has been seldom, be increased significantly. This would not only benefit the European bison's physical and behavioural well-being, but would also be improving the habitat for all three species. Building up several heaps of regularly supplemented branches would offer an addition also to the Exmoor ponies' and Dybowski deer's diet, but would additionally provide more habitat structure, cover and auto-grooming sites, retreating possibilities for deer calves and shedding sites for the stags. Additionally, heaps of branches are not only important microhabitats for uncounted small animals, they are also stepping stones for plants (BENJES 1997). This will enrich the vegetation and further improve the diet and habitat for all species.

The second recommendation also involves the vegetation of the compound. Being vegetated with old woodland-pasture trees, these have been dated to be several hundred years old. Some are already showing signs of dying off or are already just remaining dead wood. As trees need several decades before they can provide shade and cover and have to be secured against being eaten for years, it would be reasonable to start reforesting as soon as possible. Trees have been shown to be one of the most important enclosure structures for the well-being of the animals. This would ensure enough time to let those young trees develop to full-grown habitat structures, replacing the old ones in the long-term.

The last recommendation relates to the fencing of the enclosure. No aggressive behaviour of the animals towards visitors, dogs, keepers or cars could be documented, but, originating from the 1970s, large proportions of the wooden fence posts and bracings are no longer stable and could probably not withstand any effort of the animals to overcome it. To minimise any risk it is strongly recommended that the enclosure fencing be replaced. This would not only improve the safety for both visitors and animals, but also improve the public image by appearing well-maintained.

6 Summary

From spring 2010 to early summer 2011, the behaviour, intra- and interspecific interactions, as well as the habitat use of European bison (*Bison bonasus*), Exmoor ponies (*Equus ferus*) and Dybowski deer (*Cervus nippon hortulorum*) were documented in a 14ha-wide enclosure at Tierpark Sababurg. Fifteen individuals were observed by focal-animal and scan sampling during all hours of daylight for 605 hours in total.

Regarding the main behaviours as a mean over the complete observation period, the European bison spent 47.73% of the day on feeding, 43.05% on resting, 6.79% on locomotive and 1.68% on comforting behaviour. The Exmoor ponies fed for 58.62% and rested for 34.54% of the day, used 3.87% for locomotion and 1.37% for comforting behaviour. The Dybowski deer fed for 47.22% of the day and rested for 43.64%, with 4.55% dedicated to locomotive and 2.44% to comforting behaviour. Those main behaviours of all three species were organised in a species-specific daily activity rhythm of alternating phases of ingestion and resting behaviour. The proportions of all behaviours and, as a result, the daily activity rhythms varied throughout the seasons and thus in different environmental conditions.

All species could be proven to behave in the normal range of results for their free-ranging conspecifics and displayed natural social behaviours uninfluenced by management or by living in an enclosed environment. Interspecific interactions did occur to a certain extent, positive interspecific interactions being restricted to the Exmoor ponies and Dybowski deer. Agonistic relations occurred mostly as simple threatening gestures or as indirect interactions without physical contact. A species hierarchy is established and maintained, with the European bison being the dominant species, followed by the Exmoor ponies and the Dybowski deer.

The analysis of the habitat use showed clear preferences for special areas and enclosure features of the compound in the different species. As with behaviour, the habitat use was also influenced by the different seasons and varied across these. Whereas the open, grassy areas were preferred in spring and autumn, the more sheltered areas were used to a greater extent in summer, as they provided shaded resting places, and in winter due to harsh weather conditions.

In conclusion, the cohabitation of European bison, Exmoor ponies and Dybowski deer at Tierpark Sababurg is without problems and can be taken as an example project for future research on possibilities for grazing projects in nature conservation.

7 Zusammenfassung

Vom Frühjahr 2010 bis Frühsommer 2011 wurden Verhalten, intra- und interspezifische Interaktionen sowie Raumnutzung von Wisenten (*Bison bonasus*), Exmoor-Ponys (*Equus ferus*) und Dybowski-Hirschen (*Cervus nippon hortulorum*) auf einer 14 ha großen Gemeinschaftsanlage im Tierpark Sababurg untersucht. 15 Individuen wurden dazu insgesamt für 605 Stunden mittels focal-animal und scan sampling beobachtet.

