Fachgebiet Wildbiologie und Wildtiermanagement

# Impact of man on wolf behaviour in the Białowieża Forest, Poland

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### CONTENTS

1.	. General introduction				
	1.1	Background	5		
	1.2	Human impact on wolves: demographic and behavioural responses	5		
	1.3	Spatio-temporal behaviour under human influence	6		
		Anti-predator behaviour	7		
		Foraging strategy	8		
	1.4	Objectives and structure of this thesis	9		
	1.5	Study area	10		
		Project partners	10		
		Physical characteristics and vegetation	11		
		Forest protection	12		
		Humans	13		
		Wolves	15		
		Trapping and radio-tracking wolves	15		
	1.6	Literature cited	17		
2.	Accura	cy of radiotelemetry to estimate wolf activity and locations	21		
	2.1	Abstract	21		
	2.2	Introduction	21		
	2.3	Methods	22		
	2.4	Results	24		
	2.5	Discussion	26		
	2.6	Management implications	28		
	2.7	Acknowledgments	28		
	2.8	Literature cited	29		
3.	Impact	of human activity on daily movement patterns of wolves	30		
	3.1	Abstract	30		
	3.2	Introduction	30		
	3.3	Study area	31		
	3.4	Methods	31		
	3.5	Results	32		
	3.6	Discussion	33		
	3.7	Acknowledgments	34		
	3.8	Literature cited	34		
4.	Daily p	patterns and duration of wolf activity	35		
	4.1	Abstract	35		
	4.2	Introduction	35		
	4.3	Methods	36		
		Study area	36		
		Radio-tracking of wolves	37		
		Prey of wolves and activity of humans	39		
	4.4	Results	40		
		General activity patterns of wolves and humans	40		
		Prey	41		
		Breeding season	43		
		Weather	45		

	4.5	Discussion	46
	4.6	Acknowledgments	48
	4.7	Literature cited	48
5.	Selecti	on of den, rendezvous and resting sites by wolves	50
	5.1	Abstract	50
	5.2	Introduction	50
	5.3	Study area and methods	50
	5.4	Results	52
	5.5	Discussion	54
	5.6	Acknowledgements	55
	5.7	References	55
6.	Spatio	-temporal segregation of wolves from man	57
	6.1	Abstract	57
	6.2	Introduction	57
	6.3	Study area	58
	6.4	Methods	60
		Wolves	60
		Human activity	61
	6.5	Results	62
		Permanent man-made structures	62
		Temporary human presence	65
		Reserves	67
	6.6	Discussion	68
	6.7	Management implications	70
	6.8	Acknowledgements	71
	6.9	Literature Cited	71
7.	Genera	Il discussion	74
	7.1	Impact of man on wolf behaviour	74
		Accuracy of radio-telemetry and its influence on wolf behaviour	74
		Temporal patterns of wolf activity and movements	75
		Spatial avoidance of humans by wolves	77
		Spatio-temporal segregation of wolves from man	79
		Conclusions	80
	7.2	Implications for wolf conservation and management	81
		Human disturbance	81
		Habitat fragmentation	82
		Impact of roads on wolves	83
		Suitable areas for wolf recovery	84
		Wolf conservation and wolf control	85
	7.3	Literature cited	86
Su	immary		91
Ζı	isamme	nfassung	93
A	knowle	edgements	96

#### **1. GENERAL INTRODUCTION**

#### 1.1 Background

Wolves (*Canis lupus*) were originally distributed throughout the northern hemisphere, but by the mid 20<sup>th</sup> century, they had been extirpated from most populated areas (Mech 1970, Boitani 1995). People's attitudes towards nature changed in the 1960s with the onset of the environmental revolution. This also led to a shift of conceptions about wolves, whose status was raised from "the vile wolf to the unjustly persecuted wolf" (Mech 1995). Legal protection of wolves followed in many European countries as well as in the USA, and consequently wolves have been slowly expanding their ranges in Europe and North America (Promberger & Schröder 1993, Mech 1995, Boitani 2000).

Because wolves mainly survived in sparsely populated areas, they became a symbol of wilderness (Theberge 1975) and were considered as intolerant to human disturbance (Chapman 1979). This concept about wolves may be the reason why little attention was given to the study of human influence on wolf behaviour. Recent reports indicate that wolves can be highly tolerant to human presence. For example, a wolf pack in Minnesota inhabited a military training area with a high road density (Merrill 2000). In Minnesota and Wisconsin, some wolves even tolerated humans close to their den sites (Thiel et al. 1998). In Romania, several wolves paid regular nightly visits to a dump site located in a town of over 300,000 inhabitants (Promberger et al. 1997). However, Thurber et al. (1994) showed that wolves are not indifferent to human activity and avoid roads and settlements in Alaska.

The results of these studies could appear contradictory at first sight. They indicate on the one hand that wolves can be tolerant to human activity and on the other hand that they avoid contact with man. Boitani (2000) highlighted the need for knowledge on the capacity of wolves to coexist with human activity, a factor he regarded as a key element for the conservation of wolves in Europe. Better insights into the mechanisms that determine the behavioural response of wolves towards humans would therefore contribute to the understanding of wolf ecology in general and improve the ability of wildlife managers to identify suitable habitats for wolf recovery.

#### 1.2 Human impact on wolves: demographic and behavioural responses

Previous studies on the impact of humans on wolves have mostly focussed on the influence of human-caused mortality on wolf populations (e.g. Fritts & Mech 1981, Peterson et al. 1984, Ballard et al. 1987, Fuller 1989, Frkovic et al. 1992, Jędrzejewska et al. 1996). Wolf populations are able to withstand human-caused mortality rates of up to 30-40% per year (Peterson et al. 1984, Ballard et al. 1987, Haight et al. 1998, Larivière et al. 2000). However, once this threshold is passed, wolf densities decrease, leading to extirpation if hunting does not lighten. Studies in North America have found road density to be an indicator of human-caused mortality (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Mech 1989). Roads not only cause casualties but also facilitate

human access and therefore hunting or poaching. These studies considered a road density of about 0.6-0.7 km/km<sup>2</sup> as the threshold for wolf occurrence. Road density was therefore a major factor used to predict suitable wolf habitats in the USA and Italy (Mladenoff et al. 1995, Mladenoff & Sickley 1998, Corsi et al. 1999, Mladenoff et al. 1999).

The human impact on wolves is, however, not limited to mere demographic responses. A comprehensive study on the impact of humans must take into account the behavioural ecology of wolves. Behavioural ecology is concerned with the evolution of adaptive behaviour in relation to ecological circumstances (Krebs & Davies 1993). Optimisation models play an important role in behavioural ecology. These models predict that the evolutionary process favours characteristics that maximise the fitness of an individual (Krebs & McCleery 1984). An optimal behaviour should follow the economic principle: maximising benefits to the animals (e.g. the exploitation of food resources) while minimising the risk of predation (Lima & Dill 1990). The impact of human persecution is equivalent to that of a natural predator. Human persecution can therefore be considered an element of the ecological conditions that apply to wolves. Persecution by humans, sustained over long time periods, should therefore have selected animals with the best adapted avoidance behaviour.

Wolves do not necessarily distinguish between humans that intend to kill them and those who do not. Any encounter with a human should therefore induce an avoidance behaviour that is independent of the actual risk of being killed. Such a deviation in an animal's behaviour from patterns occurring without human influences is referred to as disturbance (Frid & Dill 2002). Disturbance by humans is therefore analogous to predation risk and should result in anti-predator behaviour (Gill et al. 1996, Frid & Dill 2002).

Besides adaptations, many species have the ability to adjust their behaviour to new situations by learning. Human persecution and disturbance could therefore induce general behavioural adaptations as well as acquired responses to specific conditions. The difference between adaptive and acquired behaviour would become clear if persecution or disturbance by humans are removed. An acquired behaviour would quickly change with a new situation whereas an adaptive behaviour would persist.

#### 1.3 Spatio-temporal behaviour under human influence

Animals can avoid contact with humans temporally and spatially. An optimal behaviour towards human persecution may be nocturnal activity and avoidance of settled areas. However, factors other than anti-predator behaviour, such as foraging strategy, play an equally important role in shaping the activity rhythm and home range use of a species. If the night was a worse period for hunting, nocturnal behaviour would lower the hunting success of wolves. Nocturnal wolves may therefore feed less and have a disadvantage in reproduction. On the other hand, day-active wolves may face a higher risk of being killed. An optimal strategy would therefore involve optimising food intake while minimising the risk to encounter humans. My main hypothesis was therefore that spatio-temporal avoidance of humans by wolves is an adaptation that allows wolves to optimise their temporal and spatial pattern of home range use towards food acquisition.

#### Anti-predator behaviour

Man has long been the most important predator of large carnivores even if carnivores are protected (see chapter 1.2). It is therefore likely that centuries of persecution have favoured wolves that avoided humans (Linnell et al. 2002). In fact, wolves seem to fear humans in most regions with the exception of arctic regions where they had no contact with man (Mech 1988). Creel et al. (2002) showed that the intensive use of snowmobiles in national parks increased the physiological stress of wolves. Wolves should therefore try to reduce the possibility of encounter with humans. They could avoid humans in time by adjusting their activity to times when humans are less active and in space by keeping away from areas where an encounter with humans is likely.

Human activity influenced the activity patterns of foxes, *Vulpes vulpes* (Weber et al. 1994), mountain lions, *Felis concolor* (Van Dyke et al. 1986), and black bears, *Ursus americanus* (Larivière et al. 1994). Up to now, no study has investigated the influence of human activity on activity patterns of wolves. Nocturnal behaviour of wolves in Italy (Ciucci et al. 1997) and Spain (Vilà et al. 1995) may be a sign for temporal avoidance of humans. However, because the foraging strategy also influences activity patterns of wolves, it is necessary to compare activity patterns of wolves under different levels of human activity to confirm an influence of humans. Kitchen et al. (2000) conducted such a test on coyotes (*Canis latrans*). The disturbance in this study was, however, not human activity but persecution. They found that coyotes moved less in the day during a period of persecution compared to animals that had not been persecuted for more than 8 years. Selection could not have been responsible for this quick change in activity patterns. The activity pattern was therefore not an adaptation to human persecution but an acquired behaviour. When persecution ceased, coyotes learned that it was no longer dangerous to move during daylight.

Besides temporal avoidance, wolves can also be spatially separated from man. This can be on a large scale when wolves live in sparsely populated areas. In populated areas, wolves can avoid humans on a smaller scale by selecting nature reserves, forests or other areas with limited human access. In Italy, wolves selected forest over open areas (Ciucci et al. 1997). Forest may act as a cover whereas in open areas wolves face the danger of being easily killed during daylight. Thurber et al. (1994) are the only ones so far to have quantified spatial avoidance of man-made structures by wolves. In this study, wolves avoided intensively used roads and a settled area in Alaska. Finally, spatial and temporal avoidance can be combined. Grizzly bears (*Ursus arctos*) for example used roads at night but avoided them in the day (McLellan & Shackleton 1988). The eventuality of such a spatio-temporal avoidance behaviour in wolves was the focus of my research.

#### Foraging strategy

In most regions, wolves select large ungulates as prey (Mech 1970, Okarma 1995). Depending on their local occurrence and abundance, the most important prey species are red deer (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), reindeer (*Rangifer tarandus*), Dall sheep (*Ovis dalli*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and various mountain species of Caprinae (Fritts & Mech 1981, Ballard et al. 1987, Reig & Jędrzejewski 1988, Jędrzejewski et al. 1992, Śmietana & Klimek 1993, Dale et al. 1995, Mattioli et al. 1995, Mech et al. 1995, Meriggi et al. 1996, Poulle et al. 1997, Castroviejo 1998, Spaulding et al. 1998, Kunkel et al. 1999). Wolves may also use anthropogenic food sources in regions where they live close to humans. The most important anthropogenic food sources are domestic animals and carrion (Pulliainen 1965, Macdonald et al. 1980, Bibikov et al. 1985, Meriggi et al. 1991, Patalano & Lovari 1993, Papageorgiou et al. 1994, Meriggi et al. 1996, Vos 2000). Wolves also feed at garbage dumps (Reig et al. 1985, Salvador & Abad 1987, Ciucci et al. 1997, Promberger et al. 1997), although this is relatively rare and localised (Meriggi & Lovari 1996).

Curio (1976) suggested that predators follow the activity patterns of their prey. Activity patterns of wolves feeding on wild prey should therefore be influenced by the activity rhythms of their main prey species. In the wild, the endogenous circadian rhythms of animals are regulated by extrinsic factors, called Zeitgeber (Aschoff 1958), which shape daily activity patterns. One of the most important Zeitgeber is the daily cycle of light and darkness (Nielsen 1984). Many species are therefore most active around sunrise and sunset. This bimodal activity pattern is common in red deer (Georgii 1981, Georgii & Schröder 1983), roe deer (Ellenberg 1978, Cederlund 1981, Jeppesen 1989), white-tailed deer (Montgomery 1963, Kammermeyer & Marchinton 1977), and moose (Geist 1963). Large carnivores that prey on wild ungulates may therefore also have bimodal activity patterns. Hunting strategies have however evolved to optimise hunting success. Temporal hunting patterns should therefore not only follow the activity patterns of the prey species but be also depend on the abilities of the predator. The good vision of predators is particularly important when attacking their prey and as a mean of preventing fatal injuries (Asa & Mech 1995). The vision of canids is best adapted to daylight and the phase between day and night (Kavanau & Ramos 1975, Roper & Ryon 1977). Taking this visual ability into account, the best time for wolves to hunt ungulates with bimodal activity rhythms may be during crepuscular phases.

Wolves that rely mainly on anthropogenic food sources do not have to fit their activity patterns to those of their prey. However, anthropogenic food sources are usually near human settlements. To avoid encounter with humans, wolves would have to exploit such food sources during the absence of humans (e.g. at night). This occurred in a region of Italy where wolves mainly fed at garbage sites (Zimen 1993). During the day, these wolves retired to forested areas in the mountains where they were far from settlements (Zimen 1993).

#### 1.4 Objectives and structure of this thesis

The aim of this thesis was to clarify if and how human activity affects the activity rhythm and spatial distribution of wolves. I further tested the hypothesis that wolves are spatio-temporally segregated from man.

To analyse spatial and temporal responses of wolves to human activity, it was necessary to obtain a large data set on locations and activity of wolves and humans over the whole day. The only method allowing an extensive monitoring of wolves over long time was radio-telemetry. Radio-tracking does away with the need to have visual contact with the wolf, which could influence the wolf behaviour. A detailed monitoring of human activity was also essential. Under the term human activity, I understand the spatial and temporal distribution of humans. Human activity could be quantified directly, both by visual counts and with automatic counter systems. I also mapped permanent man-made structures such as roads, settlement, and agricultural land. I analysed the data by combining the temporal distribution of humans and wolves with their spatial distribution using a geographic information system (GIS). I addressed in five articles (chapters 2-6) written for scientific journals the five main questions:

- Do radio-trackers influence wolf behaviour?
- Does human activity reduce the daytime movements of wolves?
- Does human activity modify the activity patterns of wolves?
- Do wolves select areas of low human activity for resting and raising young?
- Do wolves spatio-temporally avoid contact with man?

The Białowieża Forest in east Poland was an appropriate site for the research. The forest is under different regimes of human activity, which range from strictly protected with little human activity to commercially exploited with a high road density and intensive human use. The good road network of the Białowieża Forest allowed to intensively follow the wolves by radio-tracking. Furthermore, the Predator Ecology Group of the Mammal Research Institute in Białowieża had already gathered experience with catching and radio-tracking wolves.

Because the influence of man was the core interest of my research, I had to first test if the radio-tracking method might influence the behaviour of wolves. There were two potential sources of bias in the radio-tracking method. First, estimates based on radio-tracking may not accurately represent the actual activity and locations of wolves. Second, the radio-tracker could influence the behaviour of wolves, which would interfere with the analysis of human impact. I therefore tested the accuracy of the radio-tracking estimates as well as the possible influence of radio-trackers on wolves in chapter 2 (*Accuracy of radiotelemetry to estimate wolf activity and locations*). The most important result regarding the impact of humans on wolves was that the presence of the radio-tracker had no detectable influence on wolves.

To test if human activity caused wolves to reduce their daytime movements, I compared the movement patterns of wolves in areas with different levels of human

activity in chapter 3 (*Impact of human activity on daily movement patterns of wolves*). The main result of this chapter was that human activity did not cause wolves to reduce their daytime movements.

To clarify which factors generally determine the temporal patterns of wolf activity, I analysed the role of human activity, hunting for prey, weather and the reproduction period in shaping the movement and activity rhythms of wolves in chapter 4 (*Daily patterns and duration of wolf activity*). The daily activity patterns of wolves were mainly shaped by the hunting of prey. Extreme weather and the reproduction period had a minor impact on activity patterns. Human activity did not significantly influence the activity patterns of wolves.

As wolves appeared not to react to human activity by changing their temporal patterns of activity, I tested the spatial influence of human presence. Wolves are probably the most sensitive to human presence when they stay with their young at the den, because young wolves are less able to escape. I therefore analysed if man-made structures influenced the spatial distribution of den, rendezvous and resting sites of wolves in chapter 5 (*Selection of den, rendezvous and resting sites by wolves*). The main findings were that den and rendezvous sites were as far away as possible from the forest edge, human settlements and public roads. Resting sites were not influenced by these man-made structures.

Temporal aspects alone appeared to insufficiently explain wolf reactions to human activity (chapters 3 and 4) and spatial aspects were only important for den and rendezvous sites (chapter 5). I therefore tested the hypothesis that the influence of man on wolf behaviour is spatio-temporal in chapter 6 (*Spatio-temporal segregation of wolves from man*). This analysis revealed that wolves react spatio-temporally to human activity, which explained why wolves in the Białowieża Forest were able to live in the same area as man without adjusting their activity patterns to those of humans.

The five articles (chapters 2-6) were written for independent publication in different journals. Each of these chapters has therefore its own abstract, introduction, description of the study area and methods, results, discussion, acknowledgements, and references, and follows the structure, style and conventions of the journal to which it was submitted. In these chapters, I use the plural form "we", because I am publishing the corresponding articles with co-authors. For all five articles, I defined the objectives, analysed the data and wrote the article myself but considered comments by the co-authors and persons mentioned in the acknowledgements.

#### 1.5 Study area

#### Project partners

I conducted the field work at the Mammal Research Institute (Polish Academy of Sciences) in co-operation with the Predator Ecology Group. The Predator Ecology Group started wolf research in 1985 (Reig & Jędrzejewski 1988, Jędrzejewski et al. 1989, Jędrzejewski et al. 1992, Jędrzejewska et al. 1994, Okarma 1995, Okarma et al.

1995, Jędrzejewska et al. 1996) and conducted a first radio-tracking project on wolves from 1994 to 1996 (Musiani et al. 1998, Okarma et al. 1998, Jędrzejewski et al. 2000). In December 1996, we started a second radio-tracking study on wolves. In this work, the Predator Ecology Group conducted the project "Mechanisms of regulatory impact by wolves on populations of ungulates in Białowieża Primeval Forest" financed by the Polish State Committee for Scientific Research (Jędrzejewski et al. 2001, Jędrzejewski et al. 2002, other articles in preparation). My themes were the impact of human activity and prey distribution on the spatio-temporal habitat use by wolves (chapters 2-6, other articles in preparation).

The scientific staff of the Predator Ecology Group who worked in the wolf project were Włodzimierz Jędrzejewski (group leader), Krzysztof Schmidt, Henryk Okarma (1994-1996), and Roman Gula (1998-1999). During the period of my participation, we always had 1-2 field assistants at any time: Stanisław Śnieżko (1996-1997), Ireneusz Ruczyński and Przemysław Wasiak (1997-1998), Marek Chudziński and Roman Kozak (1998-1999). Lucyna Szymura and Karol Zub dealt with the data entering and organisation. Besides, volunteers (see acknowledgements) helped us with the field work. Nuria Selva, who conducted a Ph.D. research on scavengers of wolf prey, co-operated with us when searching for prey from 1997 to 1999. Sophie Rouys participated in our project in the summer of 1997 to study habitat characteristics of wolf den, rendezvous and resting sites.

#### Physical characteristics and vegetation

The Białowieża Forest (1450 km<sup>2</sup>) straddles the Polish-Belarussian border (52°30'-53°00'N, 23°30'-24°15'E) and has remained in contact with other forested areas (Fig. 1.1). The study area is a lowland forest (altitude 134-202 m) in the transition zone between boreal and temperate climate (Mitchell & Cole 1998). The mean daily temperature is -5°C in January and 18°C in July. Snow cover persists for 0-157 days (mean 92 days), with a maximal depth of about 1 m (about 10 cm on average). Mean annual precipitation is 641 mm. The surface geological formations result from the last glaciation and are mainly sandy gravel deposits (Faliński 1994).

The forest is composed of deciduous, mixed and coniferous stands and differs from west Central European forests by the absence of beech (*Fagus sylvatica*). A common vegetation type in the Białowieża Forest is the oak-lime-hornbeam forest (Fig. 1.2), which occurs mainly on brown soils. Common tree species in oak-limehornbeam forests are oak (*Quercus robur*), lime (*Tilia cordata*), spruce (*Picea abies*), maple (*Acer platanoides*), and hornbeam (*Carpinus betulus*) (Faliński 1986). Mixed spruce-oak-pine forests with pine (*Pinus sylvestris*), spruce, oak, aspen (*Populus tremula*), and birch (*Betula verrucosa*) grow on podzolic soils. Coniferous forests with pine and spruce usually grow on oligotrophic sandy soils. Alderwoods with alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and elm (*Ulmus scabra*) grow mainly near rivers and in depressions.



