ORIGINAL ARTICLE

Marta Kołodziej-Sobocińska · Andrzej Zalewski Rafał Kowalczyk

Sarcoptic mange vulnerability in carnivores of the Białowieża Primeval Forest, Poland: underlying determinant factors

Received: 24 July 2013 / Accepted: 8 December 2013 / Published online: 24 December 2013 © The Author(s) 2013. This article is published with open access at Springerlink.com

Abstract Sarcoptic mange caused by *Sarcoptes scabiei*, is a highly contagious worldwide mite infection responsible for epizootic skin disease in populations of wild and domestic mammals. It causes skin disorders that may lead to severe generalized skin disease (mange). We investigated the spread and dynamics of sarcoptic mange in one of the best preserved carnivore communities in the Białowieża Primeval Forest over the last 20 years. Sarcoptic mange was found in 6 of 10 investigated species. The highest percentage of infected individuals was recorded in red foxes (19 %), European badgers (9 %), grey wolves (7 %), raccoon dogs (6 %), and stone martens (5 %). Other species were not infected (least weasel, American mink, European polecat, pine marten) or infected sporadically (Eurasian lynx—1 case). Rate of infection was correlated with the sum of ecological and behavioral features, which may increase the spread of infection. Outbreaks of sarcoptic mange occurred simultaneously in several species of carnivores, which indicates the occurrence of between species transmission. We found that the source of investigated individuals (trapped, culled and found dead) may influence the results of the analysis. Our study shows that in carnivore communities such as in Białowieża Forest, numerous species may serve as a reservoir of the pathogen and favor its persistence in the environment. This study indicates that sociality and use of den sites are important factors affecting sarcoptic mange spread and prevalence in wild populations of carnivores.

Keywords Sarcoptes scabiei · Vulpes vulpes Carnivores · Ectoparasite · Epizootic outbreak

M. Kołodziej-Sobocińska (⋈) · A. Zalewski · R. Kowalczyk Mammal Research Institute, Polish Academy of Sciences,

Waszkiewicza 1, 17-230 Białowieża, Poland E-mail: mksobocinska@ibs.bialowieza.pl

Tel.: +48-85-6827750 Fax: +48-85-6827752

Introduction

Skin lesions in wildlife can be caused by several parasitic arthropod species such as Sarcoptes sp., Notoedres sp., Chorioptes sp. and Psoroptes sp. Sarcoptic mange caused by mites, Sarcoptes scabiei (L, 1758, Latrielle, 1802) (Acari: Astigmata, Sarcoptidae), is a highly contagious skin disease with a world-wide distribution and is observed most frequently in mammals. It has been found in 104 domestic and wild species in Europe, North America, Australia and Africa (Bornstein et al. 2001). In Europe, S. scabiei infections have been detected in red foxes (Vulpes vulpes), arctic foxes (Alopex lagopus), grey wolves (Canis lupus), Eurasian lynx (Lynx lynx), European badgers (Meles meles), raccoon dogs (Nyctereutes procyonoides), pine martens (Martes martes), stone martens (Martes foina) (Holt and Berg 1990; Mörner 1992; Gortázar et al. 1998; Bornstein et al. 2001; Ryser-Degiorgis et al. 2002; Nowak et al. 2008), as well as in domestic dogs (Canis lupus familiaris) and cats (Felix silvestris catus) (Lindquist and Cash 1973; Hawkins et al. 1987; Bornstein et al. 2004). Mange is transmitted by direct contact between animals or indirectly through using the same sites as infected hosts. Direct transfer of S. scabiei to an uninfected host is possible where larvae and nymphs wander on the skin surface (Arlian and Vyszenski-Moher 1988). Alternatively, indirect transfer of the pathogen, for example from common nests or burrows, is possible as mites are able to survive independently from a host and remain infectious for a new host individual (Arlian 1989); for example, S. scabiei transmission was observed amongst red foxes occupying the same den even if they did not use it simultaneously (Gerasimov 1958). The transmission of sarcoptic mange in wildlife also appears to be density-dependent; at higher population densities, a higher prevalence of mange was observed (Pence and Windberg 1994; Skerratt et al. 1998). Heavily infected individuals suffer hyperkeratosis, alopecia and general wasting (Burgess 1994; Newman et al. 2002). Death may be caused by a wide variety of factors including starvation and hypothermia (Arlian et al. 1990).