Die Mittelwerte der Hauptverhaltensweisen über den gesamten Beobachtungszeitraum ergaben bei den Wisenten Tagesanteile von 47,73 % für Nahrungsaufnahme, 43,05 % für Ruheverhalten, 6,79 % für Fortbewegung und 1,68 % für Komfortverhalten. Die Exmoor-Ponys fraßen 58,62 % des Tages, ruhten 34,54 %, nutzten 3,87 % für die Fortbewegung und verbrachten 1,37 % mit Komfortverhalten. 47,22 % der Zeit wurden von den Dybowski-Hirschen zur Nahrungsaufnahme verwendet, 43,64 % geruht, 4,55 % zur Fortbewegung genutzt und 2,44 % mit Komfortverhalten verbracht. All diese Verhaltensweisen waren Bestandteil eines artspezifischen Tagesrhythmus aus alternierenden Nahrungsaufnahme- und Ruhephasen.

Die prozentualen Anteile und somit auch die Ausprägung dieses Tagesrhythmus variierten dabei allerdings teilweise stark zwischen den einzelnen Jahreszeiten und den damit verbundenen klimatischen und umweltbedingten Veränderungen.

Die Individuen aller drei Arten verhielten sich dabei völlig normal im Rahmen der nachgewiesenen Bandbreite des natürlichen Verhaltens ihrer wildlebenden Artgenossen, unbeeinflusst von den Gehegebedingungen und Eingriffen des Zuchtmanagements.

Interspezifische Interaktionen traten regelmäßig auf, positive Kontakte blieben dabei allerdings auf die Exmoor-Ponys und die Dybowski-Hirsche beschränkt. Agonistische Interaktionen waren meist lediglich als einfache Drohgebärden oder als indirekte Interaktionen ohne körperlichen Kontakt feststellbar. Eine feste Artenhierarchie ist etabliert und wird von allen Tieren akzeptiert, wobei die Wisente die dominante Rolle einnehmen, gefolgt von den Exmoor-Ponys und den Dybowski-Hirschen.

Die Habitatnutzungsanalyse ergab für alle drei Arten bevorzugte Aufenthaltsbereiche und genutzte Gehegeobjekte. Dabei war wie das Verhalten auch die Habitatnutzung stark von den jahreszeitlich veränderlichen Umweltbedingungen beeinflusst. Während die offeneren Areale insbesondere im Frühjahr und Herbst genutzt wurden, bevorzugten die Tiere im Sommer und Winter eher die geschützteren Anlagenbereiche, im Sommer hauptsächlich als Schattenbereich, im Winter als Wetterschutz.

Zusammenfassend betrachtet funktioniert das Zusammenleben der Wisente, Exmoor-Ponys und Dybowski-Hirsche im Tierpark Sababurg ohne Probleme und kann als Beispiel-Projekt für die zukünftige Forschung über die Möglichkeiten für Beweidungsprojekte mit heimischen Wildtieren im Naturschutz dienen.

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9 Index of tables and figures

10 Acknowledgements

I am grateful to Prof. Dr. Rainer Willmann for enabling me to conduct this research as well as for his academic support and the good cooperation. I also thank Prof. Dr. Dr. Matthias Gauly and Prof. Dr. Michael Mühlenberg for useful comments and ideas on the research design and becoming the additional supervisors of the doctoral project.

This project would not have been possible without the support, interest and endurance of my colleagues at Tierpark Sababurg. Thanks not only for offering the possibility to conduct this research, but for all the numerous help and assistance.

I additionally thank Dr. Rebecca Klug for her tireless and continual support and advice on this thesis as well as for many discussions and manuscript corrections. I also owe a great deal of thanks to Thomas James Newman, who was a big help in editing and proofreading the thesis.

Finally, I particularly want to thank my family for the everlasting endorsement, patience, tolerance and support. Without you, it would not have been possible to follow my way through the last years. Danke, Sippe!