**Figure 1.1.** Distribution of forest (grey area) in the surroundings of the Białowieża Forest (continuous line). The dashed line is the state border between Poland and Belarus (map modified after Jędrzejewska et al. 1997). The wolf distribution mainly matches that of the forest distribution.

In the strict reserve of the Białowieża National Park, most tree stands are of natural origin and older than 100 years. The commercial forest consists of less than 30% of old growth while more than half of the area is covered by replanted stands of coniferous tree species (Jędrzejewska & Jędrzejewski 1998). In the strict reserve, three quarters of the tree stands are dominated by deciduous trees (Jędrzejewska & Jędrzejewski 1998). The landscape around the forest is dominated by agriculture and small villages (Fig. 1.2).

#### Forest protection

The Białowieża Forest was protected as a hunting ground for Polish kings, Lithuanian dukes and Russian tsars from the 15<sup>th</sup> century to the begin of the 20<sup>th</sup> century (Jędrzejewska et al. 1997). Large parts of the forest were historically closed to exploitation to preserve big game (especially European bison Bison bonasus) and mass timber exploitation only begun during the 1<sup>st</sup> World War. However, the forest has been subjected to at least a thousand years of human use, which have affected its landscape (Faliński 1986, Faliński 1994, Mitchell & Cole 1998). Today, the Polish part of the Białowieża Forest consists of a commercial forest (480 km<sup>2</sup>), in which timber harvest, reforestation and hunting take place, and the Białowieża National Park (Fig. 1.3). The core area of the national park (50 km<sup>2</sup>) has been protected as a strict reserve since 1921. There is no hunting, forestry or motorised traffic in the strict reserve and public access is limited. In the 1970s, the UNESCO granted the reserve the status of Man and Biosphere Reserve and World Heritage Site (Jedrzejewska et al. 1997). In July 1996, the Białowieża National Park was enlarged to 100 km<sup>2</sup>. The extended part of the national park is opened to the public, but vehicle access is restricted and hunting and forestry operations are not allowed, except for occasional cutting of sick trees and fencing off existing regeneration areas.

There are 22 small (0.1-3.7 km<sup>2</sup>) nature reserves in the Białowieża Forest, which are less protected against forestry operations than the National Park. The whole Belarussian part of the Białowieża Forest (870 km<sup>2</sup>) is protected as a national park, but hunting and limited logging are allowed. A fence was erected along the Belarussian side of the state border in 1981 (at a distance of 0-1.5 km to the border). The zone between the border and the fence is little used by man and can be considered a "strict reserve" in its own right.



**Figure 1.2.** Top: Aerial photo of the boundary between the Białowieża Forest and agricultural land (Photo: R. Gula). Bottom: Humid oak-linden-hornbeam forest in the strict reserve of the Białowieża National Park during snow-melt (Photo: J. Theuerkauf).

#### Humans

Human density is about 7 inhabitants per km<sup>2</sup> on the Polish side of the Białowieża Forest and 70 inhabitants per km<sup>2</sup> on the regional scale (Białystok administration district). The density of forest roads suitable for 2-wheel-drive vehicles is about 1.2 km per km<sup>2</sup> in the commercial forest, but only about 50 km of paved roads (0.1 km per km<sup>2</sup>) are intensively used by the public. Most human activity in the commercial forest consists of forestry operations. Mushroom collectors contribute to a quarter of forest visitors from July to October and hunters 15% from September to January. Tourists contribute to a third of humans from May to September, but only 4% from October to April. From May to September, about 100 tourists visit the strict reserve daily, but the number of tourists decreases to about 20 per day from October to April (estimate based on data of B. Jaroszewicz, personal communication). The area visited by tourists is restricted to a 4-km tourist trail near the park's entrance. The rest of the strict reserve is open to permit holders for research or education purposes. People use mostly cars (80%), but also lorries, tractors (10%) and bicycles (10%) to move around in the commercial forest. Tourists mainly go on foot or bicycle and usually stay on roads and trails.



**Figure 1.3.** The Białowieża Forest with distribution of the commercial forest (light grey), nature reserves and national parks (middle grey), the strict reserve of the Polish Białowieża National Park (dark grey), human settlements (black area), intensively used public roads (double lines), forest roads (dashed lines), and the cumulative area of wolf home ranges (continuous lines) of the National Park pack, the Ladzka pack and the Leśna packs.

#### Wolves

At the beginning of this study, three wolf packs inhabited the Polish part of the Białowieża Forest (Okarma et al. 1998). The core area of one pack (National Park pack) was the strict reserve (Fig. 1.3). Another pack lived in the north-western part of the Białowieża Forest where there are a few small nature reserves (Ladzka pack). The third pack lived in the southern part of the study area, which includes most of the small nature reserves and a large part of the border zone. In December 1997, this pack split into two packs (Leśna packs), but their home ranges overlapped largely after the separation. In the region around the Białowieża Forest, the wolf distribution mainly matches that of the forest distribution (Fig. 1.1).

Wolves have been protected since 1989 in the Polish part of the Białowieża Forest but humans remain the main cause of wolf mortality. During this study, half of our 12 radio-collared wolves were shot or died in poachers' snares set for wild boar. In the Belarussian part, the annual hunting bag of wolves was on average 80% of the wolf population (Jędrzejewska et al. 1996).

The main prey of wolves in the Białowieża Forest (Jędrzejewski et al. 2000) is the red deer, followed by wild boar and roe deer. During 1994-1999, the mean densities of prey species for the whole study area were about 3-7 red deer, 1-6 wild boar, and 1-5 roe deer per km<sup>2</sup> (Kossak 1997, Kossak 1999, Jędrzejewski et al. 2000). Wolves occasionally fed on carrion in garbage dumps or killed cattle.

#### Trapping and radio-tracking wolves

The *fladry*-and-net technique was our main method of catching wolves (Okarma & Jędrzejewski 1997). The use of this method was facilitated by the organisation of the forest, which was divided into compartments of about 1 km<sup>2</sup>. Most compartments were surrounded either by roads or forest lanes directed north-south and west-east. We located wolves at resting sites, either by snow-tracking or by telemetry and surrounded the forest compartment in which the wolves were resting with *fladry*. *Fladry* are lengths of rope to which coloured strips of cloth of about  $40 \times 15$  cm are attached at intervals of about 50 cm (Fig. 1.4). Wolves usually do not cross lines of *fladry* that are correctly placed (i.e. that is visible at a height of about 60 cm). We then placed nets that were 100-150 m long at a distance of 100-500 m outside the surrounded area. Once the nets were set, we added *fladry* corridors that funnelled into the nets. Once this was done, we set a line of beaters at the end of the compartment opposite the nets and drove the wolves towards the nets. If a wolf was caught in the nets, we tranquillised it and fitted it with a radio-collar (Fig. 1.4).

We located the radio-collared wolves by ground triangulation. In this method, the observer determines the bearing to the transmitter's signal. The intersection of at least 2 bearings taken from different places gives the estimated position of the wolf. We noted the wolves' location every 15 min. This interval gave observers enough time to take several bearings and drive to different places in order to obtain an intersection. Besides

noting the location of radio-collared animals, we estimated their activity. When radiocollared animals are moving, vegetation interferes with the signal of the radiotransmitter. As a result, the intensity of the signal received by the radio-tracker changes. We considered such changes in signal strength as indication that the animals were active. Some of the radio-tracked wolves had transmitters with activity sensors, which helped the estimate of activity. These transmitters have a switch that induces a change in the pulse frequency of the signal when the animal moves its head up and down.



**Figure 1.4.** Top: Line of *fladry* in a coniferous forest. Bottom: An immobilised wolf with its new radio-collar (both photos: J. Theuerkauf).

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### 2. ACCURACY OF RADIOTELEMETRY TO ESTIMATE WOLF ACTIVITY AND LOCATIONS<sup>1</sup>

#### 2.1 Abstract

We analyzed radiotracking data from wolves (Canis lupus) in the Białowieża Forest, Poland, to determine (1) differences between methods of estimating mean wolf activity and daily activity patterns, (2) whether activity estimated by changes in signal strength is dependent on the distance between the radiotracked wolf and the tracker, (3) radiotracker influence on wolf activity estimates, and (4) accuracy of radio locations. Daily patterns of wolf activity estimated by changes in signal strength, movements, and activity sensors were similar. However, the mean time spent active estimated by changes in signal strength (55% of the time) was higher than those estimated by movements (34%) or sensors (32%). We obtained the most accurate estimates of activity by a combination of movement, signal strength, and sensor data (43%) or by combining movement and signal strength data (44%). Activity estimated by changes in signal strength did not vary with the distance between radiotracked animals and radiotrackers. The trackers had no detectable influence on activity and movements of wolves when the tracker-to-wolf distance was >200 m. There was a small but not significant influence if trackers were <200 m away during the day. The mean radiotracking error was 194 m (95% CI: 157-231 m). We recommend that data on movements always be included in estimates of mean time spent active because activity sensors lead to underestimates and changes in signal strength to overestimates. Distances traveled obtained by radiotracking should not be regarded as minimal distances traveled, since the likelihood that they are overestimated or underestimated depends on the relation between the accuracy of radio locations and the mean distance that an animal travels per radiotracking interval.

#### 2.2 Introduction

Researchers employing radiotelemetry to study activity patterns of wolves have used a variety of methods: Kolenosky and Johnston (1967) and Ciucci et al. (1997) relied on changes in signal strength, Ballard et al. (1991) and Vilà et al. (1995) used activity sensors, and Vilà et al. (1995) and Ciucci et al. (1997) used distances traveled by wolves to determine daily patterns of activity. Each method is subject to specific errors. To estimate activity by changes in signal strength, it is necessary that a radiotracked animal moves the transmitter past objects such as trees that interfere with the radio signal thus causing changes in signal strength. Activity estimates may therefore depend on the distance between the radiotracker and the radiotracked animal, as the potential amount of interference between transmitter and receiver increases with distance. The

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information from activity sensors does not depend on the distance between the radiotracked animal and the tracker, but activity sensors that work with a head position switch may not indicate activity if wolves keep their heads in 1 position while moving. Ground tracking to estimate travel distances may also be subject to errors, not only because they are straight-line distances and do not exactly represent the wolves' itinerary, but also because they depend on the accuracy of radio locations. In addition, the accuracy of locations is important for studies of habitat use (e.g., Heezen and Tester 1967, Springer 1979, Saltz 1994). Finally, researchers who relocate radiocollared wolves may disturb the wolves, thus influencing their activity.

The objectives of our study were to (1) compare different methods of estimating mean wolf activity and daily activity patterns, (2) determine if the activity estimated by changes in signal strength was dependent on the distance between the radiotracked wolf and the tracker, (3) determine tracker influence on wolf activity estimates, and (4) determine the accuracy of radio locations.

#### 2.3 Methods

From March 1994 to September 1999, we radiotracked 11 wolves (9 F, 2 M) over 11,500 hours in the Polish part of the Białowieża Forest, which is located on the border between Poland and Belarus (52°30'-53°00'N, 23°30'-24°15'E). The study area is a forest comprising deciduous, coniferous, and mixed tree stands in the transition zone between boreal and temperate climates and is described in detail in Jędrzejewska and Jędrzejewski (1998). The Polish part of the Białowieża Forest (580 km<sup>2</sup>) consists of a commercial forest (480 km<sup>2</sup>), in which timber harvest, reforestation, and hunting occur, and the Białowieża National Park (100 km<sup>2</sup>). In the commercial forest, the density of forest roads suitable for 2-wheel-drive cars is approximately 1.2 km/km<sup>2</sup>, but only about 50 km of paved roads (0.1 km/km<sup>2</sup>) are intensively used by the public. Wolves have been protected since 1989 in the Polish part of the Białowieża Forest, but are hunted in the Belarussian part (Jedrzejewska et al. 1996). The home ranges of 2 of the 4 wolf packs living in the study area lay partly in Belarus, where hunters occasionally killed members of these packs. In the Polish part, some wolves died during our study in poachers' snares set for wild boar (Sus scrofa) or were shot. Wolves usually flee when they encounter humans in the forest.

We captured wolves with foot snare traps equipped with radio-alarm systems or with the *fladry*-and-net method (Okarma and Jędrzejewski 1997). Captured wolves were immobilized (Okarma et al. 1998) and fitted with radiocollars (Telonics, Mesa, Arizona, USA; AVM Instrument Company, Livermore, California, USA; ATS Advanced Telemetry Systems, Isanti, Minnesota, USA; Telemetry Systems, Mequon, Wisconcin, USA). The radiocollars on 4 wolves were equipped with head-position activity sensors that doubled the pulse frequency when the wolf's head was down, and 1 wolf had a transmitter with a 3-dimensional head movement sensor. The other transmitters used were not equipped with activity sensors. During 24-hr radiotracking sessions of usually

6 days (range 1-9 days), we noted wolf activity and location continuously every 30 min (Mar 1994–Dec 1996) or every 15 min (Dec 1996–Sep 1999).

We measured wolf locations by ground triangulation with 3-element Yagi antennas on forest roads from at least 2 bearings taken from different locations no more than 5 min apart. The distances between wolves and trackers ranged between 200 and 1,200 m most of the time (75% of cases). We obtained wolf locations by drawing bearings on maps during radiotracking. From March 1994 to August 1997, we used maps with horizontal and vertical grid lines spaced 267 m apart. During this period, we used the coordinates of the nearest grid line intersection as coordinates of a wolf location. As vertical and horizontal distances between these intersections were 267 m, the wolf location coordinates used in our analysis averaged 101 m (calculated with 1,000 random points inside a 267×267-m square) away from the location actually drawn on our maps in the field. Because we expected that this mapping method would increase the radiotracking error, we measured the wolf locations more precisely from September 1997 to September 1999. During this period, we used maps with a metric coordinate system upon which we could measure wolf locations to the nearest 10 m.

We calculated the distances traveled by the wolves as the straight-line distance between 2 consecutive locations. Because the sum of straight-line distances depends on the interval length, we calculated the difference between 15-min and 30-min relocation intervals. For 3,573 hours of radiotracking from December 1996 to August 1997, we first calculated the straight-line distances for 15-min intervals and then for 30-min intervals by disregarding every second location. The sum of straight-line distances between consecutive locations at intervals of 15-min was 1,560 km, whereas the sum of straight-line-distances considering only every second location was 1,344 km. We therefore corrected the data obtained by 30-min intervals by a factor of 1.16 (1,560/1,344) to make them comparable to the 15-min interval data.

We compared 6 methods of estimating mean wolf activity and daily activity patterns. We considered a wolf active if (1) the intensity of the signal was uneven or beats were missed during 1 min, (2) the activity sensors indicated movements of the wolf's head, and (3) the wolf had changed its location since the last radio location. (4) We combined the first 3 methods and considered a wolf active when it moved its head or when its location changed while the signal strength indicated activity. (5) We combined the data obtained by changes in signal strength and location changes by assigning a value of 1 when the wolf was active and changed its location, a value of 0 when the wolf was not active and did not change location, and a value of 0.5 when the wolf was active but did not change location or the wolf was not active during monitoring but changed its location. (6) Additionally, for daily patterns, we used the hourly distances traveled.

Data on animal activity gathered by 24-hr radiotracking are not necessarily temporally independent (Salvatori et al. 1999). Therefore, when conducting statistical tests, we used daily activity patterns of individual wolves as sample units rather than single relocations. To obtain the daily activity pattern of a wolf, we calculated, for each

hour of the day, the mean time spent active or distance traveled. As these means were normally distributed, we compared daily activity patterns using ANOVA.

To determine if activity estimated by changes in signal strength changed with increasing tracker-to-wolf distance, we divided mean activity estimated by changes in signal strength for 200-m distance classes by mean activity estimated by sensors of the same distance classes. We then tested whether the slope of the linear regression for these means was different from 0.

To determine if the proximity of human trackers influenced the wolf activity estimates, we focused on places where wolves were not active and did not move during the last 15-min interval. For 200-m tracker-to-wolf distance classes, we calculated the percentage of cases when a wolf became active or changed its location in the next 15-min interval. We compared these percentages with expected percentages by a Fisher's exact test. The expected percentages were the mean percentages for all tracker-to-wolf distance classes.

To assess the accuracy of our radio locations, we field-checked the places where wolves stayed at least an hour (prey and resting sites) or followed wolf trails in the snow (120 different locations were visited in 74 days of radiotracking). Mills and Knowlton (1989) showed that the accuracy of radiotelemetry increased when field personnel were aware that the accuracy of their relocation data was being evaluated. In our study, none of the radiotrackers knew their radiotracking data would be assessed later. During snow-tracking, we recorded wolf trails with a Garmin 45 Global Positioning System (GPS; Garmin, Lenexa, Kansas, USA), which worked with a position accuracy of 15 m. Because we noticed during the fieldwork that the accuracy degraded in the forest to approximately 50 m, we measured the location of prey and resting sites by compass and pacing to reduce the GPS location error.

#### 2.4 Results

We obtained simultaneous data for activity estimated by changes in signal strength, activity sensors, and movements for 12,671 radiotracking intervals. The mean percentage of time the sensor indicated activity (32.0%, SE = 0.4%) and the mean percentage of time that the wolf had changed its location (33.7%, SE = 0.4%) were similar, but the mean percentage of time wolves were active, estimated by changes in signal strength, was higher (54.9%, SE = 0.4%). The activity sensors indicated that the wolves were moving their heads, which they also do while stationary. Conversely, if the wolves were travelling without changing their head position, the activity sensor would not have registered activity. The wolves actually changed their location in 52% of 4,054 cases when the sensor indicated the wolf was active and in 17% of 8,617 cases when the activity sensor did not record head movement. Therefore, the combination of sensor, movement, and signal strength data indicated that wolves were active 43.3% (SE = 0.4%) of the time they were monitored. When we combined signal strength and movement data, we found that wolves were active 44.3% (SE = 0.4%) of the time. The

daily activity patterns obtained by the 6 methods used (Fig. 2.1) were not different (P = 0.864) and highly correlated (all  $r^2 > 0.82$ , all P < 0.001). The pattern obtained by the combination of sensor, signal strength, and movement data, and the pattern obtained by the combination of the activity estimated by changes in signal strength and movements were almost identical (Fig. 2.1).



**Figure 2.1.** Daily activity patterns obtained by 6 methods of expressing activity for 5 wolves wearing radiocollars equipped with activity sensors in the Białowieża Forest, Poland, from 1997 to 1999 (n = 12,671 radio locations): changes in signal strength (open circles), location changes (closed circles), activity sensors (open triangles), a combination of movement, signal strength and sensor data (continuous line), the mean between changes in signal strength and location changes (dashed line), and the distances traveled (plus signs). The units for the first 5 methods are percentages of time; km/hr was used for method 6.

The AVM head position activity sensor indicated a higher activity (37%) than the expected mean (32%) sensor activity ( $\chi^2$  test: P = 0.024), whereas the means of time spent active indicated by Telonics or Telemetry Systems sensors did not differ from the expected value (all  $P \ge 0.141$ ). However, the combined activity estimate calculated with location and signal strength data of the wolf with the AVM transmitter was not higher than the mean (P = 0.105). Therefore, we pooled the sensor data for analysis.

The ratio of mean time active estimated by changes in signal strength to mean time active estimated by sensors (Fig. 2.2) was not dependent on the tracker-to-wolf distance (linear regression: P = 0.618).

When trackers were closer than 200 m to a wolf in daylight, the percentages of cases when the wolf became active or changed its location appeared higher than the expected percentages (Fig. 2.3). However, the sample size for the tracker-to-wolf distance class under 200 m during the day was small (29 cases, corresponding to 0.4% of all cases) and the percentages were not significantly different from the expected percentages (Fisher's exact test: P = 0.760 for activity and P = 0.504 for movements).

The sample sizes of all other distance classes (for day and night separately) were large (426–1,009) and their percentages were not different from expected (all  $P \ge 0.257$ ).



**Figure 2.2.** Ratio of the mean time spent active by wolves as estimated by changes in signal strength to the mean time spent active as estimated by sensor information in relation to the distance between a radiotracked wolf and a tracker in the Białowieża Forest, Poland, from 1997 to 1999. The dotted line represents the mean of the ratios for all distances (n = 6,802 pairs of activity estimates); the slope of the line was not different from 0 (P = 0.618).

There was a difference in the accuracy of radio locations during the period when we mapped locations to the nearest 267 m and the period when we mapped to the nearest 10 m (*t*-test: P = 0.002). During the first period, radio locations of wolves averaged 291 m (95% CI: 244–337 m; n = 40) from where the wolves had actually been. After increasing the precision of mapping, the error was 194 m (95% CI: 157–231 m; n = 80). The daily patterns of distance traveled by wolves were not affected by the different levels of precision (P = 0.176). There was no dependence between the tracker-to-wolf distance (up to 3 km) and the accuracy of our radio locations (linear regression: P = 0.978). During the period when we mapped to the nearest 10 m, the error of radio locations was lower (*t*-test: P < 0.001) when wolves were at resting sites (110 m, 95% CI: 78–142 m; n = 18) than when they were not (219 m, 95% CI: 173–264 m; n = 62).