The epizootiology of S. scabiei infection in wildlife depends on the geographical area and the host populations, and sarcoptic mange may have a significant impact on wild animals (Lindström 1992; Henriksen et al. 1993; Martin et al. 1998; Kalema-Zikusoka et al. 2002). The short-term effects of mange epizootic were observed after its transmission to the naïve host population of red foxes in Fennoscandia in the 1960s and 1970s. Mortality of up to 90 % was observed in some areas and it was not until the late 1980s that the population eventually began to recover (Mörner 1992; Lindström et al. 1994). In remnant or isolated populations severe mange outbreaks can have a much more serious effect and cause extinction of populations as recorded in red foxes on a Danish island (Henriksen et al. 1993). Sarcoptic mange outbreaks also pose a threat to endangered species such as chamois (Rupicapra rupicapra) and ibex (Capra ibex) in the southern European Alps (Rossi et al. 1995; Fernandez-Moran et al. 1997), wombats (Vombatus ursinus) in Australia (Martin et al. 1998), and the mountain gorilla (Gorilla berengei berengei) in Africa (Kalema-Zikusoka et al. 2002).

On the contrary, sarcoptic mange does not seem to have any severe effects on red fox populations in other European countries such as Ukraine, Spain or Germany (Gerasimov 1958; Gortázar et al. 1998). Investigations based on the long-lasting epidemic among wild animals have shown evidence of parasite-host adaptation as the parasite has occurred in hosts as non-fatal, restricted or subclinical infections (Mörner and Christensson 1984; Pence and Windberg 1994). There is also evidence that foxes may recover from sarcoptic mange (Storm et al. 1976). The recovery from small *S. scabiei* burdens has also been confirmed in experimentally infected dogs as the development of immunity was observed (Arlian et al. 1996, 1997).

Numerous papers describe the epizootiology of *S. scabiei* in one or two species in a particular area; however, the epizootiology of *S. scabiei* is rarely investigated in a whole carnivore community. The Białowieża Primeval Forest (BPF) has one of the most abundant and best preserved European carnivore communities of 12 carnivore species—10 native and 2 introduced—providing ideal conditions for this investigation. Most carnivores inhabiting BPF exist at moderate to high numbers and are shaped mainly by natural factors (e.g., food abundance) and a network of intra- and interspecies interactions such as intra-guild predation, shared use of space and den sites (Jędrzejewska and Jędrzejewski 1998; Zalewski 2007; Kowalczyk et al. 2008, 2009; Schmidt et al. 2009).

The aim of this paper is the long-term analysis of sarcoptic mange in a multi-species community of carnivores in natural conditions of a large forest area; as well as the examination of factors that increase susceptibility to mange infection at a local and geographical scale. We hypothesized that sociality and long-term use of den

sites increase transmission and prevalence of sarcoptic mange in carnivores.

Study area

The study was conducted in the Polish part (595 km²) of the Białowieża Primeval Forest (52°30′–53°00′N, 23°30′–24°15′E) located on the Polish-Belarusian border. It is one of the best preserved temperate lowland forests in Europe. Coniferous and mixed forests (mainly pine *Pinus silvestris* and spruce *Picea abies*, with admixtures of birch *Betula verrucosa* and *B. pendula*, aspen *Populus tremula*, and oak *Quercus robur*) cover 62 % of the area, wet alder-ash forests (black alder *Alnus glutinosa*, ash *Fraxinus excelsior*, rarely elms *Ulmus* spp.) cover 18 %, rich deciduous forests (oak, hornbeam *Carpinus betulus*, lime *Tilia cordata*, maple *Acer platanoides*) cover 14 %, and open habitats 6 % (Jędrzejewska and Jędrzejewski 1998).

The only large human settlement localized in the Forest is Białowieża village with 2,300 inhabitants. There are several other small settlements within the forest area (up to 100 inhabitants), but most of the human settlements are localized out of the forest.