11 Appendix

Table 11.1: Abbreviations and definitions of the observed behaviours

Abk.	Verhaltensweise	Abbr.	Behaviour
Nahrungs-aufnahme		Ingestion	
fre (insg.)	Alles Fressverhalten	fee (in total)	feeding
fre (HR)	Fressen an der Heuraufe	fee (Hay rack)	feeding on the hayrack
fre (Stall)	Fressen im Stall	fee (Stable)	feeding in the stables on feed given by keepers
fre (FR W)	Fressen an der Futterraufe der Wisente	fee (Feedyard Europ. b.)	feeding on the European bison feedyard
fre (TP-Futter)	Fressen von Tierpark-Futter (Füttern durch Besucher)	fee (TP-Feed)	feeding on zoo-authorised food given by visitors
stf	Stehen und fressen	gra	grazing
kaf	Kauern und fressen	grr	grazing recumbent
std	Stehen und fressen von Erde	pic	pica
stl	Stehen und fressen von Laub	bro	browsing
gef	Gehen und fressen (mehr als 10 m pro Minute)	waf	walking and feeding
kna	Knabbern von Holz (Zweige, Baumrinde oder ähnliches)	nib	nibbling
scr	Scharren auf dem Boden (auch als Sozialverhalten beobachtet)	paw	pawing on the ground
tri	Trinken	dri	drinking
sau	Saugen (bis auf wenige Ausnahmen nur beim Muttertier)	suc	suckling
Lokomotion		Locomotion	
lok (insg.)	Alle Bewegungsverhaltensweisen	loc (in total)	
ste	Stehen (z.B. beim Kraulen, Sichern, Sozialkontakten etc.)	sta	standing
ste (sau)	Stehen beim Säugen	sta (suc)	standing while offspring is suckting
sch	Schritt	wal	walking
tra	Trab	tro	trotting
gal	Galopp	gal	galloping
Ruhe-verhalten		Resting behaviour	
ruh (insg.)	Alles Ruheverhalten	res (in total)	all resting behaviour
doe	Dösen, stehend mit entspanntem Gesichtsausdruck, waagerecht gehaltenem Hals, bei den Ponys auch mit angewinkelter Hinterhand	rst	rest standing
kau	Kauern, liegend mit unter dem Rumpf angewinkelten Beinen	rre	rest recumbent

Abk.	Verhaltensweise	Abbr.	Behaviour
lie	Liegen auf der Seite mit entspannten oder zeitweilig erhobenem Kopf, Extremitäten ausgestreckt oder leicht angewinkelt	rly	rest lying down
wkl	Wiederkäuen im Liegen	rur	rest recumbent and ruminating
wks	Wiederkäuen im Stehen	rus	standing and ruminating
Stoff-wechsel		Elimination	
kot	Koten	def	defecating
har	Harnen	uri	urinating
Komfortver halten		Comforting behaviour	
kom (insg.)	Alle Verhaltensweisen des Komfortverhaltens	com (in total)	
rei	Reiben, Scheuern an Gegenständen zur Hautpflege	rub	rubbing against sth.
wae	Wälzen auf dem Boden, ein- oder beidseitig	rol	rolling
krz	Kratzen mit dem Hinterlauf an Kopf, Ohren und Hals oder mit Zähnen an Hals oder Flanke	scr	scratching
lek	Sich selber das Fell lecken/Putzknabbern	atg	autogrooming
deh	Dehnen, meist nach dem Aufstehen	str	stretching
pla	Plantschen im Wasser	spl	splashing
Sozial-kontakte		Social contact	
soz + (insg.)	Alle freundlichen Verhaltensweisen	soc + (in total)	
kra	Kraulen, freundliches Verhalten, soziale Hautpflege von Flanken, Rücken, und Hals des Kraulpartners durch Beknabbern	gro	mutual grooming
auf	Aufsuchen, aktives Gehen zu einem Individuum, freundliches Verhalten	seo	seeking out
fol	Folgen, aktives Hinterhergehen, freundliches Verhalten	fol	following
scw	Schritt weg, aktives Fortbewegen von einen Tier nach einem stattgefundenen, freundlichen Verhalten	sta	stepping away
nan	Naso-nasaler Kontakt, freundliches Verhalten	nnc	nose-to-nose-contact
nak	Nasen-Kruppen-Kontakt, freundliches Verhalten	ncc	nose-to-croup-contact
naf	Nasen-Flanken-Kontakt, freundliches Verhalten	nfc	nose-to-flank-contact
nah	Nasen-Hals-Kontakt, freundliches Verhalten	nec	nose-to-neck-contact