#### 2.5 Discussion

Activity estimated by changes in signal strength, activity sensors, movements, or combinations of these methods provided similar results to document daily activity patterns of wolves. Similarly, Palomares and Delibes (1991) showed that activity patterns of Egyptian mongooses (*Herpestes ichneumon*) were comparable when estimated by movements, net time activity, or activity estimated at 30-min radiotracking intervals. We conclude that it is possible to document daily activity patterns of wolves with or without sensors or only with movement data. However, the values obtained for activity measured with these methods differed. In our study, activity estimated by

changes in signal strength overestimated and activity sensors or movements underestimated the time spent active by wolves. The most reliable estimates appeared to be obtained either by a combination of data on location changes and data from activity sensors, or by calculating the mean between movement data and data estimated by changes in signal strength.



**Figure 2.3.** Percentage of cases when a wolf that was not active and had not moved during the last 15 min became active (open circles) or changed its location (closed circles) during the following 15 min after a tracker was at a given distance to a wolf in the Białowieża Forest, Poland, from 1997 to 1999. The dotted line represents the expected percentage (mean percentage for all tracker-to-wolf distance classes; n = 6,802) of cases where wolves became active and the dashed line the expected percentage of cases where wolves began moving.

Straight line distances between radio locations can underestimate actual distances traveled, especially when wolves move in circular patterns rather than linearly as, for example, at prey sites (Musiani et al. 1998). On the other hand, radiotracking may overestimate distances traveled if errors in taking bearings appear as movements that have not actually occurred. This occurs particularly when animals move short distances between 2 consecutive radio locations (Rouys et al. 2001). The likelihood that distances traveled are overestimated or underestimated by radiotracking should depend on the

relation between the accuracy of radio locations and the mean distance that an animal travels per radiotracking interval. A relatively small radio location error in relation to the straight-line distance traveled per radiotracking interval would, therefore, lead to underestimates and vice versa. Thus, both types of error can neutralize each other as found by Musiani et al. (1998) who radiotracked wolves in the Białowieża Forest and, after radiotracking, used snow-tracking to verify the actual distance traveled by wolves. They found that straight-line distances estimated with radiotracking intervals of 15 min accurately represented the actual distance traveled. In this case wolves traveled about 900 m on average between 2 consecutive radio locations, while the location accuracy was about 300 m.

We expected that mapping to the nearest 267 m could increase the location error up to 101 m. There was indeed a 97-m difference in accuracy between the periods when we measured the wolf locations to the nearest 267 m and to the nearest 10 m. Therefore, we attribute the difference between the 2 periods to the mapping precision and consider the 194-m error as the error inherent to our radiotracking system. In our study, this error was independent of the distance between wolf and tracker, implying that, unlike in other studies (e.g., Springer 1979, Mills and Knowlton 1989), our bearing error was not constant. We assume that the tracker-to-wolf distance made no difference to the accuracy of our locations because we were usually relatively close to the wolves (200-1,200 m) and used several bearings to locate each animal.

#### 2.6 Management implications

We suggest that activity estimated by changes in signal strength, activity sensors, location changes, or distances traveled are suitable to document daily activity patterns of wolves. To obtain a reliable estimate of the time wolves are active, however, mean activity should be calculated by a combination of different methods, regardless of whether activity was estimated with sensors or not. We also recommend researchers determine the minimal distance at which wolves will react to their presence. When trackers are then as close as possible to the tracked animal, error polygons of a radio location can be minimized. The optimal radiotracking distance in our study was between 200 m and 400 m, but in areas where wolves are not used to humans or in areas where they are persecuted, they may be more sensitive to the presence of trackers.

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# 3. IMPACT OF HUMAN ACTIVITY ON DAILY MOVEMENT PATTERNS OF WOLVES<sup>1</sup>

#### 3.1 Abstract

It is important for the management of recolonizing wolves (*Canis lupus*) in Europe to understand the wolves' reactions to human activity. The aim of this study was to find out if human activity affects the daily movement patterns of wolves. During 3 winters (1996-1999), we radio-tracked six female wolves and monitored the pattern of human activity in the Białowieża National Park and in the commercial part of the Białowieża Forest, eastern Poland. The 24-hour movement patterns of wolves living in the commercial part of the Białowieża Forest with high human activity were negatively correlated with the activity pattern of humans. The movement patterns of wolves from the national park – where human activity was low – were not correlated with the human activity. However, there was no difference in movements between wolves from the national park and those from the commercial forest during the time of maximum human presence from 0800 to 1500 h. We concluded that human activity affected the wolves' daytime movements.

#### **3.2 Introduction**

As a result of their protection in many European countries, wolves are expanding their range into Central Europe. It is critical for management of this species to determine where these animals will be able to settle (Schröder and Promberger 1993). Human activity is an important factor because it can influence the activity patterns and distribution of wolves (Thurber et al. 1994, Vilà et al. 1995, Ciucci et al. 1997). Vilà et al. (1995) and Ciucci et al. (1997) found that wolves in agricultural landscapes reduced their movements during the daytime to avoid man. In forested areas, the movements of wolves and the activity of humans should also be negatively correlated. Wolves confronted with high human activity should move less during the day than animals that live in parts of the forest where there is low human activity. We studied the impact of human activity on the wolves of the Białowieża Forest (eastern Poland) where the effects of human activity on the daily movement patterns of wolves in the Białowieża Forest.

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#### 3.3 Study area

The Białowieża Forest is on the border between Poland and Belarus (52°30'-53°N, 23°30'-24°15'E). The Polish part of the Białowieża Forest (580 km<sup>2</sup>) comprises the Białowieża National Park (100 km<sup>2</sup>) and a commercial forest (480 km<sup>2</sup>). Human density is about 10 inhabitants per km<sup>2</sup> in the Białowieża Forest and 70 inhabitants per km<sup>2</sup> on the regional scale (Białystok administration district). The home range of 1 wolf pack covers the national park, three other packs live in the commercial forest. In winter, few people penetrate the Białowieża National Park, so the impact of humans on wolves can be considered negligible. The core area of the national park pack is in the strictly protected part of the Białowieża National Park (Okarma et al. 1998) where there is no motorized traffic. The road density in the commercial forest is about 2 km/km<sup>2</sup>. During winter, human activity in the commercial forest consists mainly of forestry operations. In the Polish part of the Białowieża Forest, wolves have been protected since 1989; however, they are hunted in the Belarussian part (Jędrzejewska et al. 1998).

#### 3.4 Methods

During the three winters from 1996 to 1999, we radio-tracked 5 female and 2 male wolves living in the commercial forest and 3 females of the wolf pack living in the national park. In this paper, we only used the winter movements of 6 adult female wolves to avoid differences that could be a result of age, sex, or season. We followed wolves by continuous telemetry over 1-week periods and noted the wolf's location every 15 min by ground triangulation. We calculated distances traveled as the straight-line distance between 2 consecutive locations. Therefore, we obtained mean movements for 96 intervals of 15 min per day as a measure of the wolves' movement patterns. Musiani et al. (1998) showed that radiolocations taken at 15-min intervals accurately represent the actual distance traveled by wolves in the Białowieża Forest.

We used 12,630 intervals of 15 min for the analysis, which corresponds to about 131 full days of radio tracking. To compensate for individual differences in daily travel distances, we used relative movements to compare the daily movement patterns of each wolf. We calculated the relative movements of each wolf by dividing the mean movement of each 15-min interval (from 0000 to 0015 h, from 0015 to 0030 h, etc.) by the mean distance the given wolf had traveled during all 15-min intervals. This procedure gave mean relative movements for 96 intervals/d. The value 1 represented the expected mean movement over a full 24 h, so a <1 for movements indicated that the wolf was moving less than the daily mean. We compared the movement patterns of wolves with Student's *t*-test for matched pairs.

During winter 1998-1999, we used a magnetic traffic counter card (NC-30, Nu-Metrics, Uniontown, Pennsylvania, USA) to record the number of passing vehicles on dirt roads in the commercial forest in 1-h intervals for periods of 1 week. The results of the traffic count are based on 35 days of continuous counting of vehicles on 5 dirt roads in the forest. To compare the patterns of traffic with those of wolf movement, we calculated relative traffic by dividing the mean number of vehicles for each hour by the daily mean.

#### 3.5 Results

The movement patterns of wolves from the commercial forest and the national park were similar (Fig. 3.1). A negative correlation existed between the relative hourly movement of wolves from the commercial forest and the relative hourly traffic in the commercial forest (r = -0.514, P = 0.010). To ensure that the correlation is based on a dependence and is not random, we also compared the movements of wolves from the national park with the traffic in the commercial forest, which should not be correlated since results were obtained from separate areas. Indeed, no correlation occurred between the movement pattern of wolves from the national park and the traffic pattern in the commercial forest (r = -0.309, P = 0.142).



**Figure 3.1.** Relative wolf movement patterns (mean hourly travel distances expressed as the proportion of the daily mean, 1=daily mean) and relative traffic pattern (mean hourly numbers of vehicles expressed as the proportion of the daily mean, 1=daily mean) in the Białowieża Forest during the winters of 1996 to 1999.

When comparing individual movement patterns of the 6 wolves with the traffic pattern in the commercial forest (Tab. 3.1), we found negative correlations for 2 wolves (Bura, Siwa) in the commercial forest. The individual movement patterns of wolves (Ruda, Chytra, Chyża) from the national park were not correlated with traffic. Interestingly, the third wolf (Sroga) from the commercial forest was the least correlated with traffic.

	Relative movements of wolves (0800-1500 h)		Movements of wolves compared to those of Bura		Correlation of wolf movements with traffic	
Wolf	$\bar{\mathbf{x}}$	SD	<i>t</i> (27 df)	Р	r	Р
Ruda (NP)	0.88	0.45	4.10	< 0.001	-0.042	0.847
Chytra (NP)	0.88	0.53	3.76	0.001	-0.079	0.714
Chyża (NP)	0.74	0.42	2.56	0.016	-0.252	0.235
Sroga (CF)	0.88	0.24	5.95	< 0.001	-0.041	0.848
Siwa (CF)	0.75	0.39	3.58	0.001	-0.447	0.029
Bura (CF)	0.49	0.24	-	-	-0.697	< 0.001

**Table 3.1.** Mean relative movements of 6 female wolves in the daytime (0800-1500 h) compared to the daytime movement of the wolf Bura and correlation of wolf movements with the traffic in the commercial forest during the winters of 1996 to 1999. Białowieża Forest (NP: national park, CF: commercial forest).

No difference occurred (t = 1.15, 27 df, P = 0.262) between the mean relative movements for 15-min intervals of wolves from the national park and those of the commercial forest during the time of maximum human presence from 0800 to 1500 h (Fig. 3.1). When we compared the daytime movements of wolves, 1 wolf (Bura) from the commercial forest moved less during the day than all other wolves (all  $P \le 0.016$ , Tab. 3.1). No significant differences occurred in relative movement during the daytime among the other wolves.

#### **3.6 Discussion**

In the Białowieża Forest, wolves reacted differently to human activity. The 2 wolves whose movements correlated the most and the least with traffic were both from the commercial forest. The road density in the home range core area of the wolf least influenced by humans was not lower than the road density in areas used by other wolves. The impact of human activity did not appear strong enough to reduce the daytime movements of wolves in the commercial forest compared to movements of wolves in the national park. The daytime drop in movements seems to be affected by other factors than human activity. Spanish and Italian wolves studied in agricultural mountainous regions with human densities of 20-30 inhabitants per km<sup>2</sup> hardly move in the daytime (Vilà et al. 1995, Ciucci et al. 1997). In Minnesota and Alaska in the United States, in areas where human densities are probably lower, wolves moved for 28% (Mech 1992) and 50% (Peterson et al. 1984) of the daylight hours, respectively. Although they lived close to people, wolves in the Białowieża Forest did not reduce their movements during the day, probably because the area is well forested. In Italy and Spain, less than 40% of the area in wolves' home ranges was forested (Vilà et al. 1995, Ciucci et al. 1997). Wolves in the Białowieża Forest left the forest only at night (Theuerkauf et al., unpublished data). We conclude that, in the Białowieża Forest, wolves did not reduce their movements in the daytime because of human activity. However, the daylight prevented them from leaving the forest cover.

#### 3.7 Acknowledgments

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#### 4. DAILY PATTERNS AND DURATION OF WOLF ACTIVITY<sup>1</sup>

#### 4.1 Abstract

We studied the influence of human activity, hunting of prey by wolves, reproduction and weather conditions on daily patterns and duration of activity of 11 radio-tracked wolves (*Canis lupus*) in the Białowieża Forest (Poland) from 1994 to 1999. On average, wolves were active 45% of time and traveled 0.92 km/h. The mean length of an activity bout was 0.76 h and of an inactivity bout 1.02 h. Wolves were active throughout the day but their activity peaked at dawn and dusk, which coincided with the periods when they killed most prey. Periods of reproduction and high temperatures had less pronounced effects on activity patterns. Human activity and other factors did not significantly affect the wolves' daily activity patterns. The influence of humans may however be indirect if hunting of ungulates by humans modifies the activity patterns of the wolves' prey. We conclude that the daily activity patterns of wolves in our study area were mainly shaped by their pattern of hunting prey.

#### 4.2 Introduction

Radio-tracking studies of wolves (*Canis lupus*) have suggested several factors that are likely to influence their activity patterns. These factors are human activity (Ciucci et al. 1997; Vilà et al. 1995), the hunting of prey (Ballard et al. 1991; Harrington and Mech 1982; Mech and Merrill 1998; Murie 1944), reproduction (Ballard et al. 1991; Harrington and Mech 1982; Vilà et al. 1995) and weather (Fancy and Ballard 1995; Kolenosky and Johnston 1967). However, the importance of each of these factors will vary according to the geographic area, which causes dissimilarities in the activity patterns of wolves from different study sites: Wolves were nocturnal in Italy (Ciucci et al. 1997), nocturnal with a tendency to bimodal activity in Spain (Vilà et al. 1995), active throughout day and night in Ontario (Kolenosky and Johnston 1967), and in Alaska wolves were most active from 2200-0600 h in summer and from 0700-1600 h in winter (Fancy and Ballard 1995). Wolves also show significant variation in daily activity patterns among individuals of a pack as observed at denning and rendezvous sites (Ballard et al. 1991; Harrington and Mech 1982).

We hypothesized that human and prey activity would have the most important influence on the activity patterns of wolves. The activity patterns of wolves and their prey are theoretically dependent on one another because prey strive to avoid wolves, whereas wolves adapt their temporal hunting pattern to the times when prey are most vulnerable. Knowledge about the temporal distribution of wolf kills could improve the understanding of the interactions between wolves and their prey, but the information available is limited to data based on the times at which wolves leave den sites for

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hunting and return afterwards (Ballard et al. 1991; Harrington and Mech 1982; Mech and Merrill 1998; Murie 1944). The influence of humans on activity of wolves is especially important to determine. Wildlife managers need information about the potential influence of humans on the behavior of wolves in areas where wolves are currently extending their range, such as Central Europe (Promberger and Schröder 1993) or the USA (Mech 1995). We expected that wolves living in areas with high human activity would either change their activity patterns to avoid encounters with humans or become used to the presence of people. In Central Europe, where hunting by humans strongly influences the activity patterns of ungulates (Briedermann 1971; Georgii 1981; Georgii and Schröder 1983; Jeppesen 1989), hunting patterns of recolonizing wolves could cause a shift in the activity patterns of their prey.

To obtain daily patterns of wolf activity, kills by wolves and human activity, we radio-tracked wolves, determined the time when wolves killed prey, and recorded human activity in the Białowieża Forest, Poland. This area lies on the western edge of the large wolf range that encompasses the boreal and temperate forest zone of Eurasia. The aim of our study was to determine how human activity, the wolves' hunting pattern, reproduction and weather conditions affect the activity of wolves.

#### 4.3 Methods

#### Study area

The Białowieża Forest straddles the Polish-Belarussian border (52°30'-53°00'N, 23°30'-24°15'E) in the transition zone between boreal and temperate climate. The forest consists of deciduous, coniferous and mixed tree stands. The mean daily temperature is -5°C in January and 18°C in July, annual precipitation is 641 mm, and the length of snow cover averages 92 days, but ranges between 0 and 132 days (Faliński 1994). The maximum depth of snow during this study was 63 cm. Our study area was the Polish part of the Białowieża Forest (580 km<sup>2</sup>), which includes the Białowieża National Park (100 km<sup>2</sup>) and a commercial forest (480 km<sup>2</sup>). Timber harvest, reforestation and hunting take place in the commercial forest. See Jędrzejewska and Jędrzejewski (1998) for a detailed description of the study area.

Human density is about 7 inhabitants/km<sup>2</sup> in the Białowieża Forest and 70 inhabitants/km<sup>2</sup> in the region surrounding the study area (Białystok administration district). The density of forest roads suitable for 2-wheel drive cars is about 1.2 km/km<sup>2</sup> in the commercial forest, but only about 50 km of paved roads (0.1 km/km<sup>2</sup>) are intensively used by the public. Foresters are the main source of human activity in the commercial forest. Tourists contribute largely to human activity in summer, particularly in the National Park. Mushroom collectors and hunters are active seasonally. Traffic in the forest consists mostly of cars, trucks or tractors. Tourists mainly move on foot or bicycle, and usually remain on roads and trails.
Three wolf packs roamed the Polish part of the Białowieża Forest at the beginning of this study. The core area of 1 pack (National Park pack) was the strict reserve (50 km<sup>2</sup>) of the Białowieża National Park, where there is no motorized traffic and human access is restricted. Another pack inhabited the northwestern part of the Białowieża Forest (Ladzka pack). The 3<sup>rd</sup> pack lived in the southern part of the study area. This pack split in December 1997 into 2 packs (Leśna packs) but their home ranges overlapped nearly completely after the separation. Wolves have been protected since 1989 in the Polish part of the Białowieża Forest but humans are still the main mortality factor. During our study, 6 of 12 radio-collared wolves were shot or died in poachers' snares set for wild boar (*Sus scrofa*). In the Belarussian part, hunters killed 80% of the wolf population per year on average (Jędrzejewska et al. 1996). Wolves usually flee when they meet humans in the forest.

The main prey of wolves in the Białowieża Forest (Jędrzejewski et al. 2000; Jędrzejewski et al. 2002) is the red deer (*Cervus elaphus*), followed by wild boar and roe deer (*Capreolus capreolus*). During this research, the mean densities of prey for the whole study area were about 3-7 red deer, 1-6 wild boar, and 1-5 roe deer/km<sup>2</sup> (Jędrzejewski et al. 2000; Kossak 1997; Kossak 1999).

#### Radio-tracking of wolves

We captured 12 wolves from 4 packs, either with Aldrich foot-snares equipped with radio-alarm systems (3 wolves) as described in Okarma et al. (1998) or by the fladry and net method (9 wolves) as described in Okarma and Jędrzejewski (1997). Wolves were immobilized with 1.2-1.8 ml of a xylazine-ketamine mixture (Okarma et al. 1998) and fitted with radio-collars. The radio-collars of 5 wolves were equipped with activity sensors. The other transmitters were without activity sensors. We estimated the approximate age of wolves to range between 5 months and 9 years during the period of radio-tracking, based on the date of capture, body mass, and tooth wear (Okarma et al. 1998).

During 24-h radio-tracking sessions of usually 6 days (range 1-9 days), we noted activity and location of a radio-collared wolf continuously every 30 min (March 1994 to December 1996) or every 15 min (December 1996 to September 1999). We obtained the locations of a wolf by ground triangulation from forest roads. We determined the position of the wolf from at least 2 bearings taken from different places at intervals of no more than 5 min apart. The number of locations of 11 radio-tracked wolves (9 females, 2 males) ranged from 557-8,336/wolf during 3-42 months of radio-tracking (total 40,305 radio-locations), which we considered to be large enough for analysis.

From March 1994 to August 1997, we mapped the locations of wolves using a grid of 267 m square length with a mean radio-location error of 291 m (95% confidence interval: 244-337 m). From September 1997 to September 1999, we estimated the wolves' positions to the nearest 10 m, which reduced the mean radio-tracking error to 194 m (95% CI: 157-231 m). The daily patterns of the mean distance traveled by

wolves were not affected by the different levels of mapping precision (Theuerkauf and Jędrzejewski 2002). We calculated the distances traveled by the wolves as the straight-line distance between 2 consecutive locations. Because the sum of straight-line distances between radio-locations depends on the interval length, we corrected the straight-line distances obtained with an interval of 30 min by the factor 1.16 provided by Theuerkauf and Jędrzejewski (2002), which made the results comparable to those obtained with 15-min intervals.

We used 3 methods to determine if a wolf was active or not active during a radiolocation. We considered wolves active if the intensity of the signal was uneven or signal pulses were missed during 1 min, the activity sensors indicated vertical movements of the wolf's head, or if the wolf had changed its location since the last radio-location. We calculated the mean time spent active by a wolf by assigning a value of 1 when the wolf was active (estimated by changes in signal strength) and changed its location, a value of 0 when the wolf was not active and did not change location, and a value of 0.5 when the wolf was active but did not change location or the wolf was not active during monitoring but changed its location. This provided an accurate estimate of wolf activity and did not require wolves to have radio-collars with activity sensors (Theuerkauf and Jędrzejewski 2002).