The climate of BPF is transitional between Atlantic and continental types with clearly marked cold and warm seasons. The mean annual temperature is +7 °C. In January mean temperatures are approximately -4.8 °C and in July approximately +18.4 °C. The range of daily temperatures varies from -33.4 to +33.4 °C. The vegetative season lasts, on average, 208 days. Snow cover persists for an average of 86 days per year (range 61–137) with a maximum recorded depth of 95 cm. Mean annual precipitation is 639 mm (Jędrzejewska and Jędrzejewski 1998).

The BPF is inhabited by a rich community of carnivores, which includes altogether 12 species—10 native and 2 introduced. The raccoon dog colonized BPF from the east and was first recorded in the early 1950s (Bunevich and Dackevich 1985). The second alien species in BPF is American mink (*Neovison vison*), which was first recorded in 1972 (Ruprecht et al. 1983).

Methods

Between 1994 and 2013, all carnivores that were trapped (mainly for radio-collaring), culled by local hunters or found dead were inspected for presence of sarcoptic mange and skin disorders. An individual was recorded as being positive for infection with *S. scabiei* based on the presence of visible, hairless lesions, hyperkeratosis and crusting dermatitis (Pence and Ueckermann 2002; Almberg et al. 2012). Twenty percent of specimens of different species were investigated clinically by a vet to confirm mange presence or absence based on skin changes and microscopic investigation of skin scrapings. Sarcoptic mange was confirmed in all veterinary

investigated specimens. We assumed that the presence or absence of clinical signs of mange reflected an individual's infection status; however, the possibility of asymptomatic or early infection before clinical signs have occurred cannot be ruled out. In total, 680 individuals of 10 species were investigated (Table 1). Due to a very low number of individuals, stoat (*Mustela erminea*) and European otter (*Lutra lutra*) were not involved in the analysis.

Hierarchical cluster analysis (HCA) was used to classify species based on their behavioral traits. When selecting predictor variables for analysis, we focused on those presumably increasing vulnerability to mange infections or those already mentioned by other authors (Kauhala and Holmala 2006; Collins et al. 2010; Oleaga et al. 2011; Almberg et al. 2012) (Table 2). We did not include body size-dependent variables such as density. home range size or lifespan, because they are auto-correlated and have an opposite influence (e.g., density and lifespan). The presence or absence of behavioral traits in different carnivore species was attributed based on published data (from the Białowieża Forest, amongst other areas) concerning ecology of these species (social system, den/resting sites use and intra-guild predation) (Table 2). The Euclidean distance measure was used and clustering was performed with complete linkage. This method uses the most distant pair of objects in two clusters to compute between-cluster distances. The procedure was implemented in SYSTAT 13.

Results

Sarcoptic mange was found in 6 of 10 investigated species (Table 1). The highest percentage of infected individuals was recorded in 5 species: red foxes (19 %), badgers (9 %), wolves (7 %), raccoon dogs (6 %), and stone martens (5 %). One species, lynx, was infected sporadically and four others were not infected (American mink, least weasel *Mustela nivalis*, European polecat *Mustela putorius*, pine marten) (Table 1). Data from dead individuals (191) showed mange caused mortality

Table 1 Sarcoptic mange infection in ten species of carnivores of the Białowieża Primeval Forest (BPF) in 1994–2013

Species	Number of investigated animals	% of infected animals	% of infected animals that died due to mange
Red fox	59	19	27
Badger	33	9	0
Wolf	27	7	0
Raccoon dog	116	6	14
Stone marten	62	5	0
Lynx	49	2	100
Pine marten	27	0	0
Polecat	41	0	0
American mink	57	0	0
Weasel	209	0	0
All species	680	-	_

in 3 % (5) and in total was only observed in three species (red fox, raccoon dog, lynx) (Table 1). Rate of infection was correlated with the sum of ecological and behavioral features (sociality, den use and share, intra-guild predation), which may increase spread of infection ($r_s = 0.902$, n = 10, P < 0.001) (Table 2). The HCA divided studied species into two groups (Fig. 1). The first included all social species and those who share dens with other species, and the second included all solitary species (Fig. 1).

When comparing the origin of investigated individuals in infected species, we found a significantly higher proportion of infected animals among those found dead than the culled or trapped individuals (log-linear model: $\chi^2 = 4.5853$, df = 1, P = 0.032; Table 3). There was no significant differences between species ($\chi^2 = 10.357$, df = 5, P = 0.066), neither for interaction between origin of sample and species ($\chi^2 = 8.061$, df = 5, P = 0.153).