Abk.	Verhaltensweise	Abbr.	Behaviour
nag	Naso-genitaler Kontakt, freundliches Verhalten	ngc	nose-to-genital-contact
rea	Reiben an, Scheuern an einem anderen Tier zur Fellpflege	rui	rubbing against other individuals
lec	Lecken von Herdenmitgliedern	lii	rubbing of other individuals
bet	Betteln (Nur Besuchern gegenüber)	beg	begging
soz - (insg.)	Alle agonistischen Verhaltensweisen	soc - (in total)	
zwi	Zwicken, leichtes Beißen mit den Schneidezähnen, dominantes Verhaltes	nip	nipping
ver	Verfolgen, aufdringliches Hinterherlaufen, dominantes Verhalten	pur	pursuing
vtr	Vertreiben, Verfolgen eines Individuums, um es zu verjagen, aggressives Verhalten	dro	driving another animal off
dro	Drohen, schwache Form des Beißdrohens, angelegte Ohren oder Drohbewegungen mit dem Kopf (z.B. zum Verscheuchen anderer Individuen)	thr	threatening
bed	Beißdrohen, Freilegen des Schneidezahngebisses und angelegte Ohren	thb	threatening to bite
sld	Schlagdrohen, Anheben des Hinterteiles und/ oder des Hinterbeines, Drohhaltung	thk	threatening to kick
bei	Beißen	bit	biting
sla	Schlagen, Ausschlagen mit einem oder meist beiden Hinterbeinen	kic	kicking
ang	Angehen, Angriff auf ein Individuum, aggressives Verhalten	att	attacking
tre	Treiben, Haltung des Hengstes mit waagerecht gestrecktem Hals und angelegten Ohren, gehobenen Schweif und teilweise Schlenkerbewegungen des Kopfes, zum Zusammenhalten der Herde und Rückführung von Stuten, aggressives Verhalten	cha	chasing
anf	Anflehmen, wie flehmen, aber submissives Verhalten	fla	flehmen as submissive gesture
unk	Unterlegenheitskauen, Aufeinanderklappern der Zähne und geduckte Körperhaltung, seitlich abfallende Ohren, eingeklemmter Schweif, meist bei Jungtieren	inc	inferiority chewing

Abk.	Verhaltensweise	Abbr.	Behaviour
unh	Unterlegenheit, unterwürfige Körperhaltung mit gesenktem Kopf, seitlich gekippten Ohren und eingezogenem Schweif, bei Adulten	inf	inferiority
mei	Meiden, aktives Fortbewegen von einem Individuum	flg	fleeing
auw	Ausweichen, Aus-dem-Weg- gehen, um einen störenden Kontakt zu verhindern (auch als Reaktion auf vtr, ver etc.)	avo	avoiding
Sichern		Vigilant behaviour	
sic (insg)	Alle ein Sichern hervorrufenden Ereignisse	sat (in total)	
sic allg.	Allgemeines Sichern, Aufwerfen des Kopfes, Habachtstellung, aufgestellte Ohren	sal	standing alert
sic gg. Störung	Sichern gegenüber Störung	sad	standing alert because of a general disturbance
Besucher	Sichern gegenüber Besuchern	svi	standing alert because of visitors
Besucher + Hund	Sichern gegenüber Besuchern mit Hunden	svd	standing alert because of visitors with dogs
Besucher-gruppe	Sichern gegenüber Besuchergruppen (>10 Personen)	svg	standing alert because of a group of visitors
Kindergruppe	Sichern gegenüber Kindergruppen (z.B. Schulklassen)	ssc	standing alert because of a class of pupils
TP-Auto	Sichern gegenüber Tiepfleger-Auto	skc	standing alert because of a keepers car
HW-Auto	Sichern gegenüber Handwerker-Auto	scc	standing alert because of a craftsmen car
PF-Auto	Sichern gegenüber Raumpflegerinnen-Auto	sdc	standing alert because of a detergencies' car
Auto	Sichern gegenüber allen anderen außer oben aufgeführten Autos	soc	standing alert because of other cars
Traktor	Sichern gegenüber Traktor(en)	str	standing alert because of tractors
Bau-fahrzeug	Sichern gegenüber Baufahrzeugen	scv	standing alert because of construction vehicles
Luchs	Sichern gegenüber Luchs (-Rufe während der Ranz-Zeit)	slc	standing alert because of the lynxes calls
Gibbon	Sichern gegenüber Gibbon-Rufen	sgc	standing alert because of the gibbons calls
Nilgänse	Sichern gegenüber wilden Nilgänsen an den im Gehege befindlichen Teichen	seg	standing alert because of the Egyptian geese
Wisente	Sichern gegenüber den Wisenten	seb	standing alert because of the European bison
TP	Sichern gegenüber Tierpflegern	ske	standing alert because of the keepers