We calculated the duration of activity bouts with uninterrupted series of 15-min intervals for which we had data on activity sensors, estimated activity and movements (2,607 bouts over 2,334 h radio-tracking of 5 wolves). We defined the length of an active (inactive) bout as an uninterrupted block of radio-locations during which the animal was active (inactive) and that was preceded and followed by an interval during which the wolf was inactive (active). Short activity changes between 2 radio-locations (i.e. rising up for a moment while resting) were not detected with this method unless they happened to occur during the radio-location.

Data on animal activity gathered by 24-h radio-tracking are often not temporally independent (Salvatori et al. 1999). Temporal independence can be obtained by analyzing radio-tracking data in time-series (e.g. Doncaster and Macdonald 1997) or by assessing the interval of independence (e.g. Salvatori et al. 1999). We did not use time-series to analyze our data, because we were not able to follow wolves without short breaks during which we lost contact. Time intervals that ensure temporal independence are often large, which can lead to an important underestimate of home range size and movements of radio-tracked animals (Rooney et al. 1998). We therefore decided not to reduce our radio-tracking data to temporally independent locations, which would have resulted in a lower accuracy of results, but to eliminate autocorrelation among consecutive radio-locations by calculating 1 value for each wolf. Accordingly, we used the variation among wolves and not among radio-location data for statistical testing.

In 15% of the time during which we followed the four wolf packs, we radiotracked 2 wolves in a pack simultaneously instead of 1 wolf. Activity and movements of the radio-tracked wolves of a pack could therefore have been partly auto-correlated. However, wolf packs are no fixed units, as wolves show significant variation in daily activity patterns among individuals in a pack at denning and rendezvous sites (Ballard et al. 1991; Harrington and Mech 1982). Also in our study, we noted both activity and location of radio-tracked wolves separately, because wolves did often not show the same behavior at the same time and packs often separated. Nonetheless, to test if activity patterns of wolves in our study area were more often correlated within than among packs, we calculated correlation coefficients among the 11 radio-tracked wolves (55 comparisons). The daily activity patterns were not more often significantly correlated (1-sided Fisher's exact test, P = 0.448) and the correlation coefficients were not higher among wolves of the same pack than among wolves of different packs (*t*-test, t = 1.14, d.f. = 53, P = 0.260). We therefore decided to use the individual wolf rather than the wolf pack as the sample unit. Also Otis and White (1999) recommended to use individual animals as sample units for studies on resource selection.

We defined dawn and dusk as beginning 1 h before and ending 1 h after sunrise or sunset. Moonlit night-h were the 5 lightest h of the night in the week around the full moon, whereas dark nights began 1 h after sunset and lasted until 1 h before sunrise (excluding moonlit night-h). We defined the denning period as the time during which breeding females stayed mostly at the den site (from 2 weeks before a birth until 6 weeks after the birth) and the post-denning period as the time when wolves had left the den site but still met at rendezvous sites (6 weeks until 5 months after the birth).

## Prey of wolves and activity of humans

From 1997 to 1999, we made an effort to find the remains of all prey killed during continuous radio-tracking sessions. We snow-tracked wolf trails to find prey remains or, if there was insufficient snow cover, organized a search party that included a dog whenever possible. If we found the place where wolves had killed their prey, we defined the time at which wolves killed the prey as the moment when they were 1<sup>st</sup> radio-located at this point. Although we think that we found most prey when conditions were favorable (snow cover), we probably missed some prey remains in summer, especially during periods when wolves also take small prey such as calves of deer or young wild boar. We therefore did not compare differences in the time wolves killed prey among seasons.

To document the daily pattern of human activity in the study area, we observed vehicular and foot traffic either visually or with a magnetic count card at 39 counting points on roads in the forest from 1997 to 1999. During the visual counts, which lasted for units of 2-24 h (total 569 h), volunteers counted people and vehicles that passed a given counting point. In addition, a magnetic traffic counter card (NC-30, Nu-Metrics, Uniontown, PA, USA) placed in forest roads recorded the number of passing vehicles for continuous periods of 1 week (total 5,712 h). We checked the reliability of the card during 150 h of direct observations, and it appeared that the card had registered 144 vehicles when 142 vehicles had actually passed. We therefore considered that the card recorded the number of vehicles precisely enough and pooled these data with those

gathered visually (together 1,440 h for winter and 4,841 h for summer). We defined each of these counting h as an h with or without human presence, according to whether or not a human or vehicle had passed the observation point during that h. We used this measure of human presence as an expression of human activity.

If human activity modified the activity pattern of wolves, wolves in regions with higher human activity should reduce their activity and movements during the time of human presence compared to wolves of regions with lower human activity. We therefore compared mean activity and movements of wolf packs during the time of highest human activity to assess the impact of humans on activity patterns of wolves. We did not correlate human and wolf activity directly, because this would have been no reliable measure to assess the influence of humans. Many other factors can cause nocturnal activity of a species and because humans are usually diurnal, a direct comparison could have resulted in a pseudo-correlation.

#### 4.4 Results

#### General activity patterns of wolves and humans

Wolves were active 45% of the day on average, but the mean activity and inactivity bouts were relatively short (Tab. 4.1).

**Table 4.1.** Time spent active, time spent moving, and distance traveled by 11 wolves, and duration of activity of 5 wolves with activity sensors for the whole day (24 h), daylight (10 h), dawn and dusk (4 h), and night (10 h) in the Białowieża Forest, from 1994 to 1999.

Whole day		e day	Daylight		Dawn/dusk		Night	
Variable	x	SE	x	SE	x	SE	x	SE
Time active (%)	45.2	0.9	39.2	2.6	50.8	1.6	48.9	1.5
Time active (h)	10.8	0.2	3.9	0.3	2.0	0.6	4.9	0.1
Time moving (%)	35.9	1.6	30.7	2.4	40.6	2.1	39.2	1.8
Time moving (h)	8.6	0.4	3.1	0.2	1.6	0.1	3.9	0.2
Distance traveled (km/h)	0.92	0.05	0.67	0.07	1.06	0.09	1.10	0.06
Length of active bout (h)	0.76	0.05	0.68	0.06	0.93	0.12	0.81	0.04
Length of inactive bout (h)	1.02	0.07	1.05	0.08	0.75	0.09	1.06	0.11

Most active and inactive bouts lasted only 15 min (46% and 37%, respectively) or 30 min (18% and 16%), whereas only 19% of active and 30% of inactive bouts were longer than 1 h. The longest activity bout lasted 7 h and the longest inactivity bout 9.5 h. The activity of wolves was highest at dawn and dusk, which also coincided with the longest activity bouts (Tab. 4.1). The mean length of activity bouts decreased (linear regression, 0.03 h/year) with increasing age of wolves ( $r^2 = 0.649$ , d.f. = 7, P = 0.009), but not the mean length of inactive bouts ( $r^2 = 0.050$ , d.f. = 7, P = 0.562), the time spent active ( $r^2 = 0.002$ , d.f. = 25, P = 0.847) or the distance traveled ( $r^2 = 0.002$ , d.f. = 25, P = 0.820). In

all months, wolves in the Białowieża Forest were active throughout the day, but with peaks at dawn and dusk and troughs in the middle of the day and of the night (Fig. 4.1). The peaks of wolf activity followed the seasonal changes in the timing of sunrise and sunset (Fig. 4.2).



**Figure 4.1.** Daily patterns of mean percentage of time spent active and mean distance traveled/h by 11 wolves for periods of 2 months in the Białowieża Forest, from 1994 to 1999. The bars indicate the length and variation of night (black), dawn and dusk (gray) and day (white) during the 2-month periods.

Human activity was lowest both in intensity and length in the home range of the National Park pack, especially in winter (Fig. 4.3). However, during the main period of human activity (0700-1700 h), the distances traveled by wolves of the national park were not greater than those of wolves living in the commercial forest in winter (t = 0.12, d.f. = 9, P = 0.906) and summer (t = 1.87, d.f. = 7, P = 0.104). During the same part of the day, wolves from the national park were also not more active than wolves from the commercial forest in winter (t = 0.95, d.f. = 9, P = 0.365), but were even less active in summer (t = 2.77, d.f. = 7, P = 0.028).

Prey

Wolves killed most of the prey that we found and for which we could estimate the time of killing (n = 54) in the 6 h around sunrise (on average 2.3 h ± 0.5 SE before sunrise) and in the 1<sup>st</sup> 4 h after sunset (on average 2.7 ± 0.6 h after sunset). They killed less often in the night and rarely in the middle of the day (Fig. 4.4). Compared to the length of

each section of day during the days of hunts, wolves killed 1.8 times more than expected at dawn, dusk and during moonlit nights (1-sided Fisher's exact test, P = 0.047), with 1.2 times not significantly more than expected during the night (P = 0.282), and 3.6 times less than expected in the day (P = 0.002).



**Figure 4.2.** Patterns of mean percentage of time spent active and mean distance traveled/h by 11 wolves in relation to sunrise and sunset in the Białowieża Forest, from 1994 to 1999. The bars indicate night (black), dawn and dusk (gray) and day (white).

The mean length of time wolves were active and moved before they made a kill was 1.7  $\pm$  0.2 h. The hourly activity and distance traveled by wolves were highest during the 2 h before a kill (Fig. 4.5). The mean distance traveled dropped immediately after wolves made a kill, but the wolves remained mostly active and moved short distances in the h after a kill. We compared activity and movements of wolves the day before a kill with the day after a kill for two parts of the day. From evening to morning (3 h before sunset to 3 h after sunrise), wolves were less active (45.9  $\pm$  2.1%) and traveled shorter distances (0.79  $\pm$  0.06 km/h) the day after a kill compared to their mean activity (58.1  $\pm$  2.5%) and distance traveled (1.37  $\pm$  0.13 km/h) the day before the kill (*t*-test for paired samples, t = 4.53, d.f. = 9, P = 0.001 for activity and t = 4.20, d.f. = 9, P = 0.002 for distance traveled). However, in the middle of the day (3 h after sunrise to 3 h before sunset), wolves did not reduce their activity (49.4  $\pm$  7.2% before and 44.2  $\pm$  3.2% after a kill, t = 0.69, d.f. = 8, P = 0.507) and movements (0.84  $\pm$  0.16 km/h before and 0.85  $\pm$  0.13 km/h after a kill, t = 0.06, d.f. = 8, P = 0.950) after a kill. The length of active (t =



1.15, df = 3, P = 0.241) and inactive bouts t = 0.79, df = 3, P = 0.487) did not differ the day before and after a kill.

**Figure 4.3.** Daily patterns of mean percentage of time spent active and mean distance traveled/h by wolves compared to the patterns of mean percentage of time with human presence in the home ranges of the National Park pack (4 wolves), the Ladzka pack (3 wolves), and the Leśna packs (4 wolves) in the Białowieża Forest, from 1994 to 1999. The bars indicate the length and variation of night (black), dawn and dusk (gray) and day (white).

## Breeding season

Wolves were least active and mobile during the period of pup raising (April-July), whereas activity and movements were highest in August and in February and March during the mating season (Fig. 4.6). Breeding females reduced their activity and movements during the period of denning compared to non-breeding females at night, but not from dawn to dusk (Tab. 4.2). The only adult male that we radio-tracked during the denning period was no more active (t = 0.48, d.f. = 4, P = 0.655), but traveled longer distances (1.04 km/h, t = 6.41, d.f. = 4, P = 0.003) than the breeding females. Breeding females stayed near the den  $67 \pm 4\%$  of the time during the whole 8-week long denning period ( $37 \pm 18\%$  of time the 2 weeks before birth;  $86 \pm 3\%$  during the 1<sup>st</sup> 2 weeks after birth;  $73 \pm 6\%$  during 3<sup>rd</sup> and 4<sup>th</sup> week after birth;  $32 \pm 10\%$  during 5<sup>th</sup> and 6<sup>th</sup> week

after birth). During the 1<sup>st</sup> 2 weeks after birth, breeding females were the least active  $(28.7 \pm 1.5\%)$  and mobile  $(0.42 \pm 0.10 \text{ km/h})$ .



**Figure 4.4.** Temporal distribution of 54 wolf kills in the Białowieża Forest, from 1994 to 1999 (continuous line: number of prey killed in 2-h classes, broken line: start of hunting). The bars indicate the length and variation of night (black), dawn and dusk (gray) and day (white).



**Figure 4.5.** Mean percentage of time spent active and mean distance traveled/h by 10 wolves 24 h before and after the time of 54 kills in the Białowieża Forest, from 1994 to 1999.

In the post-denning period, the time spent active and distances traveled by breeding females increased compared to those of non-breeding females (Tab. 4.2). From dawn to dusk, breeding females moved even more than non-breeding females (Tab. 4.2). In the post-denning period, the activity (t = 0.61, d.f. = 4, P = 0.573) and distance traveled (t = 1.68, d.f. = 4, P = 0.168) by breeding females were not significantly higher than those of the male. During the rest of the year, the means of activity or distance traveled by breeding females did not differ to those of non-breeding females (t = 0.25, d.f. = 9, P = 0.804 for activity; t = 1.15, d.f. = 9, P = 0.278 for movements) or males (t = 0.53, d.f. = 5, P = 0.619 for activity; t = 0.78, d.f. = 5, P = 0.472 for movements).

	ц			Denning	Denning			Post-denning				
	aypa	Breeding		Non-b	Non-breed.		Bree	Breeding		Non-breed.		
Variable	<u> </u>	$\bar{\mathbf{x}}$	SE	x	SE	Г	x	SE	x	SE	Г	
Activity	ght	37.5	4.0	72.1	11.2	0.012	46.8	2.9	40.5	12.2	0.467	
Distance	ŠĨ	0.77	0.37	1.18	0.12	0.006	1.05	0.14	0.83	0.21	0.441	
Activity	ay	36.0	3.0	34.1	9.0	0.788	43.9	4.7	38.7	4.7	0.553	
Distance	Ď	0.55	0.03	0.50	0.22	0.854	0.83	0.08	0.49	0.01	0.011	

**Table 4.2.** Time spent active (%) and distance traveled (km/h) by 5 breeding and 2 non-breeding females during the night and in the day (including dawn and dusk) in the Białowieża Forest, from 1994 to 1999.



**Figure 4.6.** Monthly means of percentage of time spent active and distance traveled/h by 11 wolves in the Białowieża Forest, from 1994 to 1999.

#### Weather

Wolves reduced their mean activity from 44.1  $\pm$  1.4% on days with no or light rain (up to 10 mm/day) to 32.6  $\pm$  3.8% on days with more rain than 10 mm/day (*t*-test for paired samples, t = 2.80, d.f. = 8, P = 0.023). Simultaneously, they reduced their movements from 0.89  $\pm$  0.05 km/h to 0.55  $\pm$  0.11 km/h (t = 2.41, d.f. = 8, P = 0.043) and the length of their activity bouts from 0.79  $\pm$  0.06 h to 0.39  $\pm$  0.06 h (t = 8.26, d.f. = 2, P = 0.014), whereas they increased the length of inactive bouts from 1.09  $\pm$  0.09 h to 1.51  $\pm$  0.06 h (t = 4.59, d.f. = 2, P = 0.044). In contrast, activity (t = 0.00, d.f. = 10, P = 0.998) and distance traveled (t = 0.81, d.f. = 10, P = 0.437) by wolves were not different on days with and without snowfall. However, wolves decreased their mean time spent active (0.6%/cm snow depth) and distance traveled/h (0.02 km/cm snow depth) with increasing snow depth (linear regression, both P < 0.001) for snow depths ranging between 1-63 cm.

We tested the influence of extreme weather conditions (high and low temperatures, heavy rainfall, heavy snowfall and deep snow) on the daily patterns of wolf activity, but the animals only significantly modified their activity patterns on days when the mean daily temperatures were 20°C or above. On such hot days, wolves reduced their movements compared to mild summer days (10-19°C from May to August) during the evening (1800-2400 h) from  $1.15 \pm 0.19$  km/h to  $0.57 \pm 0.12$  km/h (*t*-test for paired samples, t = 2.76,  $d_{f} = 7$ , P = 0.028) and increased their movements from  $1.09 \pm 0.11$  km/h to  $1.33 \pm 0.21$  km/h in the morning (0400-0800 h), although this was not significant (*t*-test for paired samples, t = 0.84,  $d_{f} = 6$ , P = 0.432).

## 4.5 Discussion

Wolves in Europe had to adapt to over 1,000 years of heavy persecution by man, whereas they were hunted intensively over shorter periods in many areas of North America. If wolves had adapted their behavior to avoid direct contact with humans, they might be less active during the day. Indeed, wolves studied in agricultural mountainous regions of Spain and Italy with human densities of 20-30 inhabitants/km<sup>2</sup> hardly moved in daylight (Ciucci et al. 1997; Vilà et al. 1995). In Alaska, where human density is low, wolves moved in 50% (Peterson et al. 1984) of the daylight. In forests of Minnesota, where human density in the wolf range was 1.5 inhabitants/km<sup>2</sup> (Mladenoff et al. 1995), wolves moved during 28% of the daylight in winter (Mech 1992). In the Białowieża Forest, persecution does not seem to have caused wolves to reduce their activity and movements in daylight, perhaps because our study area is mostly covered by forest. In Italy and Spain, where less than 40% of the area in the wolves' home ranges was forested (Ciucci et al. 1997; Vilà et al. 1995), perhaps there was not enough cover for daylight movements. Human activity therefore does not seem to significantly influence the temporal activity patterns of wolves in regions where they have the opportunity to avoid direct contact with man. Our hypothesis that wolves would adapt their activity patterns to human activity was insufficient to explain the wolves' behavior in our study area. We suggest that man and wolves are spatio-temporally separated, i.e. wolves do not change their temporal activity patterns under human influence, but they avoid being at the same time and at the same place as humans. In Romania, a wolf pack regularly visited a dump site at night in a town of 300,000 inhabitants, but remained in the forest in the day (C. Promberger et al. in litt.).

However, there are other possible reasons why wolves could reduce their activity and movements during the day. On hot days, wolves in our study area moved less in the evening but more in the morning, when ambient temperatures are usually lowest. Mech (1970) reported that wolves quickly get overheated in summer and usually reduce their daylight movements. Temperature may therefore have partly caused the nocturnal activity patterns of the wolf radio-tracked in Italy from June to November by Ciucci et al. (1997). Human influences can however be indirect through prey. Ungulates under human hunting pressure often reduce their daytime activity (Briedermann 1971; Jeppesen 1989), which could drive wolves to be more nocturnal and hunt more in the night than they would do in areas without humans. Although it is possible that human activity caused the nocturnality of wolves in Spain and Italy, the influence of humans may be confounded with factors such as temperature and prey activity. It is therefore difficult to clearly determine the impact of human activity on the temporal patterns of wolf activity.

In our study, the number of prey taken by wolves was highest when the light was dim, i.e. at dawn, dusk and on moonlit nights. This is not astonishing considering that vision of canids is best adapted to daylight and the phase between day and night (Kavanau and Ramos 1975; Roper and Ryon 1977). Wolves that are kept in enclosures and do not have to hunt were almost exclusively active during daylight (Kreeger et al. 1996). We therefore think that the crepuscular and nocturnal activity of wolves is probably caused by the need to hunt. We suggest that dim light provides the best hunting chances for wolves and that prey are more readily available during this period. Red deer in the Białowieża Forest are active throughout the day with a tendency to activity peaks at dawn and dusk (E. Kaniowska and B. Jędrzejewska in litt.).

Peaks in activity and especially movements of wolves were closely related to the hunting pattern, and after a successful hunt, wolves reduced their activity. However, wolves did not decrease their activity and movements in the middle of the day after a kill in comparison with the day before a kill. This time may be used to eat, socialize, play or keep diurnal scavengers such as ravens away from the kill.

During the period of reproduction, wolves (especially breeding females) spend much of their time at denning and rendezvous sites (Ballard et al. 1991; Harrington and Mech 1982). Because other wolves from the pack usually assure the feeding of breeding females during this time (Mech 1999; Mech et al. 1999; Murie 1944), females do not have to maintain an activity pattern based on hunting. In our study, breeding females reduced during the denning period their activity and movements at night, which indicated that other wolves may have provided females with food. If other wolves cannot supply the breeding female with enough food, her activity pattern should be shaped both by hunting and the need to attend pups. In Spain, such a situation caused breeding females to leave the den mainly in the day, whereas they were mainly active at night in other periods of the year (Vilà et al. 1995). Vilà et al. (1995) assumed that in Spain, where packs are usually small, it would be the safest for females to leave the den for hunting during the day, because sunlight would help keep the unattended pups warm and potential predators are less active. The activity patterns of breeding females therefore seem to depend greatly on the ability of other pack members to provide them with food.

We conclude that daily activity patterns of wolves in our study area were mainly shaped by their pattern of hunting prey. Human activity appeared to have no significant influence on temporal activity patterns of wolves. The influence of humans may however be indirect if hunters of ungulates modify the activity patterns of the wolves' prey. The pup raising had a temporary influence on activity patterns and mean time spent active. Weather markedly modified the behavior of wolves only under extreme situations such as high temperature and heavy rain. Although some information on daily activity patterns of wolves has been gathered (Ballard et al. 1991; Ciucci et al. 1997;

Fancy and Ballard 1995; Harrington and Mech 1982; Kolenosky and Johnston 1967; Vilà et al. 1995; this study), it is still not possible to completely explain activity patterns of wolves in different sites.