During 20 years of investigation, sarcoptic mange occurred simultaneously in the same years in several species of carnivores. During the study period we observed two outbreaks of sarcoptic mange, which lasted 2–3 years each between 1997–1999 and 2011–2013 (Fig. 2). During the first outbreak, 21 % of red foxes and 7 % of raccoon dogs exhibited skin lesions suggestive of mange. Since 1994 a long period of disease persistence in populations of carnivores in the Białowieża Primeval Forest has been observed. In two of the most numerous species (red fox and raccoon dog) we found no relationship between number of annually investigated and infected individuals ($r^2 = 0.23$ and 0.29, respectively, P > 0.05).

Discussion

Sarcoptic mange was found in six of ten investigated carnivores from the Białowieża Primeval Forest. These species of carnivores are most often reported as mange carriers in the literature review (Table 4); indicating that these species are more vulnerable to mange infections than other species of carnivores. This is probably due to sociality and den use being characteristic traits for these species, thus increasing direct and indirect risk of mange transmission between individuals of the same and different species. Sarcoptic mange is most often transmitted directly from animal to animal (Pence and Ueckermann 2002). Close contact between pair mates or group members may strongly increase risk of disease transmission; thus sociality is probably one of the main factors influencing sarcoptic mange infections. As sarcoptic mange may alternatively be transferred indirectly, for example by using the same dens or nests (Arlian 1989), shared use of den sites by individuals of the same or different species seems to be the second most important factor of pathogen transmission. Simultaneous den use by different carnivore species was reported in numerous studies (Goszczyński and Wójtowicz 2001; Theuerkauf

Table 2 Behavioral traits of carnivore species investigated for sarcoptic mange in the BPF

Species	Sociality	Seasonal or permanent use of shelters	Shared use of dens with other carnivores	_	Sum	References
Red fox	1	1	1	1	4	Jędrzejewska and Jędrzejewski 1998; Kowalczyk et al. 2008
Badger	1	1	1	1	4	Jędrzejewska and Jędrzejewski 1998; Kowalczyk et al. 2000, 2003, 2008
Wolf	1	1	1	1	4	Jędrzejewska and Jędrzejewski 1998; Schmidt et al. 2009; Theuerkauf et al. 2003
Raccoon dog	1	1	1	0	3	Jędrzejewska and Jędrzejewski 1998; Kowalczyk et al. 2008; Kowalczyk and Zalewski 2011
Stone marten	0	1	0	0	1	Herr 2008; A. Wereszczuk, unpublished data
Lynx	0	0	0	1	1	Schmidt et al. 1997, 2009; Jędrzejewska and Jędrzejewski 1998
Pine marten	0	1	0	0	1	Zalewski 1997, 2007; Jędrzejewska and Jędrzejewski 1998; Zalewski and Jędrzejewski 2006
Polecat	0	1	0	0	1	Jędrzejewska and Jędrzejewski 1998; A.Z. et al. unpublished data
American mink	0	1	0	0	1	Jędrzejewska and Jędrzejewski 1998; A.Z. et al. unpublished data
Weasel	0	1	0	0	1	Jędrzejewska and Jędrzejewski 1998; Jędrzejewski et al. 2000; Zub et al. 2008

¹ Presence, 0 absence

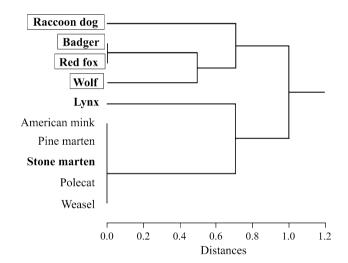


Fig. 1 Dendrogram showing the results of a hierarchical cluster analysis (HCA) of behavioral traits of carnivore species from the Białowieża Primeval Forest (BPF) that may increase risk of sarcoptic mange infections. The data matrix of presence (1) or absence (0) of traits is used (Table 2). Clustering is based on complete linkage and the Euclidean distance measure is used. Species with sarcoptic mange presence are marked in *bold*. Social carnivores are framed. Behavioral traits based on published data—see Table 2

et al. 2003; Hendrickson et al. 2005; Kauhala and Holmala 2006). Red foxes and raccoon dogs frequently use badger setts for reproduction and wintering, respectively (Neal and Cheeseman 1996; Kowalczyk et al. 2000, 2008; Kauhala and Holmala 2006; Kowalczyk and Zalewski 2011), and may even use the same sett chambers (Kowalczyk et al. 2008). In the Białowieża Primeval Forest, wolves also often settle into badger or red fox dens for reproduction (Theuerkauf et al. 2003).