Abk.	Verhaltensweise	Abbr.	Behaviour
Dybowski	Sichern gegenüber Dybowski-Hirschen	sdd	standing alert because of the Dybowski deer
Schuss	Sichern gegenüber Schüssen während der Wildabschüsse in anderen Parkbereichen	ssh	standing alert because of shots
Laut-äußerung		Vocalisation	
qui	Quieken, Kontaktlaut bei den Hirschen	squ	squealing
wie	Wiehern	whi	whinnying
röh	Röhren. Brunftruf der männlichen Hirsche	bar	barking and roaring of the stag during the rutting season
Territorialverhalten		Territorial behaviour	
imt	Territoriales Imponieren, Imponierhaltung mit gespitzten Ohren und meist im Trab	tim	territorial impressing
mar	Markieren, Koten oder Harnen auf Kothaufen an Gehegegrenzen	mar	marking
for	Forkeln, mit Gehörn oder Geweih an Boden, Totholz oder Gebüsch	for	forkeln with horns or antlers
feg	Fegen, Abstreifen der Basthaut nach Wachstumsvollendung des Geweihs, meist an Gebüsch oder Ästen	sha	shedding the antlers
Spiel-verhalten		Playing behaviour	
spk	Spielkampf, Spielerischer Kampf mit Zwicken, Anrempeln und gegenseitigem Jagen, meist im Schritt mit kurzen Laufphasen	plf	play fighting
lau	Laufspiel, Bewegungsspiel im Galopp oder Trab mit Sprüngen und meist ohne bestimmtes Ziel, einzeln oder mit anderen Tieren	lop	locomotive play
sex	Sexualspiel, Spielerisches Besteigen der Jungtiere untereinander, ohne Erektion	psb	play sexual behaviour
Sexual-verhalten		Sexual behaviour	
ims	Sexuelles Imponieren, Imponierhaltung mit aufgewölbten Hals und im Trab	sim	sexual impressing
aus	Ausschachten, Erektion der Rute	ere	erection
ona	Onanieren, klatschendes Schlagen der erigierten Rute an den Bauch	mas	masturbating

Abk.	Verhaltensweise	Abbr.	Behaviour
sae	Sägebockstellung, sägebockartig gespreizte Beine, schwach gesenkte Hinterhand und leicht erhobener Schweif, bei paarungsbereiten weiblichen Tieren	saw	sawbuck-posture
bli	Blitzen, Abspritzen von Urin und Brunstschleim während der Rosse	rhm	releasing of heat mucus
fle	Flehmen, geruchliche Orientierung mit den Jacobsonschen Organ, charakteristische Körperhaltung, zur Untersuchung von Kot- und Harnstellen und von rossigen Stuten, ferner zur Identifizierung fremdartiger Gerüche (sexueller Hintergrund)	fle	flehmen
vor	Vorspiel, Zwicken in die Schulter und Flanke, naso-genitaler Kontakt und Flehmen, Zeichen einer bevorstehenden Paarung, freundliches Verhalten	for	foreplay
bes	Besteigen, Aufreiten, auch von Jungtieren	mou	mounting
int	Koitus, Penetration	pen	penetration
rih	Riechen von Harn oder Kot, Beriechen von Exkrementen	ine	investigation of excrement