## 4.6 Acknowledgments

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## 5. SELECTION OF DEN, RENDEZVOUS AND RESTING SITES BY WOLVES<sup>1</sup>

## 5.1 Abstract

We studied the selection of den, rendezvous and resting sites by wolves (*Canis lupus*) in the Białowieża Forest (Poland). The aim of the study was to find out whether wolves selected sites that were far from villages, forest edge and roads, and had a dense ground cover with good hiding possibilities. We also tested whether wolves selected a particular forest type for their den sites. Den and rendezvous sites were located as far away as possible from villages, the forest edge, and intensively used public roads. Locations of resting sites were not affected by these man-made structures. Wolves selected dry coniferous forests for den sites but also used other forest types. We conclude that the suitability of an area for pup raising depends mainly on the spatial distribution of forest, human settlements and public roads and to a lesser extent on habitat characteristics.

## 5.2 Introduction

Wolves (*Canis lupus*), in both Europe and the USA, are expanding back into areas from which they had been extirpated (Mech 1995, Boitani 2000). The success of their recovery depends as much on public acceptance as on the suitability of the habitat, which should provide adequate food resources as well as quiet areas where the animals can retire (Boitani 2000). The ability to predict potential den and rendezvous sites is necessary to plan the protection of these areas during the breeding season (Wisconsin Wolf Advisory Committee 1999). There are some studies on den and rendezvous sites from North America (Murie 1940, Ballard and Dau 1983, Fuller 1988, Ciucci and Mech 1992) and Russia (Tehsin 1987, Ryabov 1988). There is, however, a lack of data about the habitat selection of denning wolves as well as on the potential influence of man on den, rendezvous and resting site selection. We therefore tested whether wolves of the Białowieża Forest (Poland) selected den, rendezvous and resting sites that (1) were far from villages, the forest edge and roads, and (2) had a dense ground cover offering good hiding possibilities. We also analysed if (3) wolves selected a particular forest type for their den sites.

#### 5.3 Study area and methods

The study area was the Polish side of the Białowieża Forest (580 km<sup>2</sup>), which is situated on the border with Belarus. One hundred km<sup>2</sup> of the forest are protected as the Białowieża National Park (Fig. 5.1). The core area of the national park (50 km<sup>2</sup>) is a strict reserve in which harvesting of plants or animals is prohibited, entry is limited to

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permit holders and no motorised traffic is allowed. There are a further 22 small (0.1-3.7 km<sup>2</sup>) nature reserves in the Białowieża Forest (Fig. 5.1). Human presence in the strict reserve of the National Park is low except for a small area close to the park's entrance where tourists are taken on guided tours. Human penetration is more intense in the rest of the forest, which is exploited commercially. Human density is about 7 inhabitants per km<sup>2</sup> in the Białowieża Forest and 70 inhabitants per km<sup>2</sup> in the region surrounding the study area (Białystok administration district). The density of forest roads suitable for 2-wheel-drive vehicles is about 1.2 km per km<sup>2</sup> in the commercial forest, but only about 50 km of paved roads (0.1 km per km<sup>2</sup>) are intensively used by the public. The Belarussian part of the Białowieża Forest (870 km<sup>2</sup>), which is adjacent to the study area, is protected as a national park (partially in Fig. 5.1). Wolves have been protected since 1989 in the Polish part of the Białowieża Forest, but are hunted in the Belarussian part (Jędrzejewska et al. 1996). In the Polish part, some wolves died during our study in poachers' snares set for wild boar (*Sus scrofa*). For a detailed description of the study area see Jędrzejewska and Jędrzejewski (1998).

Kwiatkowski (1994) described 19 vegetation types of the Białowieża Forest, which we grouped into four forest types according to dominant species and ground humidity. We classified habitats as dry or wet forests (ground water level lower or higher than 2 m) and coniferous or deciduous forest depending on the dominating tree species. Accordingly, the category dry coniferous forests covered Kwiatkowski's (1994) classifications of fresh pine (*Pinus sylvestris*) forests, pine-spruce (*Picea abies*) mixed forests, and thermophilous pine-spruce forests. Dry deciduous forests covered fresh oak (*Quercus robur*)-linden (*Tilia cordata*)-hornbeam (*Carpinus betulus*) forests, pine-oak mixed forests, thermophilous oak forests, thermophilous oak-hornbeam forests, and eutrophic oak-linden-hornbeam forests. We considered the following as wet coniferous forests: alder (*Alnus glutinosa*)-spruce forests, bog spruce forests, bog pine forests, humid pine forests, and humid oak-spruce forests. As wet deciduous forests we considered humid oak-linden-hornbeam forests, ash (*Fraxinus excelsior*)-elm (*Ulmus campestris*) flood plain forests, ash-alder flood plain forests, bog oak forests, bog alder forests, and bog birch (*Betula pubescens*) forests.

We understand as den site a place where a breeding female raised pups up to weaning, as rendezvous site a place were young wolves stayed for several days and to which the adults returned regularly, and as resting site a place where wolves had been located for several hours by radio-tracking while being not active but which wolves did not reuse later. For analyses, we used den sites for which we had either found a burrow (n = 9), a surface bed with signs of prolonged wolf use (n = 5) or when we did not find a burrow or surface bed but a radio-collared female stayed stationary during the first weeks of May (n = 5). Our mean radio-tracking error was 110 m when wolves were not active (Theuerkauf and Jędrzejewski 2002), we therefore considered the location of a radio-located den site sufficiently accurate for analysis of distances to roads, villages and the forest edge as well as to determine the forest type using the vegetation map of Kwiatkowski (1994). We only included rendezvous and resting sites in the analysis

when we found signs of wolf use at these sites (beds with wolf hairs, scats, wolf tracks, gnawed bones), or when we confirmed a resting site by snow-tracking. Most sites used by wolves stemmed from a radio-tracking study of wolves from 1994 to 1999 (Jędrzejewski et al. 2001), but we included data on den sites found incidentally.

We calculated distances between the location of sites used by wolves and the nearest man-made structure (villages, forest edge, roads) and determined the forest type after Kwiatkowski (1994) for all 19 den, 10 rendezvous and 31 resting sites (11 for summer, 20 for winter) using a GIS (Geographic Information System). We assessed selection by comparing distances and forest type of sites used by wolves with those of 100 random points located inside the study area, which we created by GIS. We considered three types of forest roads for the analysis following a classification by J. Theuerkauf et al. (unpublished data): primary roads, which were intensively used by the public (1,000-10,000 vehicles per week), secondary roads (48-500 vehicles per week) and tertiary roads (less than 40 vehicles per week).

We described the habitat structures of 6 den, 7 rendezvous, and 10 resting sites found during the summer of 1997. These habitat descriptions were done within a 50-m radius of the site's centre. For each of these 23 sites, we described in the same manner the habitat of a point randomly chosen within the home range of the given wolf. The habitat structures that we described were (1) the sight distance at wolf eye level (about 50 cm) in the four compass directions, (2) the estimated percentage of sight blocking structures on the ground (young trees, shrubs, fallen trees), and (3) the estimated percentage of open canopy in the 50-m circle.

## 5.4 Results

The den and rendezvous sites of wolves were located as far away as possible from the edge of the forest, settlements, and public roads (Fig. 5.1). All den and rendezvous sites of wolves which home ranges included the Białowieża National Park were in the strict reserve of the national park, whereas all den and rendezvous sites of wolves living in the commercial forest laid outside nature reserves (Fig. 5.1).

The den and rendezvous sites of wolves were further away from the forest edge, villages, and intensively used roads than the random sites (Tab. 5.1). On the other hand, wolves did not avoid any man-made feature for their resting sites (Tab. 5.1). The ground vegetation around den, rendezvous or resting sites was no denser than around random points and the vision distance at sites used by wolves did not differ from that of random points (Tab. 5.1). There were always small glades in the 50-m circles around den or rendezvous sites but the canopy cover of these sites was not more open than that at random sites (Tab. 5.1).



**Figure 5.1.** Locations of den (black dots circled in white) and rendezvous (white dots) sites of four wolf packs in the Białowieża Forest with distribution of the commercial forest (light grey), nature reserves (mean grey), the strict reserve of the Polish Białowieża National Park (dark grey), human settlements (black area), heavily used public roads (double lines) and forest roads (dashed lines).

**Table 5.1.** Means ( $\pm$  difference to 95% confidence limits) of habitat characteristics and distances to manmade structures of den, rendezvous and resting sites, compared with random sites in the Białowieża Forest using a *U*-test.

	Den		Rendezvous		Resting		Random
Habitat structure or distance	$\overline{X} \pm CI$	Р	$\overline{x} \pm CI$	Р	$\overline{x} \pm CI$	Р	$\overline{x} \pm CI$
Dense vegetation (%)	11±8	0.808	24±6	0.270	17±10	0.489	25±9
Canopy cover (%)	43±43	0.746	44±37	0.523	25±20	0.074	49±14
Vision distance (m)	18±11	0.435	11±5	0.082	20±14	0.450	21±6
Distance to villages (km)	4.3±0.7	< 0.001	4.5±0.8	< 0.001	$2.8 \pm 0.5$	0.168	2.4±0.3
Distance to forest edge (km)	3.9±0.6	< 0.001	4.2±0.6	< 0.001	$2.5 \pm 0.5$	0.154	2.1±0.3
Distance to primary roads (km)	5.8±0.7	< 0.001	7.1±0.9	< 0.001	3.3±0.8	0.948	3.4±0.5
Distance to secondary roads (km)	2.2±0.6	0.005	3.2±0.4	< 0.001	1.6±0.4	0.296	1.4±0.2
Distance to tertiary roads (km)	1.1±0.5	0.041	0.9±0.7	0.678	0.8±0.3	0.300	0.5±0.1

Four of the den sites that we found were in thermophilous pine-spruce forests, four in humid oak-linden-hornbeam forests, three in fresh oak-linden-hornbeam forests, two in humid pine forests, two in fresh-pine forests, one in an ash-alder flood plain forest, one

in an alder-spruce forest, one in a bog spruce forest, and one in a pine-spruce mixed forest (all forest types after Kwiatkowski 1994). Considering the availability of forest types with random points, the only forest type that wolves selected were dry coniferous forests for den (Tab. 5.2) and rendezvous sites (Fisher's exact test, P = 0.013). Wolves did not select a particular type of forest for their resting sites (all P > 0.35). When wolves dug a burrow as den site, they most often enlarged one or two entrances of former badger setts or fox dens. The burrows in wet forests (Tab. 5.2) were usually on small hillocks with sandy soil. When wolves used surface beds at their den sites, they were either under roots of fallen trees or between the roots of large standing spruces. We never found that a female reused a den in the following years.

 Table 5.2. Numbers (percentages) of 19 den sites occurring in different forest types, compared with 100 random sites in the Białowieża Forest using a Fisher's exact test.

Forest type	Burrows	Surface beds	Radio-located	All dens	Random points	Р
Dry coniferous	4	2	1	7 (37%)	14 (14%)	0.004
Dry deciduous	2	0	1	3 (16%)	34 (34%)	0.176
Wet coniferous	2	0	2	4 (21%)	15 (15%)	0.503
Wet deciduous	1	3	1	5 (26%)	37 (37%)	0.441

## 5.5 Discussion

Ballard and Dau (1983) described the tree cover at den and rendezvous sites in Alaska as homogenous or mixed stands with semi-open canopies interspersed with glades, and Fuller (1989) noted that dens in Minnesota tended to be in coniferous forest with a semi-opened to closed canopy. Although we also found glades to be a constant at rendezvous or den sites, we could not highlight a preference for a particular forest structure. We suggest that the characteristic that plays the greatest role in selection of dry coniferous forest for den sites is the soil type as sandy soil seems to be the only substrate in which such dens occur (Murie 1944, Mech 1970, Ballard and Dau 1983, Ryabov 1988, Fuller 1989, this study). However, as wolves may forego the excavated dens and use other features such as surface beds, hollow logs or the base of fallen trees (Joslin 1967, Mech 1970, Ryabov 1988, Fuller 1989, this study) to give birth to their pups, the protection of particular habitats as potential wolf den sites does not seem necessary.

In the Superior National Forest in Minnesota, where we expect that human activity compared to our study area is low, wolves located their dens randomly throughout their territory and only avoided a 1-km strip at the edge of their territory, probably to minimise confrontation between packs (Ciucci and Mech 1992). In the Northwest Territorium of Canada, wolves avoided denning in the forest (Heard and Williams 1992). Wolf den and rendezvous sites in the Białowieża Forest, however, were only in the forest and as far away as possible from the edge of the forest, villages and

public roads. Den and rendezvous sites of wolves were probably located in areas where encounters with humans were the least likely but did not select forest parts with a denser ground cover where they would be more concealed. Wolves living in the national park located their dens and rendezvous sites in the strict reserve (50 km<sup>2</sup>) but the packs living in the commercial forest did not use small nature reserves (up to 4 km<sup>2</sup>) although their dens were close to these reserves. Our results indicate that small nature reserves do not improve the suitability of an area for wolf breeding.

The reason why wolves in our study did not re-use dens and avoided locating their den sites close to villages and roads may be a behavioural adaptation to persecution by man. Between 1975 and 1994, people in the Białowieża Forest took about 30% of pups from the dens to use as pets or to receive a bounty (Jędrzejewska et al. 1996). However, wolves did not react strongly to human activity in the forest as we observed during radio-tracking that occasional forestry work within 200 m of the den sites did not cause the breeding female to abandon the den. Wolves in our study area have to live at close quarters with human beings, which probably explains why they tolerated forestry work within a close distance of their den. Examples from North America also suggest that wolves can adapt to human activity even at the den (Mech et al. 1998, Thiel et al. 1998) whereas wolves in wilderness areas seem to be intolerant to human proximity (Chapman 1979). We conclude that, in areas where wolves co-exist with man, the forest distribution, public roads, and villages are the main factors determining the wolf selection of den or rendezvous sites whereas habitat characteristics play an accessory role.

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# 6. SPATIO-TEMPORAL SEGREGATION OF WOLVES FROM MAN<sup>1</sup>

## 6.1 Abstract

Knowledge about the impact of human activity on the behavior of wolves (*Canis lupus*) is important to predict habitats suitable for wolf recolonization and for planning management zones. We tested the hypothesis that wolves live spatio-temporally segregated from man. From 1994 to 1999, we radiotracked 11 wolves of 4 packs and monitored human activity in the Białowieża Forest (Poland). Wolves avoided permanent man-made structures (settlements, forest edge to arable land, roads, tourist trails) more in the day than at night. The avoidance increased with increasing human use. Particularly large settlements and intensively used public roads reduced the area used by wolves. Wolves avoided temporary human presence in the forest (traffic, forestry operations) by selecting areas from which man was absent. One of the wolf packs selected a strict reserve of 50 km<sup>2</sup> as core area of its home range in the day and at night, whereas wolf packs living in a commercial forest with small nature reserves (up to 4 km<sup>2</sup>) did not select reserves in the day or at night. We conclude that spatio-temporal segregation is an adaptation of wolves to co-exist with man whilst keeping their activity pattern optimized towards food acquisition. The distribution of areas with restricted human access, forest, settlements, and intensively used public roads are the main factors determining the suitability of an area for wolves.

## 6.2 Introduction

Boitani (2000) highlighted the need for knowledge on the capacity of wolves (Canis lupus) to coexist with human activity, a factor which he regarded as a key element for the conservation of wolves in Europe. Wolves are now recolonizing many areas of Europe and North America from which they were formerly extirpated (Mech 1995, Boitani 2000). As some of the areas to which wolves are returning are densely populated, wildlife managers need information on the impact of human activity on wolves for predicting habitats which are most likely to be colonized and for planning management zones. However, only few studies have focused on the influence of human activity on wolf behavior. Thiel et al. (1998) documented that some wolves in Minnesota and Wisconsin tolerated humans even close to their den sites, but other studies reported that wolves usually avoided contact with man. This avoidance can be spatial, as in Alaska, where wolves avoided the surroundings of public roads (Thurber et al. 1994). In contrast, Vilà et al. (1995) and Ciucci et al. (1997) suggested that wolf and man are temporally segregated, because radiotracked wolves in Italy and Spain were mainly nocturnal. However, in the Białowieża Forest (Poland), the daily movement patterns of wolves living under various levels of human activity were not different

<sup>&</sup>lt;sup>1</sup> A similar version of this chapter has been submitted to the Journal of Wildlife Management: Theuerkauf, J., Jędrzejewski, W., Schmidt, K. & Gula, R. Spatio-temporal segregation of wolves from humans in the Białowieża Forest (Poland).

(Theuerkauf et al. 2001). We therefore hypothesized that man and wolves are spatiotemporally separated, i.e. wolves avoid being at the same time at the same place as man.

We studied the spatio-temporal home range use of wolves in relation to human activity in the Białowieża Forest to test our hypothesis on the spatio-temporal segregation of wolf and man. Detailed objectives were to find out whether (1) wolves avoid man-made structures (human settlements, forest edge with arable land, roads) more during the day than at night, (2) the home range of wolves is smaller during the day than at night, (3) the size of human settlements or the intensity of road use influences the level of wolf avoidance, (4) wolves reduce the use of forest parts when humans use them intensively compared to periods when man is absent, (5) wolves are more sensitive to human activity when resting than when active, (6) human activity close to a wolf is less than the mean human activity in the wolf's home range, (7) wolves select nature reserves more during the day than at night, and (8) wolves use an area more intensively after it has become protected as a reserve.

#### 6.3 Study area

The Białowieża Forest is a forest complex of 1450 km<sup>2</sup> (52°30'-53°00'N, 23°30'-24°15'E), which straddles the Polish-Belarussian border and is a mosaic of deciduous, coniferous and mixed tree stands (Fig. 6.1). The Polish part of the Białowieża Forest consists of the Białowieża National Park and of a commercial forest (480 km<sup>2</sup>), in which timber harvest, reforestation and hunting occur. Fifty km<sup>2</sup> of the Białowieża National Park have been protected as a strict reserve since 1921. There is no hunting, forestry or motorized traffic in the strict reserve and public access is limited. In July 1996, the Białowieża National Park was enlarged to 100 km<sup>2</sup>. The extended part of the national park is opened to the public but vehicle access is restricted, hunting is not allowed and forestry interventions are limited to cutting of sick trees and fencing off regeneration areas. There are also 22 small (0.1-3.7 km<sup>2</sup>) nature reserves in the Białowieża Forest, which are less protected against forestry operations than the National Park. The whole Belarussian part of the Białowieża Forest (870 km<sup>2</sup>) is a national park, but hunting and limited logging are allowed. On the Belarussian side, there is a guarded fence built in 1981 along the state border (in a distance of 0-1.5 km). The zone between the border and the fence is little used by man.

Human density on the Polish side is about 7 inhabitants per km<sup>2</sup> in the Białowieża Forest and 70 inhabitants per km<sup>2</sup> in the region surrounding the study area (Białystok administration district). The density of forest roads passable by 2-wheel-drive vehicles is about 1.2 km/km<sup>2</sup> in the commercial forest, but only about 50 km of paved roads (0.1 km/km<sup>2</sup>) are intensively used by the public. Most humans who penetrate the commercial forest are foresters. Mushroom collectors contribute to a quarter of forest visitors from July to October and hunters to 15% from September to January. Tourists contribute to a third of humans from May to September, but only to 4% from October to April. From May to September, around 100 tourists visit the strict reserve daily, but the number of tourists decreases to about 20 per day from October to April (estimate based on data of B. Jaroszewicz, Białowieża National Park, personal communication). The area visited by tourists is restricted to a 4-km tourist trail near the park's entrance. The rest of the strict reserve is open for permit holders to conduct research or education. To move around in the commercial forest, people use mostly cars (80%), but also lorries and tractors (10%) as well as bicycles (10%). Tourists mainly go on foot or bicycle and usually stay on roads or trails.



**Figure 6.1.** Białowieża Forest with distribution of the commercial forest (light gray), nature reserves (mean gray), the strict reserve of the Polish Białowieża National Park (dark gray), human settlements (black area), heavily used public roads (double lines), forest roads (dashed lines), state border (dashed and pointed line), and the cumulative home ranges (continuous lines) of wolf packs.

At the beginning of this study 3 wolf packs inhabited the Polish part of the Białowieża Forest (Okarma et al. 1998). The core area of 1 pack (National Park pack) was the strict reserve (Fig. 6.1). Another pack lived in the north-western part of the Białowieża Forest and the Ladzka Forest where there are a few small nature reserves (Ladzka pack). The third pack lived in the southern part of the study area, which includes most small nature reserves and a large part of the border zone. This pack split in December 1997 into 2 packs (Leśna packs), but because their home ranges overlapped largely after the separation, we pooled data of the 2 packs when comparing them with the other 2 packs. Forest road density was 0.8 km/km<sup>2</sup> in the home range of the National Park pack and

1.0 km/km<sup>2</sup> in the home ranges of packs living in the commercial forest. Wolves have been protected since 1989 in the Polish part of the Białowieża Forest but humans are still the main mortality factor. During our study, half of the radiocollared wolves died in poachers' snares set for wild boar (*Sus scrofa*) or were shot. In the Belarussian part, hunters kill 80% of the wolf population per year on average (Jędrzejewska et al. 1996).

The main prey of wolves in the Białowieża Forest (Jędrzejewski et al. 2000, 2002) is red deer (*Cervus elaphus*), followed by wild boar and roe deer (*Capreolus capreolus*). During this research, the mean densities of prey species for the whole study area were about 3-7 red deer, 1-6 wild boar, and 1-5 roe deer per km<sup>2</sup> (Kossak 1997, Jędrzejewski et al. 2000) Wolves only occasionally fed on carrion in rubbish tips (Ladzka pack) or killed cattle (Leśna I pack).

## 6.4 Methods

#### Wolves

From 1994 to 1999, we captured 12 wolves out of 4 wolf packs either with Aldrich foot snares equipped with radioalarm systems or by the fladry and net method (Okarma and Jędrzejewski 1997) and fitted them with radiocollars (Okarma et al. 1998). We relocated wolves in 24-hr radiotracking sessions of usually 6 days (range 1-9 days) as described in detail in Theuerkauf and Jędrzejewski (2002). Data samples for 11 radiotracked wolves (9 females, 2 males) were large enough for analysis (557-8336 radio locations per wolf during 3-42 months of radiotracking).

We created 10,000 random points with a geographic information system (GIS) inside the study area, which we defined as the cumulative area of all the wolves' home ranges (minimum convex polygons). We calculated selection by comparing radio locations of a wolf with the locations of random points inside the home range of the given wolf. We used Ivlev's electivity index (Jacobs 1974) to indicate selection:

# Selection index = $(p_w - p_r)/(p_w + p_r - 2 p_w p_r)$

where  $p_w$  is the proportion of wolf locations in a given category, and  $p_r$  is the proportion of random points in a given category. Selection indices can vary from +1 (total selection) to -1 (total avoidance). We categorized wolf or random point locations in classes according to the distance to man-made structures (settlements, forest border, roads, tourist trails) or parts of the study area under different protection (commercial forest, nature reserves, strict reserve, border zone). We calculated selection indices for all categories first for each wolf, and then mean selection indices and 95% confidence intervals (CI) for the variation among wolves. We considered that wolves selected (avoided) a given category if the lower (upper) limit of the 95% CI was higher (lower) than 0. To map the spatio-temporal home range use of wolves, we calculated selection indices for squares of 250 × 250 m. Because the location error during radiotracking was between 194 and 291 m on average (Theuerkauf and Jędrzejewski 2002), we used a 500-m radius around the center of the square to compensate for the radio location error. We defined summer as the period from May to September when wolves are concentrated around dens or rendezvous sites and when there are many tourists in the forest, and winter as the period from October to April when wolves use their whole home ranges (Jędrzejewski et al. 2001) and human activity in the forest is mainly limited to forestry operations and hunting. We defined the forest edge as the peripheral borders of the Białowieża Forest as well as all borders to clearings with a human settlement within the forest.

#### Human activity

We documented human activity from 1997 to 1999 either visually or with a magnetic traffic counter card (NC-30, Nu-Metrics, Uniontown, Pennsylvania, USA) at 39 counting points on roads in the Białowieża Forest. During visual counts, which lasted for units of 2-24 hr (total 569 hr), we counted people and vehicles that passed a given point. The traffic counter card dug in forest roads recorded hourly the numbers of passing vehicles for continuous periods of one week (total 5,712 hr). We checked the reliability of the card under our field conditions during 150 hr of direct observations and it appeared that the card had registered 144 vehicles when 142 vehicles had actually passed. We therefore considered that the card recorded the number of vehicles precisely enough and pooled its data with those gathered visually.

We classified roads inside the forest as primary roads (public paved roads with 1,000-10,000 vehicles per week), secondary roads (regularly used forest roads with 48-500 vehicles per week), and tertiary roads (rarely used forest roads with less than 40 vehicles per week). We calculated the mean human activity on roads in the home range of a wolf by multiplying the percentage of the length of a road class in the home range of a wolf with the mean human activity on the road class, and then adding the values for the 3 road classes.

In addition, we recorded human activity during radiotracking by noting the number of men and vehicles that passed the radiotracker. In 95% of cases, radiotrackers were between 200 and 2,200 m from the radiotracked wolf, so the count of human activity represents human activity within a radius of about 2 km around the radiotracked wolves. There was no detectable influence of the radiotracker on the behavior of the radiotracked wolf (Theuerkauf and Jędrzejewski 2002). To test if wolves select areas of low human activity, we compared the mean human activity on roads around wolves with the mean human activity on roads used for radiotracking.

The forestry administration provided us with information about daily locations of forestry operations in an area where we had radiotracked wolves continuously (3 weeks in January, February and May 1999). To evaluate the wolf reaction to the presence of forestry operations, we compared the wolf use of areas around forestry operations during working hours (day during the working week) and during non-working hours (night on all days, weekend).

#### 6.5 Results

### Permanent man-made structures

Wolves in the Białowieża Forest usually selected areas in the center of their home ranges that were as far as possible from the forest edge, especially in summer (Fig. 6.2). The mean daytime home ranges of wolves (205 km<sup>2</sup>, SE = 23 km<sup>2</sup>) were reduced (*t*-test for pairs: P = 0.001) compared to nightly home ranges (257 km<sup>2</sup>, SE = 29 km<sup>2</sup>). Wolves used only 74% (SE = 2%) of their home ranges in the day compared to 93% (SE = 2%) at night.



**Figure 6.2.** Selection of  $250 \times 250$ -m squares inside the home ranges of 11 wolves of four packs in the Białowieża Forest from 1994 to 1999 (black squares: selection index > 0.75, dark gray: selection index 0 - 0.75, medium gray: selection index -0.75 - 0, light gray: selection index < -0.75, white area: not used, continuous lines: forest edge to agriculture land with villages, dotted lines: nature reserves, dashed and pointed line: state border).

Wolves not only avoided coming out of the forest into arable land but also rarely made incursions into the 2-km wide forest zone that borders the forest edge (Fig. 6.3). Daytime avoidance of arable land was almost total and more pronounced for the 2-km

edge zone than at night. The 24-hr patterns of the mean distance between wolves and the forest edge were similar when comparing wolf packs, but the difference between distances in the day and at night were largest for the National park pack in winter when human activity in the home range of this pack was at its lowest (Fig. 6.4).



**Figure 6.3.** Mean wolf selection indices (with 95% CI of the variation among wolves) of 0.5-km-wide distance classes to the forest edge during the day (white dots) and the night (black dots) for 11 wolves of the Białowieża Forest from 1994 to 1999.



**Figure 6.4.** Temporal distribution of the mean distance between wolves and the forest edge for 4 wolves of the National Park pack (continuous lines), 4 wolves of the Leśna packs (dotted lines), and 3 wolves of the Ladzka pack (dashed lines). The bars indicate the length and seasonal variation of night (black), dawn and dusk (gray) and day (white).

Wolves increased both their avoidance level and the width of the avoided forest zone with increasing size of human settlements (Fig. 6.5). The avoidance zone for the largest town in the study area (24,000 inhabitants) was 2 km at night and 3.5 km in the day. Wolves avoided a zone of 0.5 km at night and 1 km in the day around forest settlements of a few houses.



**Figure 6.5.** Mean wolf selection indices (with 95% CI of the variation among wolves) of 0.5-km-wide zones of forest around settlements of different sizes during the day (white dots) and the night (black dots) for 11 wolves of the Białowieża Forest from 1994 to 1999.

In the commercial forest, wolves avoided a band of 0.75 km from primary roads at night and 2 km in the day (Fig. 6.6). The avoidance of secondary roads was lesser at 0.25 km for the night and 1 km for the day. Wolves avoided tertiary roads the least, leaving a 0.25-km wide strip in the day but none at night. In summer, wolves of the strict reserve avoided a 3.5-km wide zone around tourist trails in the day but did not clearly avoid tourist trails at night (Fig. 6.7). In winter, wolves only avoided a 1-km wide zone around the tourist trails in the day. Wolves did not avoid the surroundings of other, less used tracks in the strict reserve (all 95% CIs including the value 0). Wolves were not further in the day from the forest edge (*t*-test: P = 0.919), human settlements (P = 0.919), primary roads (P = 0.863), secondary roads (P = 0.896), tertiary roads (P = 0.544), or tourist trails (P = 0.381) when resting than when active.



**Figure 6.6.** Mean wolf selection indices (with 95% CI of the variation among wolves) in relation to the distance to roads inside the Białowieża Forest (excluding wolf locations in the strict reserve of the Białowieża National Park where there are no roads for motor transportation) compared to random points during the day (white dots) and the night (black dots) for 11 wolves from 1994 to 1999 (250-m-wide distance classes up to 1 km from the road and 500-m-wide distance classes when further away).

### Temporary human presence

Although the mean human activity on roads within the home ranges of wolves was higher in summer than in winter (Fig. 6.8), the mean daily number of people or vehicles on roads in a 2-km radius around wolves was not higher (*t*-test: P = 0.596 for people, P = 0.533 for vehicles) in summer ( $\bar{x} = 7.1$ , SE = 2.1 for people,  $\bar{x} = 4.7$ , SE = 1.4 for vehicles) than in winter ( $\bar{x} = 9.2$ , SE = 3.0 for people,  $\bar{x} = 6.0$ , SE = 1.5 for vehicles). In both seasons, the hourly mean numbers of men or vehicles on roads in the 2-km radius around wolves were lower than those on all roads used for radiotracking or on all roads in the home ranges of wolves (Fig. 6.8, Wilcoxon-test: all P < 0.001). Wolves used the area of up to 1.5 km around forestry operations less during working hours than during non-working hours (Fisher's exact test: P = 0.043).



**Figure 6.7.** Mean wolf selection indices (with 95% CI of the variation among wolves) in relation to the distance to tourist trails inside the strict reserve of the Białowieża National Park compared to random points during the day (white dots) and night (black dots) for 4 wolves from 1994 to 1999.



**Figure 6.8.** Daily patterns of mean human activity (mean number of men or vehicles per h) on roads in the wolves' home ranges (dashed lines), mean human activity on roads used for radiotracking during absence of wolves (dotted lines), and mean human activity on roads used for radiotracking during the presence of wolves (continuous lines) in the Białowieża Forest in 1998 and 1999.

#### Reserves

The daily patterns of reserve selection differed greatly among packs (Fig. 6.9). The National Park pack strongly selected the strict reserve but avoided other reserves and the border zone (Tab. 6.1). Wolves of the National Park pack also avoided the new national park except on winter nights. During the winter, the Leśna packs used nature reserves more than randomly, especially in the day, but they did not clearly select reserves or the border zone (Tab. 6.1). The Ladzka pack neither selected reserves (Tab. 6.1) nor showed a particular daily pattern in reserve selection (Fig. 6.9). Wolves of the National Park pack used the area of the new national park less (*t*-test: P = 0.004) before its creation (8% of time monthly, SE = 2%) than after (17%, SE = 3%). The wolf use of this area increased at a rate of 0.5% monthly (linear regression: P = 0.048) during the 3 years after the protection was established. Before the creation of the new national park, the monthly use did not increase (P = 0.818).



**Figure 6.9.** Daily pattern of reserve selection for 4 wolves of the National park pack, 3 wolves of the Ladzka pack, and 4 wolves of the Leśna packs in the Białowieża Forest from 1994 to 1999 (nature reserves: continuous lines, strict reserve: lines with closed triangles, new national park: lines with open triangles, border zone: dotted lines). For confidence intervals see Table 6.1.

		National	Par pack	Leśna	packs	Ladzka pack		
		day	night	day	Night	day	night	
	Nature reserves	-0.94±0.06	-0.86±0.15	-0.08±0.78	-0.27±1.01	-0.30±0.29	-0.68±0.44	
summer	Strict reserve	$0.91{\pm}0.07$	$0.82 \pm 0.08$	-	-	-	-	
	New National Park	-0.53±0.37	-0.20±0.19	-	-	-	-	
	Border zone	-0.70±0.19	-0.76±0.36	$0.06 \pm 0.71$	0.07±0.56	-	-	
	Nature reserves	-0.81±0.23	-0.83±0.25	0.31±0.48	0.32±0.41	-0.18±0.54	0.12±0.36	
winter	Strict reserve	$0.87 \pm 0.06$	0.61±0.17	-	-	-	-	
	New National Park	$-0.25 \pm 0.07$	0.16±0.17	-	-	-	-	
	Border zone	-0.71±0.23	-0.52±0.27	0.19±0.23	-0.12±0.11	-	-	

**Table 6.1.** Mean reserve selection indices (± difference to the 95% CI limits) for 4 wolves of the National park pack, 3 wolves of the Ladzka pack, and 4 wolves of the Leśna packs in the Białowieża Forest from 1994 to 1999.

## 6.6 Discussion

Vilà et al. (1995) and Ciucci et al. (1997) assumed that wolf and man may be temporally segregated in Italy and Spain, where radiotracked wolves were mainly nocturnal. In contrast, wolves in Alaska (Peterson et al. 1984), in forests of Minnesota (Mech 1992), and in the Białowieża Forest (Theuerkauf et al. 2001) moved also in the day. In Alaska, Thurber et al. (1994) reported a spatial segregation as wolves avoided the surroundings of public roads. This might lead to the conclusion that wolves avoid humans spatially in areas with low human density (e.g. Alaska), and temporally in regions with high human activity (e.g. Europe). However, in the Białowieża Forest, the daily movement patterns of wolves living under various levels of human activity were not different (Theuerkauf et al. 2001) and wolves were active throughout the day although human activity in some parts of the forest is high (Theuerkauf et al. 2003a). During periods when there were high numbers of people in the Białowieża Forest, wolves managed to use parts of the forest, in which human activity (e.g. forestry operations, tourist tours) was low at that moment (this study). We conclude that the segregation between wolves and man is spatio-temporal as wolves react to human activity by avoiding areas being used temporarily by man.

There may therefore be other reasons than avoidance of humans activity for the nocturnal behavior of wolves in Italy (Ciucci et al. 1997) and Spain (Vilà et al. 1995). In Ciucci et al.'s (1997) study, wolves took regular advantage of anthropogenic food sources such as rubbish tips. Because these dump sites were in the proximity of human settlements, wolves used them at night (Ciucci et al. 1997). In Romania, several wolves also regularly visited a dump site at night in a town of 300,000 inhabitants and remained in the forest in the day (Promberger et al. 1997) where they seem to be active throughout the day when in search for prey (Promberger-Fürpaß and Sürth 2002). In the

Białowieża Forest, wolves almost completely meet their food requirements by hunting red deer, wild boar and roe deer in the forest (Jędrzejewski et al. 2000). Here, wolves were active and hunted throughout the day, but both the number of prey killed and activity peaked at dawn and dusk (Theuerkauf et al. 2003a), which are periods when these prey species are usually most active (Briedermann 1971, Cederlund 1981, Georgii 1981, Georgii and Schröder 1983, Jeppesen 1989). Besides feeding on carrion and domestic animals, Spanish wolves also prey on wild ungulates, which may be the reason why the activity patterns of wolves were nocturnal but with activity peaks at dawn and just after dusk (Vilà et al. 1995). The reason why wolves were not active in the day in Ciucci et al.'s (1997) study may also be that the potential wild prey for the studied wolf pack was wild boar, which are mainly nocturnal in Italy even when not hunted (Russo et al. 1997). Nocturnal activity of wolves may therefore be as much an adaptation to shortage of wild prey in the forest or nocturnal activity patterns of prey species as to human activity in the home range.

Spatial avoidance, on the contrary, appeared to occur alongside with spatiotemporal segregation. There were man-made structures - among which human settlements, public roads and the edge to agricultural land had the greatest influence – that even at night reduced the area used by wolves. Human settlements and roads both produce noise and light, which may explain why the wolf avoidance found in our study increased with the size of settlements and the intensity of road use. Thurber et al. (1994) noted a similar behavior in Alaska where wolves avoided a public road but selected little used roads for ease of travel. In a Canadian area with little human activity on linear corridors (mostly pipeline or seismic lines), wolves were even closer to these corridors than were random points (James and Stuart-Smith 2000). The distribution of forest plays an important role in the habitat selection of wolves. In our study area as well as in Italy (Ciucci et al. 1997), wolves avoided arable land and selected forest, especially in the day. Centuries of persecution by man have probably favored wolves that avoid open areas during daylight where they can be easily killed. The forest may however act as a cover that allows wolves to be also active during daylight. It therefore seems that in areas where wolves may come into contact with man, the centers of wolf activity tend to be at maximum distances to human settlements, the forest edge, and intensively used public roads.

Spatial avoidance is especially important during the denning period, when the breeding female cannot spatio-temporally avoid human contact. She can either choose particularly quiet places or has to bear the human activity. Both strategies occur. In Minnesota and Wisconsin, some wolf packs tolerated human activity close to their den sites (Thiel et al. 1998). In the Białowieża Forest, wolf den and rendezvous sites were at maximum distances to human settlements, the forest edge and intensively used public roads, but wolves did not abandon the den when foresters worked near the den sites (Theuerkauf et al. 2003b).

# 70

### 6.7 Management implications

Wolves are protected by law in many European countries as well as in the 48 contiguous USA. As a result, wolves are slowly expanding their ranges in both Europe (Boitani 2000) and the United States (Mech 1995). Legal protection however is not the only factor that determines the speed and extend of wolf recolonization, because the first wolves are often illegally killed (Mech 1977). The human access to an area was therefore used as an indicator for wolf survival. In the USA, a density of roads that are suitable for 2-wheel-drive vehicles of about 0.6-0.7 km/km<sup>2</sup> was regarded as a threshold for wolf occurrence because of poaching and road accidents (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Mech 1989). Road density was a major factor used to predict suitable habitats for wolves in the USA and Italy (Mladenoff et al. 1995, 1999; Mladenoff and Sickley 1998; Corsi et al. 1999). However, in the Białowieża Forest (Poland), wolves survived in a commercial forest with a road density of about 1.2 km/km<sup>2</sup>, although many wolf casualties were caused by humans (Jedrzejewska et al. 1996). Similarly, Merrill (2000) reported that a wolf pack in Minnesota survived in a military area with a road density of 1.4 km/km<sup>2</sup>. Spatio-temporal segregation of wolves from man may enlarge the area where wolves are able to live. It is possible that wolves will colonize areas that are predicted as unsuitable when taking into consideration only spatial aspects of wolf response to human activity.

Fritts and Carbyn (1995) outlined the necessity for nature reserves of up to several thousand square kilometers to maintain an isolated wolf population. Such large reserves do not exist in Europe and most parts of North America, but commercial forests proved to be sufficient for wolf occurrence. Additionally, even medium sized nature reserves as the Białowieża National Park can serve as core areas for wolves. As wolves are able to disperse over distances of up to 800 km (Fritts 1983), the exchange of individuals should be high enough to ensure the survival of a wolf population even when packs are patchily distributed in landscapes with fragmented suitable habitats. However, wolves only selected reserves when they were large enough, which in our study was 50 km<sup>2</sup>. Nature reserves or similar areas with limited human access (e.g. military training areas, state border zones, mountains) can therefore improve the suitability of populated areas where wolf recovery is desired. Moreover, as nature reserves often bear higher densities of potential prey species for wolves, it would also improve the nutritional situation for wolves and may reduce depredation on livestock (Meriggi and Lovari 1996).

We conclude that spatio-temporal segregation is an adaptation of wolves to coexist with man whilst keeping their activity pattern optimized towards food acquisition. The distribution of areas with restricted human access, forest, human settlements, and intensively used public roads are the main factors determining the areas in which wolves are able to live. Nature reserves or similarly protected areas of at least 50 km<sup>2</sup> should be especially suitable habitats for wolves, but small reserves of a few square kilometers would not improve the habitat suitability for wolves.

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#### 7. GENERAL DISCUSSION

#### 7.1 Impact of man on wolf behaviour

The mechanisms by which humans influence wolf behaviour are little known, probably because wolves have long been a symbol of wilderness and considered as intolerant of human disturbance (Theberge 1975, Chapman 1979). Until now, only Thurber et al. (1994) have analysed the spatial distribution of wolves in relation to roads and human-settled areas in Alaska. The aim of my research was therefore to improve the understanding of the conditions under which human activity influences the behaviour of wolves. In the following discussion, I summarise the most important results presented in the five preceding chapters, put them in the context of the current knowledge on wolves and strive at identifying the human impact on wolf behaviour.

#### Accuracy of radio-telemetry and its influence on wolf behaviour

In order to meet the objectives of my research, it was necessary to monitor wolf activity and movements over a large area and for all periods of the day. The only method meeting these requirements was radio-tracking since it does not demand visual contact with the animals. However, estimates of an animal's activity and location that are based on radio-tracking may not accurately represent the actual behaviour of the animal. Previous studies have shown that there is an error involved when using radio-tracking to estimate locations (Heezen & Tester 1967, Springer 1979, Saltz 1994) and distances travelled by animals (Musiani et al. 1998, Rouys et al. 2001). For the aim of my study, it was important to accurately document the daily activity patterns of wolves. I chose to use as indicators of activity the movements of the wolf's head (activity sensors) or body (changes in signal strength) and, for movements on a larger scale, straight-line distances between two consecutive radio-locations (movements). It appeared that activity estimated by changes in signal strength, activity sensors, movements, or combinations of these methods provided similar results and were appropriate to document the daily activity patterns of wolves (chapter 2). The radio-tracking method did not allow more detailed information on the wolf behaviour. It was not possible to distinguish between behaviours that involve similar movements, such as lying or sleeping, playing or feeding, running or hunting. Such detailed information on wolf behaviour would have required direct observations as performed by Mech (1988) in the tundra of Ellesmere Island. Extensive direct observations were impossible in the Białowieża Forest but even had direct observations been possible, it is likely that the proximity of observers would have influenced the behaviour of the wolves that have experienced humans as predators in the past (Jedrzejewska et al. 1996).