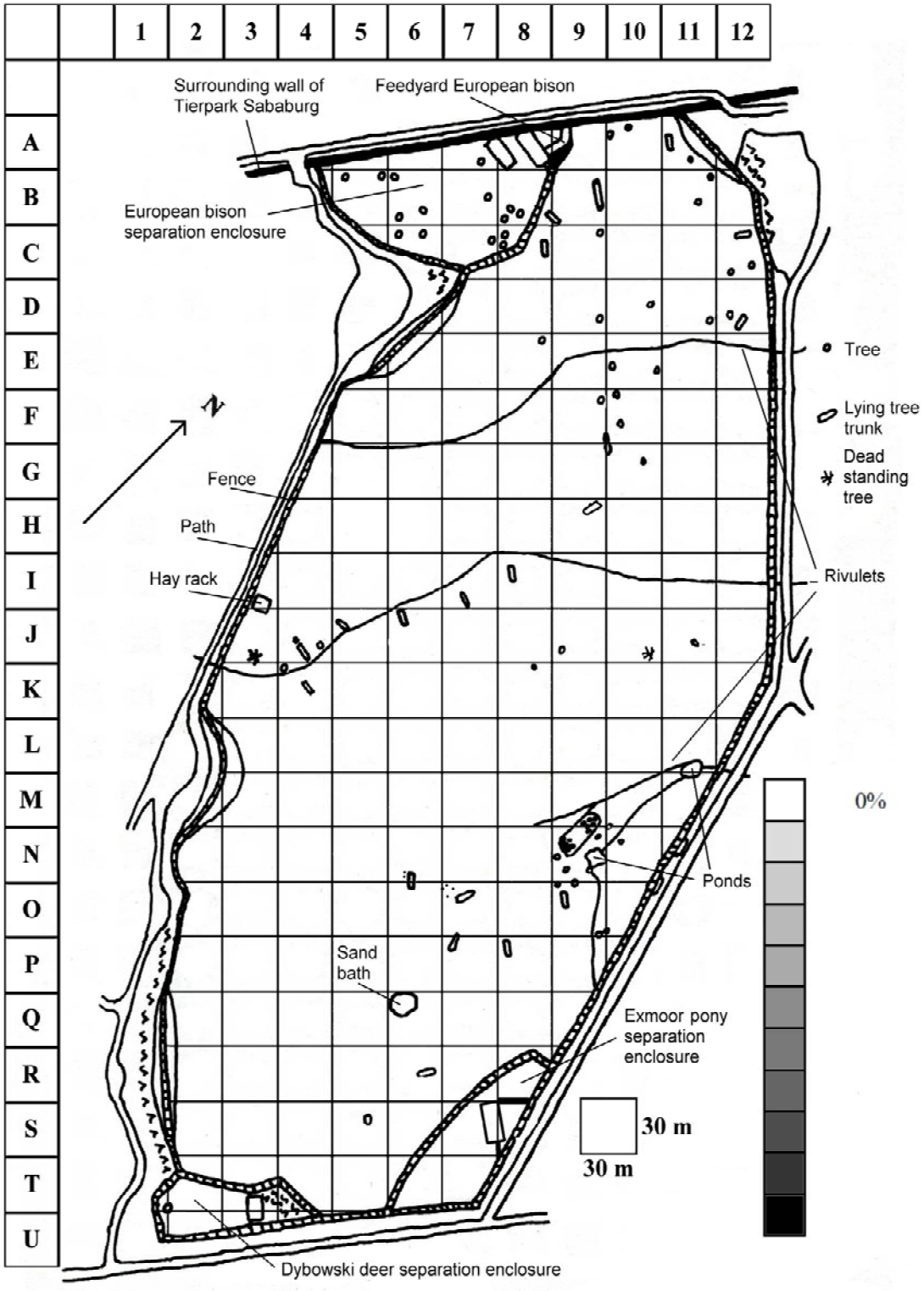

Figure 11.1: Grid map of the enclosure with schematic landscape marks. The bar on the right shows the use of single quadrants in 10% increments.