Wolves can hear better than humans and have a highly developed sense of smell (Asa & Mech 1995). As we radio-tracked wolves from a distance of 1 km on average (chapter 2), it is likely that the animals were sometimes aware of our presence. If the presence of radio-trackers had affected the behaviour of wolves, it would have

interfered with the analyses of human impact. To test whether the proximity of human trackers influenced the wolf activity estimates, I quantified changes in wolf activity in relation to the distance between wolf and tracker at resting sites of wolves (chapter 2). It appeared that the trackers had no detectable influence on the activity and movements of wolves when the distance between the wolf and the tracker was larger than 200 m (chapter 2). There was a small but non-significant influence if trackers were nearer than 200 m during the day. The presence of trackers is however unlikely to have influenced the results, because trackers were further than 200 m from the wolf in 99.6% of radio-locations.

As wolves did not react to humans who were further than 200 m from them (chapter 2), I estimate that the flight distance of wolves to humans was under 200 m in the Białowieża Forest. For more detailed information on the flight distance of wolves, it would have been necessary to directly measure the reaction of wolves to approaching observers. I did not perform such experiments since repeating tests until a reasonable sample size was obtained may have altered the behaviour of wolves in the study area. Furthermore, flight distances can be considerably smaller when a predator approaches an animal directly than when the approach is non-directional, i.e. following a direction that would pass the approached animal (Burger and Gochfeld 1990, Cooper 1998, Frid & Dill 2002). During radio-tracking, the approach of wolves is rather non-directional because radio-trackers try to stay at a certain distance. Testing flight distances by directly approaching the wolves would therefore not have been applicable to estimates of the influence of radio-tracking on wolf behaviour.

# Temporal patterns of wolf activity and movements

The daily movement patterns of wolves living in the commercial part of the Białowieża Forest were negatively correlated to the activity patterns of humans (chapter 3). This could have led to the conclusion that wolves adjusted their daily movement patterns to the daily patterns of human activity. However, such a correlation does not necessarily prove that human activity affected wolf behaviour, as activity and movement patterns of wolves may have evolved independently of human activity patterns. It was therefore necessary to compare the activity and movement patterns of wolves living in areas of different levels of human activity. I accordingly tested whether wolves of the commercial forest, where human activity was high, reduced their movements and activity in the day compared to wolves of the national park, where human activity was low. It turned out that the movements and activity of wolves of the national park and the commercial forest did not differ during periods when human presence was at its peak (chapters 3 and 4). Since an effect of humans on temporal patterns of wolf activity and movements appeared unlikely, I tested other factors that may have influenced the temporal patterns of wolf activity.

I found that the need to hunt was the most important factor shaping the temporal patterns of wolf activity in the Białowieża Forest (chapter 4). The numbers of prey

taken by wolves were highest during crepuscular phases. The temporal distribution of killings, as well as the general activity pattern, were bimodal with peaks at dawn and dusk (chapter 4). The peaks of wolf activity coincided with the periods when red deer, the main prey species of wolves in the Białowieża Forest (Jędrzejewski et al. 2000, Jędrzejewski et al. 2002) tend to be most active (Kaniowska 2002). This would support Curio's (1976) suggestion that predators follow the activity patterns of their prey. It may be that wolves can find and follow red deer more easily during crepuscular phases, which match with the activity phases of red deer and the part of day to which the vision of wolves is best adapted (Kavanau & Ramos 1975, Roper & Ryon 1977). Activity patterns of their main prey species.

The second important factor influencing temporal patterns of wolf activity appeared to be the reproduction. Denning females may become more sensitive to human activity as they are more vulnerable. One could therefore expect breeding females to become more nocturnal to avoid contact with humans. However, in the Białowieża Forest, denning females became more diurnal than non-breeding females (chapter 4). A human impact on daily activity patterns of breeding females therefore appears unlikely. It is more likely that breeding females do not have to maintain an activity pattern based on hunting (chapter 4), because other pack members usually assure the feeding (Mech 1999, Mech et al. 1999, Murie 1944).

Mean daily temperatures above 20°C caused wolves to reduce their movements and activity in the afternoon when the ambient temperature is usually highest (chapter 4). Also Mech (1970) reported that wolves quickly get overheated in summer and usually reduce their movements during the daylight hours. In hot regions, temperature may therefore play an important role in shaping the daily activity patterns of wolves.

Spanish and Italian wolves studied in agricultural mountainous regions with human densities of 20-30 inhabitants per km<sup>2</sup> hardly moved in daylight (Ciucci et al. 1997, Vilà et al. 1995), whereas wolves were also active in the day in a wildlife refuge of Alaska (Peterson et al. 1984), in forests of Minnesota (Mech 1992) with 1.5 inhabitants/km<sup>2</sup> (Mladenoff et al. 1995), and in the Białowieża Forest with 7 inhabitants/km<sup>2</sup> (chapters 3 and 4). At first sight, the nocturnal behaviour of wolves in Spain and Italy could be explained by the higher human density in these regions. However, a wolf radio-tracked in the Bieszczady Mountains of Southeast Poland with about 40 inhabitants/km<sup>2</sup> was active throughout the day with a tendency to a bimodal activity pattern (R. Gula, B. Pirga, S. Rouys & J. Theuerkauf, unpublished data).

The mode of food acquisition better explained the nocturnal activity of wolves in Italy and Spain than the influence of human activity. In the Italian study, wolves depended to a large extent on rubbish at dump sites, which they explored at night (Ciucci et al. 1997). The only readily available ungulates in Ciucci et al.'s (1997) study area were wild boar, which even when not hunted are mainly nocturnal in Italy (Russo et al. 1997). If wolves in Ciucci et al.'s (1997) study area also hunted for wild boar, they

may have followed the activity pattern of this species. Nocturnal activity of wolves may therefore be caused either by nocturnal activity patterns of their prey species or by the need to exploit dump sites without being disturbed by humans. In Spain, besides feeding on carrion and domestic animals, wolves also preyed on wild ungulates, which may be the reason why the activity patterns of wolves were mainly nocturnal but with activity peaks at dawn and just after dusk (Vilà et al. 1995).

Activity patterns are adaptations that enable animals to exploit their environment efficiently (Daan & Aschoff 1982). From an evolutionary perspective, it would be a disadvantage for wolves to adjust their temporal activity patterns to those of humans if the risk of being killed is not very high. By reducing their daytime activity, wolves may fail to effectively exploit the available food resources. Activity patterns of wolves should therefore be geared towards optimising their foraging strategy and minimising the risk of being killed by humans. In case of an extreme persecution by man, this may include a shift to a more nocturnal behaviour. For example, covotes moved less in the day during a period of persecution by man compared to animals that had not been persecuted for more than 8 years (Kitchen et al. 2000). During the period of persecution coyotes obviously adjusted their activity patterns to reduce the chance to encounter human hunters, but increased their diurnal activity quickly after the persecution had stopped. Ciucci et al. (1997) and Vilà et al. (1995) did not report a heavy persecution in their study areas of Italy and Spain. I therefore expect the influence of humans on activity patterns of wolves that are not heavily persecuted to be less important than their mode of food acquisition. The influence of man could however be indirect as ungulates under human hunting pressure can change their activity patterns to a more nocturnal behaviour (Briedermann 1971, Georgii 1981, Jeppesen 1989). This could incite wolves to hunt more at night than they would do in areas without man, and accordingly become more nocturnal.

I conclude that wolves adjust their activity patterns to optimise their food intake. I therefore expect factors related to the mode of food acquisition to be the most important in determining the activity patterns of wolves. Activity patterns are therefore likely to be adjusted to those of their prey in regions where wolves mainly feed on wild prey.

#### Spatial avoidance of humans by wolves

The analysis of the spatial distribution of wolf locations provided a better insight into how wolves avoided humans. The distribution of forest, human settlements and intensively used public roads were the most important in determining the spatial distribution of wolves in the Białowieża Forest (chapters 5 and 6). The centres of wolf activity tended to be at maximal distances to human settlements, the forest edge, and intensively used public roads. Wolves mainly selected forest and avoided arable land (chapter 6).

There are two reasons which may be instrumental in explaining the wolves' selection of forest. First, the forest reduces the chance of wolves being seen by humans

and, more importantly from an evolutionary perspective, being spotted by wolf hunters. Second, wolves in the Białowieża Forest kill prey nearly exclusively in the forest (J. Theuerkauf, W. Jędrzejewski & K. Schmidt, unpublished data), probably because prey abundance is higher in the forest than in the surrounding agricultural landscape. Similarly, a radio-tracked wolf avoided arable land and selected forest in Italy (Ciucci et al. 1997). Unlike the situation in the Białowieża Forest, the forest did not provide enough food for the wolves studied by Ciucci et al. (1997), so in that case the cover seems to play the major role. The forest selection is likely to be a result of centuries of persecution by man in Europe (Boitani 1995), which may have favoured wolves that avoided open areas as they could be more easily killed in open areas than in the forest.

Wolves generally avoided human settlements and roads (chapters 5 and 6). The avoidance increased with increasing size of human settlements and increasing use of the roads (chapter 6). Human settlements and traffic on roads produce noise and light, which may explain why wolf avoidance increased with the size of settlements and the intensity of road use. Noise may also be the reason why intensive use of snowmobiles in American national parks increased the physiological stress of wolves (Creel et al. 2002). In Alaska, Thurber et al. (1994) studied the response of wolves to roads and to an area with human settlements at the border of a wildlife refuge. They found that wolves avoided the settled area and a public road but selected little used roads for ease of travel. Wolves therefore seem to only avoid intensively used roads. When the human use is low, wolves use roads as corridors, in which they can travel at higher speed than in the forest (Musiani et al. 1998). In a Canadian area with little human activity on pipeline and seismic lines, wolves were even closer to these lines which acted as corridors than random points (James & Stuart-Smith 2000).

Wolves of the Białowieża Forest selected the strict reserve (50 km<sup>2</sup>) of the national park but did not select small nature reserves of up to 4 km<sup>2</sup> inside the commercial forest (chapter 6). Small reserves therefore appear to be no more suitable for wolves than commercial forests. Wolves also seem to quickly react to newly protected areas. After the enlargement of the Białowieża National Park, wolves immediately began to use this area more frequently and doubled their use of the newly protected area within three years (chapter 6). Besides lower human activity, wolves may select the strict reserve as a better feeding ground because the density of ungulates is much higher in the reserve than in the commercial forest (J. Theuerkauf, S. Rouys & W. Jędrzejewski, unpublished data).

Spatial avoidance is especially important during the denning period, when the nursing female cannot easily escape with the pups. Wolf den and rendezvous sites in the Białowieża Forest were as far as possible from the edge of the forest, villages and public roads, thus in areas where encounters with humans were the least likely (chapter 5). All den and rendezvous sites of the national park pack were in the strict reserve but the packs living in the commercial forest did not use the small reserves of up to 4 km<sup>2</sup> for denning (chapter 5). This indicates that the existence of small nature reserves does not improve the suitability of an area for wolf breeding. In the Superior

National Forest of Minnesota, wolves located their dens randomly throughout their territory and only avoided a 1-km strip at the edge of their territory, probably to minimise confrontation between packs (Ciucci & Mech 1992). It therefore appears that only roads that are intensively used influence the spatial distribution of wolf dens.

Occasional forestry work within 200 m of the den sites did not cause the nursing female to abandon the den (chapter 5). Wolves in our study area have to live at close quarters with human beings, which probably explains why they tolerated forestry work within a close distance of their den. In North America, wolves also tolerated human activity near the den in areas where wolves were protected (Mech et al. 1998, Thiel et al. 1998) whereas they did not tolerate humans nearer than 800 m from the den sites in open tundra where wolves were not protected from hunting (Chapman 1979). As long as the risk of being killed by humans is low, wolves seem to tolerate humans near the den rather than having to move their young, which would probably be more risky for the pups' survival.

### Spatio-temporal segregation of wolves from man

In chapters 3-5, I tested independently the influence of human activity on the temporal patterns and spatial distribution of wolves. It appeared that humans influenced the spatial distribution of wolves but not their temporal patterns of activity. The spatial analyses revealed general trends, but were not sufficient to explain all aspects of the wolves' behaviour. Resting sites of wolves were for example located no further from man-made structures than random sites (chapter 5). A further analysis that would encompass both spatial and temporal aspects simultaneously appeared appropriate to assess the impact of human on wolf behaviour. This combination provided the best insight in how wolves avoided humans and revealed that these avoidance patterns were spatio-temporal.

Home ranges of wolves are large in the Białowieża Forest and exceed 200 km<sup>2</sup> even when only considering locations obtained during daylight (chapter 6). Forestry operations therefore never occur simultaneously in the whole home range, but are concentrated in some places. Wolves avoided the surroundings of places where foresters were working in the day and moved to areas without human presence where they continued their normal activity (chapter 6). This shift to areas unused by humans at that time is the reason why temporal activity patterns of wolves were not influenced by humans (chapters 3 and 4).

The wolves' response to forestry operations is immediate. While wolves avoided zones with forestry operations during working hours, they use these areas at night in the week and during the weekend (chapter 6). The avoidance of humans by wolves is therefore not a static system, but a dynamic one in which wolves temporarily avoid human activity by avoiding areas used by man at that time. This also explains why wolf avoidance of settlements, roads, tourist trails and arable land was stronger in the day than at night (chapter 6). McLellan & Shackleton (1988) found a similar spatio-

temporal avoidance of humans for grizzly bears, which used roads at night but avoided them in the day.

In mammalian predator-prey systems, the fear of predators plays an important role in shaping the behaviour of the prey (Brown et al. 1999). Under high levels of predation, prey species are very vigilant. After a reduction of predators, the prey will rapidly become less wary (Brown et al. 1999). It is likely that human-wolf relationships follow the same principle. Wolves under heavy persecution would thus be more alert and therefore less visible to humans. This does not necessarily mean that wolves would become nocturnal, because they can spatio-temporally avoid contact with humans. The forest appeared of particular importance in spatio-temporal segregation as wolves rarely left its cover in daylight in the Białowieża Forest (chapter 6) and in Italy (Zimen 1993, Ciucci et al. 1997). In areas frequented by people, wolves therefore seem able to maintain their activity during the day by taking advantage of the cover available in the forest. Interestingly, of all the wolves in the Białowieża Forest, those living in the Białowieża National Park avoided man-made structures the most (chapter 6). The difference between the day-time and the night-time avoidance shown by the National Park pack was greatest in winter, when human activity in the pack's home range was lowest (chapter 6). It therefore seems that wolves that are not hunted are most sensitive to human activity when they have least contact with humans, which means that wolves habituate to some degree to human activity.

Spatio-temporal segregation appeared to be a strategy of wolves to co-exist with man in the Białowieża Forest. But can this mechanism be generalised to wolves living in other regions? From an evolutionary perspective, wolves should have evolved similar behavioural adaptations under similar conditions. This evolution must however have taken place independently in the different wolf metapopulations, as these were not in contact with each other in historical times (at least North American and Eurasian wolves). It is likely that in all regions where wolves were persecuted, selection has favoured those individuals that avoided humans efficiently without failing to explore the available food resources. I therefore expect that the spatio-temporal habitat use of wolves is generally adapted to human activity except in regions where they have not been persecuted. I believe that in forested areas where wolves prey on wild ungulates and co-exist with humans, wolves should spatio-temporally avoid humans. It would however be desirable to verify this statement in other wolf studies that have data allowing a spatio-temporal analysis.

### Conclusions

In the Białowieża Forest, human activity did not significantly influence temporal patterns of wolf movements (chapter 3) and activity (chapter 4). A spatial analysis revealed a response of wolves to human settlements, roads and arable land (chapter 5). The mechanism of avoidance behaviour became most clear when analysing the spatio-temporal relationship between wolves and man (chapter 6).

I conclude that spatio-temporal avoidance of humans is a behavioural adaptation of wolves, which allows the co-existence of wolf and man while minimising the chance of encounters. Forest plays an important role in this segregation as it provides cover that allows wolves to be active during daylight. The segregation can be more spatial in regions of low wolf density or in areas which wolves recolonise, as wolves have more opportunity to retire to areas of low human density. The distribution of forest, human settlements, intensively used public roads, and areas with restricted human access are the main factors determining the locations of a wolf pack's activity centres and home range. Activity patterns of wolves are probably optimised towards food acquisition rather than being shaped by human activity. However, wolves can become nocturnal in regions where the main food resources are close to human settlements or in landscapes without sufficient cover. Wolves are also able to habituate to human presence and are less sensitive to human activity when they have more contact with humans.

#### 7.2 Implications for wolf conservation and management

#### Human disturbance

Wolves are protected in many European countries by the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats) of 1979 and within the European Union by the Habitat Directive of 1992. In the USA (without Alaska), the Endangered Species Act of 1973 protects wolves. The status of wolves as protected species also implies their protection from human disturbance. As the term disturbance is ambiguous (Stock et al. 1994), it is necessary to define the circumstances under which human activity can be considered a disturbance. On the species level, disturbance is important if it affects survival and causes a population to decline (Gill et al. 2001). Applying this definition, a disturbance to wolves would be mainly restricted to direct persecution such as poaching, accidental killing (by traps set for other wildlife) and taking pups from the dens. On the behavioural level, the definition of disturbance would also apply if human activity caused breeding females to permanently abandon their young, which would result in their death.

Considering that wolves are flexible in their habitat selection, the protection of particular habitat types that wolves may select for denning does not appear necessary (chapter 5). Protecting an area that may or may not be used for dens would anyway be impractical, unless breeding females are fitted with radio-collars. However, should a den in use be found by chance, it would be desirable for the area around the den to be free of human use (e.g. forestry operations) during the denning period. The Michigan (Weise et al. 1997) and the Wisconsin (Wydeven et al. 1999) wolf management plans recommend that an area of 800 m around den and rendezvous sites should not be used by humans during the denning period. I do not think that the protection of such a large area is necessary for wolves in most European regions. It would however be desirable

for an area of at least 200 m (chapters 2 and 5) around the den to be protected from human use during the denning period.

Provided the protection of wolves is desired in areas being recolonised by wolves, wildlife managers may be concerned that human disturbance could negatively affect wolf survival. They may accordingly consider restricting human access within the home ranges of newly established wolf packs. However, human activity should not be regarded as a synonym of disturbance. Considering the ability of wolves to cope with human activity within their home ranges (chapter 6), the absence of people appears unnecessary. Allowing humans to visit areas colonised by wolves may even improve the wolves' acceptance by the public because people that are accustomed to wolves usually fear them much less than others. Furthermore, many people may not appreciate a restriction on where they can go, which could promote an anti-wolf attitude that should be avoided.

Forestry operations in commercial forests or tourists' use of roads and trails in reserves do not generally represent a disturbance for wolves. Human disturbance should also be no reason not to radio-track wolves. In the Białowieża Forest, radio-tracking did not affect the behaviour of wolves significantly (chapter 2). Since this technique is an important tool for the conservation of wildlife (Mech & Barber 2002), the recovering populations should be studied by radio-tracking in order to monitor the wolf population and its further evolution. The future of a wolf population will primarily depend on the intensity of legal or illegal killing of wolves but not on non-lethal human disturbance.

### Habitat fragmentation

Fuller (1995) suggested that clusters of 2-3 wolf packs represent the minimal number of packs necessary to support a viable population. He estimated that the necessary area for such a wolf subpopulation was about 500 km<sup>2</sup> in the USA. Home ranges of Eurasian wolves are mostly between 100 and 300 km<sup>2</sup> (Okarma et al. 1998), which would also result in a necessary area of about 500 km<sup>2</sup> for 2-3 packs. In both Europe and the USA, wolves are increasingly recolonising landscapes that have been modified by human use (Mech 1995, Boitani 2000). As a result, wildlife managers are faced with the issue of whether these sometimes highly fragmented landscapes will prove suitable for a wolf subpopulation. In California, coyotes showed a high behavioural plasticity in respect to habitat fragmentation (Crooks 2002). I expect that wolves are also able to cope with habitat fragmentation.

The results of this research showed that wolves can cope with human activity in a commercial forest without being disturbed (chapters 3-6). Commercial forests of about 500 km<sup>2</sup> may therefore be sufficient for a wolf subpopulation, provided there is enough prey and that wolves are not excessively persecuted (Fritts et al. 1994). It is however important to know the extent to which the forest can be fragmented before it is no longer suitable. It appears that the tolerance to forest fragmentation can be high, as for example observed in the Bieszczady Mountains (Southeast Poland). The home range of

a wolf pack in this region mainly consisted of two fragments of commercial forest (about 30 and 50 km<sup>2</sup>, respectively), divided by a 1-2 km wide stripe of arable land with public roads and villages (R. Gula, B. Pirga, S. Rouys & J. Theuerkauf, unpublished data). The necessary area for a wolf population could therefore also consist of several small blocks of forest within agricultural landscapes. However, the fragmentation of forest may expose wolves to a higher risk of being killed as the area is thereby more easily accessible to humans. The survival chances of wolves would therefore mainly depend on the public acceptance rather than on the habitat characteristics. The issue of accessibility leads finally to the influence of roads on wolf survival.

# Impact of roads on wolves

In the USA, a road density of about 0.6-0.7 km/km<sup>2</sup> was regarded as a threshold for wolf occurrence (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Mech 1989). Road density was therefore a major factor used to predict suitable habitats for wolves in the USA and Italy (Mladenoff et al. 1995, Mladenoff & Sickley 1998, Mladenoff et al. 1999, Corsi et al. 1999). A road density threshold is however not universally applicable because it is an indicator of many factors affecting wolf survival, which may vary in different regions. Road density represents the accessibility of an area and comprises road accidents, which depend on the intensity of road use, but also poaching or hunting, which depend greatly on the attitude of people towards wolves. Although road density is high in the Białowieża Forest (1.2 km/km<sup>2</sup>) and many wolf casualties are caused by humans (Jędrzejewska et al. 1996), wolves co-exist with man without even changing their activity patterns (chapters 3 and 4). Similarly, Merrill (2000) reported that a wolf pack in Minnesota survived in a military training area with a road density of 1.4 km/km<sup>2</sup>. It is therefore likely that wolves will recolonise areas of increasingly high road density if they are not persecuted.

Intensively used motorways may be a barrier to the dispersal of wolves into suitable areas. The main problem will not be so much wolf avoidance of motorways but rather road casualties. However, in Minnesota only about 10% of human-caused mortality was due to traffic accidents (Fuller 1989). Merrill & Mech (2000) even showed that wolves crossed highways up to over 200 times without being killed. In Wisconsin, Kohn et al. (1999) assessed the impact of a four-lane highway with about 5000 vehicles per day on wolf survival and dispersal. Their preliminary data did not indicate that the highway acted as a barrier for the dispersal of wolves. Additionally, migrating wolves were more careful in crossing the road than resident wolves (Kohn et al. 1999). In Europe where motorways are usually more intensively used, the mortality of wolves crossing motorways will probably be more important. However, in the last few decades, several wolves coming from Poland crossed large parts of northern Germany before they got shot (Promberger et al. 1993a). During their travel, they must have crossed heavily used motorways several times. Motorways will therefore slow down wolf recovery rather than totally preventing it. However, I expect that

recolonising wolves will settle first in areas that are at maximal distance to intensively used roads, as found in the Białowieża Forest (chapters 5 and 6).

# Suitable areas for wolf recovery

Wolves can adapt to human activity (chapters 3-6) and survive in any landscape provided they find enough food and humans do not increase wolf mortality rates to over 30-40% per year (Peterson et al. 1984, Ballard et al. 1987, Haight et al. 1998, Larivière et al. 2000). The identification of suitable areas for wolf recovery is, therefore, not so much a question of determining the habitats in which wolves are able to live, but rather of predicting the habitats they will recolonise first. Large commercial forests with sufficient prey are a suitable wolf habitat. In those forests that wolves will recolonise, game managers should consider predation by wolves when planning hunting quotas to avoid overexploitation of game populations. I expect that wolves will first recolonise areas where human access is restricted, which limits the risk of wolves being killed. These could be large nature reserves and national parks, but also areas that are naturally difficult to access (e.g. mountains or state border zones). Settling in such areas will also cause less conflict with humans than would colonising agricultural landscapes.

There are about 270,000 km<sup>2</sup> of national parks and preserves in the USA (Fritts & Carbyn 1995), but only about 60 European national parks of IUCN category II (protected area managed mainly for ecosystem conservation and recreation) are larger than 500 km<sup>2</sup> (Knapp et al. 1998), which represents the area necessary for a wolf subpopulation (see chapter Habitat fragmentation). However, most of the category II national parks are in the European part of Russia (41,500 km<sup>2</sup>), Norway (23,300 km<sup>2</sup>), Italy (11,700 km<sup>2</sup>) and Romania (8,400 km<sup>2</sup>). All these countries except Norway have established wolf populations. Wolves began recolonising Norway in the 1980s (Promberger et al. 1993b), but there are still only about 3 wolf packs in the southeastern part of the country near the border with Sweden (Aronson et al. 2001). The protected area in other countries that are currently experiencing wolf recovery is much less than in Norway. Whereas France has about 2,800 km<sup>2</sup> protected in 5 category II national parks, Germany (450 km<sup>2</sup>) and Switzerland (170 km<sup>2</sup>) have little protected area (Knapp et al. 1998). However, protected areas that are not large enough to contain a viable wolf population may serve as core areas for wolves provided that these areas are surrounded by buffer zones where wolves may be managed (Gula & Perzanowski 2002). A strict reserve of 50 km<sup>2</sup> can already act as a core area for a wolf pack (chapter 6). National parks of over 50 km<sup>2</sup> may therefore play an important role as stepping stones in wolf recovery. Small reserves of a few square kilometres will however have no importance for wolves (chapter 6). The existence of nature reserves could also be an advantage for wolves because sport or commercial hunting is often prohibited in reserves. The resulting higher densities of wild ungulates in such reserves improve the nutritional situation for wolves and may reduce depredation to livestock (Meriggi & Lovari 1996). Such nature reserves could additionally be important for wolf reproduction, as suitable sites for wolf dens are likely to be at a maximal distance to the forest edge, human settlements, and intensively used public roads (chapter 5). It is thus not astonishing that the first area that wolves colonised in France was the Mercantour National Park (protected core area: 685 km<sup>2</sup>) at the border to Italy (Poulle et al. 1997).

Military training areas may also prove particularly suitable for wolves. This could be especially important for countries with little protected area. For example, Germany has only 450 km<sup>2</sup> of category II national parks (Knapp et al. 1998), whereas about 4,000 km<sup>2</sup> of forest lie in military training areas (Forstverwaltungen des Bundes und der Länder, www.wald-online.de). Furthermore, many former military training areas in eastern Germany have now become nature reserves and could play an important role in the wolf recovery. Even military training areas that are still in use provide suitable habitats, as wolves are able to live spatio-temporally separated from man. These military training areas, which are only partially used and usually include large forested areas, appear particularly appropriate for wolf den sites. Training areas that are still in use have the additional advantage that they are often closed to public access, which could reduce the risk of wolves being poached. Interestingly, the first wolf pack to establish and breed in Germany settled into a functioning military training area (145 km<sup>2</sup>) near the border to Poland (Bundesforstamt Muskauer Heide 2001).

# Wolf conservation and wolf control

The determining factor in wolf conservation is public acceptance (Boitani 1995). Increased public acceptance has already resulted in wolves expanding their ranges in Europe and North America (Promberger & Schröder 1993, Mech 1995, Boitani 2000). The human dimension issue in wolf conservation is however complex (Bath 1989, Bath & Buchanan 1989, Boitani 1995, Bath 1996, Lohr et al. 1996, Pate et al. 1996, Bath 2000) and a complete discussion would be beyond the scope of my research. Knowledge on the impact of humans on wolf behaviour can help predict wolf behaviour in anthropogenic landscapes and identifying areas that wolves are most likely to recolonise. However, the decision of whether wolves will survive or not lies with the local population. Wolves may recolonise many of the areas from which they were extirpated provided the public accepts a co-existence with them. If however even parts of a local community do not accept the presence of wolves, legal protection will have little impact. In the Bieszczady Mountains, for example, following the full protection of wolves in 1998, the number of illegal killings increased (Okarma 2002). Thus the legal protection did not prevent wolves from being killed, but resulted in uncontrolled poaching and unknown numbers of killed animals. Therefore, wolf conservation can sometimes have more success when it is combined with an organised sustainable wolf control.

People living in regions to which wolves migrate may however worry that wolves living close to humans could lose their fear of man and become dangerous. In Denali National Park in Alaska, wolves began approaching campers to steal food (Linnell et al. 2002). Under extreme conditions, humans may even become prey for wolves. This occurred in India, where in some regions wolves co-exist with up to 600 humans per km<sup>2</sup> and unattended children may be the most easy and available prey for wolves (Jhala & Sharma 1997, Rajpurohit 1999). Predation on humans is usually done by few wolves that have lost their fear of man and learned to consider humans as prey. The immediate elimination of such wolves is obviously necessary, as was done in India. In most of the wolf range, the risk of wolf attacks is however very low (Linnell et al. 2002). I expect that wolves will keep their fear of man in most regions where wolves co-exist with people because there will always be some human-caused mortality, even in a protected population.

Considering the ability of wolves to cope with human activity, it appears that the most important task of wolf management for the future will not be to improve the habitat quality for wolves in regions where their recovery is possible, but to be prepared to deal with the consequences of wolf recovery. This will mainly involve achieving public acceptance, implementing measures to minimise depredations to livestock, and taking wolf predation on wild ungulates into consideration when planning hunting quotas for game management (for more details see Mech 1995 and Boitani 2000). Key elements for the success of wolf recovery will be to inform the public about the capacity of wolves to live in agricultural landscapes as well as to achieve the co-operation of hunters, farmers, foresters, wolf advocates, and scientists when establishing wolf management goals.

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### SUMMARY

Knowledge on the impact of human activity on wolf behaviour is important to assess the capacity of wolves to coexist with man. I therefore aimed at finding out if humans affect the activity rhythm or spatial distribution of radio-collared wolves in the Białowieża Forest (East Poland). In five articles (chapters 2-6), I addressed the five main questions:

- Do radio-trackers influence wolf behaviour?
- Does human activity reduce the daytime movements of wolves?
- Do humans modify the activity patterns of wolves?
- Do wolves select areas of low human activity for resting and raising young?
- Do wolves spatio-temporally avoid contact with man?

The objective of chapter 2 was to assess the reliability of the radio-tracking method and to test if the presence of radio-trackers influences wolf activity and movements. I therefore compared different radio-tracking methods of estimating activity and the reaction of wolves to various distances between the radio-tracker and the wolf. The radio-tracking method used in this research provided a representative estimate for daily patterns of wolf activity. The trackers had no detectable influence on activity and movements of wolves when the tracker-wolf distance was greater than 200 m. There was a small but non-significant influence if trackers were less than 200 m away from wolves during the day.

In chapter 3, I compared daily patterns of human activity with daily movement patterns of wolves in the Białowieża National Park and in the commercial part of the Białowieża Forest to assess if human activity can reduce the daytime movements of wolves. The daily movement patterns of wolves living in the commercial part of the Białowieża Forest with high human activity were negatively correlated with the activity pattern of humans. During the time of maximum human presence, there was however no difference in movements between wolves from the national park, where human activity was low, and those from the commercial forest. I concluded that human activity may have affected the wolves' movement pattern but that the influence was not strong enough to reduce significantly the wolves' daytime movements.

The aim of chapter 4 was to assess the influence of various factors on the temporal patterns of wolf activity. I analysed the influence of human activity, hunting by wolves, the reproductive period, and weather conditions on the daily activity patterns of wolves. Wolves were active throughout the day but their activity peaked at dawn and dusk, when they also killed most of their prey. The reproduction period and high temperatures had a less pronounced effect on the wolves' activity patterns. Human activity and other factors did not significantly affect the wolves' daily activity patterns. I concluded that the daily activity patterns of wolves were mainly adjusted towards food acquisition. An indirect influence of human hunters who may modify the activity patterns of prey, and thus that of wolves, cannot be ruled out.

Chapter 5 focused on assessing wolf selection of den, rendezvous and resting sites in relation to habitat and human proximity. I compared habitats and locations of sites used by wolves with random points in the forest. Den and rendezvous sites were located as far as possible from the forest edge, human settlements, and intensively used roads. Locations of resting sites were not affected by these man-made structures. Wolves selected dry coniferous forests for den sites, but also used other forest types. The suitability of an area for wolf breeding appeared to depend mainly on the spatial distribution of forest, human settlements and public roads and to a lesser extent on habitat characteristics.

Separate analyses of temporal and spatial aspects did not explain all wolf reactions to human activity (chapter 3-5). The aim of chapter 6 was therefore to test the hypothesis that wolves live spatio-temporally segregated from man. I compared the spatial distribution of radio-locations of wolves with that of random points for different parts of the day to determine whether wolves temporarily avoided man-made structures (settlements, edge between forest and arable land, roads, tourist trails). I also compared human activity around wolf locations with that of forest parts from which wolves were absent at that time to estimate how wolves deal with human activity in the forest (e.g. forestry operations, traffic). Wolves avoided man-made structures considerably more in the day than at night. The avoidance increased with increasing human use. Particularly large settlements and intensively used public roads reduced the area used by wolves. Wolves avoided human presence in the forest by a temporary selection of areas from which humans were absent. One of the wolf packs selected the strict reserve (50 km<sup>2</sup>) of the Białowieża National Park as core area of its home range in the day and at night, whereas wolf packs living in a commercial forest with small nature reserves (up to 4 km<sup>2</sup>) did not select these reserves at any time.

I conclude that spatio-temporal avoidance of humans is a behavioural adaptation of wolves allowing wolves to co-exist with man whilst keeping their activity patterns optimised towards food acquisition. The segregation of wolves from man can be more spatial in regions of low wolf densities as wolves can retire to areas of low human density. The distribution of forest, human settlements, intensively used public roads, and areas with restricted human access mainly determine the areas in which wolves live. Nature reserves of at least 50 km<sup>2</sup> are especially suitable for wolves, but small reserves of a few square kilometres will not improve the habitat suitability for wolves.

# ZUSAMMENFASSUNG

#### [Einfluss des Menschen auf das Verhalten von Wölfen im Białowieża-Wald, Polen]

Die Kenntnis über den Einfluss menschlicher Aktivität auf das Verhalten von Wölfen ist nötig um einschätzen zu können, unter welchen Bedingungen Wölfe in der Lage sind in Koexistenz mit Menschen zu leben. Mein Ziel war es deshalb herauszufinden, ob Menschen den Aktivitätsrhythmus oder die räumliche Verteilung telemetrierter Wölfe im Białowieża-Wald (Ostpolen) beeinflussen. In fünf Artikeln (Kapitel 2-6) habe ich die folgenden Fragen behandelt:

- Beeinflusst die Telemetrie das Verhalten der Wölfe?
- Schränkt menschliche Aktivität die Standortveränderungen der Wölfe ein?
- Beeinflussen Menschen den Aktivitätsrhythmus der Wölfe?
- Bevorzugen Wölfe für Ruheplätze und Welpenaufzucht Gebiete mit niedriger menschlicher Aktivität?
- Meiden Wölfe den Kontakt mit Menschen räumlich-zeitlich?

Das Ziel in Kapitel 2 war es, die Verlässlichkeit der Telemetrie zu bestimmen und ob die Anwesenheit der Telemetrierer die Aktivität und Standortveränderungen der Wölfe beeinflusst. Hierfür habe ich verschiedene Methoden zur Einschätzung der Aktivität mit Hilfe der Telemetrie und die Reaktion der Wölfe bei verschieden Abständen zwischen Telemetrierern und Wölfen verglichen. Die in dieser Studie verwendete Telemetriemethode ermöglichte eine repräsentative Schätzung der Aktivitätsrhythmen der Wölfe. Die Telemetrierer hatten keinen erkennbaren Einfluss auf die Aktivität und Standortveränderungen der Wölfe, solange der Abstand zwischen Telemetrierern und Wolf größer als 200 m war. Am Tage gab es einen kleinen, aber nicht signifikanten Einfluss, wenn die Entfernung zwischen Telemetrierer und Wolf kleiner als 200 m war.

In Kapitel 3 habe ich Tagesrhythmen von Menschen mit Tagesrhythmen der Standortveränderungen von Wölfen im Białowieża-Nationalpark und im bewirtschafteten Teil des Białowieża-Waldes verglichen, um einzuschätzen, ob menschliche Aktivität die Standortveränderungen der Wölfe am Tage einschränken. Die Tagesrhythmen der Standortveränderungen von im Wirtschaftswald mit hoher menschlicher Aktivität lebenden Wölfen waren negativ mit den Aktivitätsrhythmen von Menschen korreliert. Zur Tageszeit maximaler menschlicher Präsenz gab es jedoch keine Unterschiede im Ausmaß der Standortveränderungen zwischen Wölfen aus dem Nationalpark mit niedriger menschlicher Aktivität und dem Wirtschaftswald. Dies bedeutet, dass menschliche Aktivität die Tagesrhythmen der Standortveränderungen von Wölfen möglicherweise beeinflussen, aber der Einfluss nicht stark genug ist, um Standortveränderungen am Tage signifikant zu vermindern.

Das Ziel in Kapitel 4 war es, den Einfluss verschiedener Faktoren auf Aktivitätsrhythmen von Wölfen einzuschätzen. Hierzu habe ich die Wirkung menschlicher Aktivität, der Jagd nach Beute, der Saison der Welpenaufzucht und der Witterung auf die Aktivitätsrhythmen von Wölfen analysiert. Die untersuchten Wölfe waren zu jeder Tageszeit aktiv, die Aktivitätsspitzen lagen jedoch bei Sonnenaufgang und Sonnenuntergang. Während der Dämmerungsphasen rissen Wölfe auch die meisten Beutetiere. Die Saison der Welpenaufzucht und hohe Temperaturen hatten einen weniger deutlichen Einfluss auf die Aktivitätsrhythmen. Menschliche Aktivität und andere Faktoren beeinflussten die Aktivitätsrhythmen der Wölfe nicht erkennbar. Der Aktivitätsrhythmus der Wölfe scheint deshalb hauptsächlich durch die Jagd nach Beute geprägt zu sein. Es ist jedoch nicht ausgeschlossen, dass der Einfluss von Menschen indirekt sein kann, wenn Menschen die Aktivitätsrhythmen von Beutetieren durch Bejagung verändern.

Das Ziel in Kapitel 5 war zu bestimmen, wie Wölfe ihre Wurf-, Rendezvous- und Ruheplätze hinsichtlich der Habitatbeschaffenheit und Nähe des Menschen auswählen. Hierzu habe ich Habitatstrukturen und Lage solcher Plätze mit denen von Zufallspunkten im Wald verglichen. Wurf- und Rendezvousplätze befanden sich so weit wie möglich entfernt von Waldrand, Siedlungen und intensiv genutzten Straßen. Diese von Menschen geschaffenen Strukturen beeinflussten die Lage von Ruheplätzen nicht. Die Wölfe bevorzugten trockene Nadelwälder zum Anlegen der Höhlen, nutzen aber auch andere Waldtypen für die Welpenaufzucht. Die Eignung eines Gebietes für die Aufzucht von Welpen scheint deshalb in erster Linie von der räumlichen Verteilung des Waldes, der Siedlungen und der öffentlichen Straßen abzuhängen und in zweiter Linie von der Habitatbeschaffenheit.

Ohne Berücksichtigung gemeinsamer Effekte erklärten die Analysen zeitlicher und räumlicher Aspekte nicht alle Reaktionen der Wölfe auf menschliche Aktivität (Kapitel 3-5). Deshalb testete ich in Kapitel 6 die Hypothese, dass Wölfe räumlichzeitlich vom Menschen getrennt leben. Um zu überprüfen, ob Wölfe permanente vom Menschen geschaffene Strukturen (Siedlungen, Grenze zwischen Wald und Agrarland, Straßen, Wanderpfade) zeitweise meiden, habe ich die räumliche Verteilung der Lokalisierungen von Wölfen mit der von zufallsverteilten Punkten für verschiedene Tagesabschnitte verglichen. Um einzuschätzen, wie Wölfe auf Aktivität von Menschen im Wald (z. B. Forstarbeiten, Verkehr) reagieren, habe ich die Aktivität von Menschen in der Umgebung der Wölfe mit der von Waldteilen verglichen, in denen Wölfe zur gegebenen Zeit abwesend waren. Die Wölfe mieden vom Menschen geschaffene Strukturen mehr am Tag als in der Nacht. Je stärker die Nutzung durch Menschen war, um so mehr mieden Wölfe die Struktur. Vor allem große Siedlungen und intensiv genutzte öffentliche Straßen reduzierten das von Wölfen genutzte Gebiet. Die Wölfe mieden zeitweise Anwesenheit von Menschen im Wald dadurch, dass sie Gebiete aufsuchten, in denen sich zur gegebenen Zeit keine Menschen aufhielten. Ein Wolfsrudel bevorzugte das Totalreservat (50 km<sup>2</sup>) des Białowieża-Nationalparks als Kerngebiet seines Streifgebietes am Tage und in der Nacht. Wolfsrudel, die im Wirtschaftswald mit kleinen Naturschutzgebieten (bis 4 km<sup>2</sup>) lebten, bevorzugten dagegen Naturschutzgebiete weder am Tage, noch in der Nacht.

Ich schließe aus den Ergebnissen meiner Studie, dass die räumlich-zeitliche Meidung des Menschen eine Verhaltensanpassung ist, die Wölfen ermöglicht im gleichen Gebiet mit Menschen zu leben und ihren Aktivitätsrhythmus auf den Nahrungserwerb hin zu optimieren. Die Trennung der Wölfe vom Menschen kann in Gebieten mit niedriger Wolfsdichte stärker räumlich geprägt sein, da Wölfe die Möglichkeit haben sich auf Gebiete mit niedrigerer Siedlungsdichte von Menschen zu beschränken. Die räumlichen Verteilungen von Wald, Siedlungen, intensiv genutzten Straßen und Gebieten mit eingeschränktem Zugang für Menschen bestimmen hauptsächlich, welche Gebiete Wölfe besiedeln. Schutzgebiete von mindestens 50 km<sup>2</sup> Größe stellen geeignete Lebensräume dar, wohingegen kleine Schutzgebiete von wenigen Quadratkilometern Größe die Habitateignung für Wölfe nicht verbessern.

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