Table 3 Influence of sample origin on sarcoptic mange prevalence in carnivores in the BPF

Species	Trapp	ed and culled	Dead	Dead		
	\overline{N}	% infected	\overline{N}	% infected		
Red fox	28	4	31	32		
Badger	16	6	17	12		
Wolf	13	15	14	0		
Raccoon dog	26	4	90	7		
Stone marten	39	3	23	9		
Lynx	33	0	16	6		
All species	155	4	191	11		

In contrast to social mammals, the rate of encounters between individuals of solitary carnivores is much lower and often limited to a few specific periods such as mating season (Schmidt et al. 1997). They usually use separate resting sites and often their home ranges overlap in small proportions (Zalewski 1997; Zalewski and Jędrzejewski 2006). All these factors reduce the probability of infection transmission.

Another factor increasing transmission of mange to top predators may be intra-guild predation. Wolves and lynx prey upon medium-sized carnivores such as red foxes and raccoon dogs (Jędrzejewska and Jędrzejewski 1998; Linnell et al. 1998; Sunde et al. 1999; Kowalczyk et al. 2009). This may probably explain sporadic records of sarcoptic mange in solitary lynx as was observed in this and other studies (see review in Table 4). It has been proved that *S. scabiei* var. *vulpes*, identified originally in red foxes, can be transmitted by direct or indirect contact to lynx, wolves, dogs and cats (Lindquist and Cash 1973; Pence and Ueckermann 2002; Bornstein et al. 2004). Transmission of mites between wild and domestic

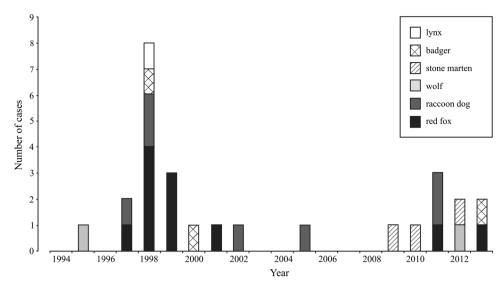


Fig. 2 Dynamics of sarcoptic mange infections in carnivores of the BPF from 1994 to 2013. Note that the number of individuals in 2013 are from the first quarter of the year

animals could also explain sarcoptic mange occurrence in stone martens that live near human settlements in the same locations as domestic cats (A.Z., personal communication). Overall, the high density of stone marten recorded during the last years in BPF (A.Z., unpublished data) may be one of the factors increasing mange infection susceptibility.

Our studies have revealed red fox as the main reservoir and carrier of sarcoptic mange. This species is reported in the literature as having the highest infection prevalence (review in Table 4). The red fox exhibits the widest geographical range of any European carnivore; it can be found in a wide diversity of habitats and often at high densities (Bartoń and Zalewski 2007). As the red fox is particularly susceptible to sarcoptic mange (Soulsbury et al. 2007), and because mangy animals may visit human settlements in search for easy accessible food sources (Todd et al. 1981; Balestrieri et al. 2006), they seem to be the main vector of mange transmission between wild and domestic animals. In addition, the red fox appears to be a persistent reservoir of scabies. A long-term study of S. scabiei infection in Norwegian red fox populations revealed the possibility of the occurrence of host/parasite adaptation (Davidson et al. 2008). The occurrence of non-fatal, restricted, subclinical or even the recovery from S. scabiei infection was observed (Storm et al. 1976; Mörner and Christensson 1984). This suggests that the red fox population may be adapting to live with the parasite and that low-grade or subclinical infections may occur amongst exposed foxes.

Dangerous sarcoptic mange outbreaks have been noted in some species worldwide (Henriksen et al. 1993; Martin et al. 1998; Kalema-Zikusoka et al. 2002). Wildlife mortality rates of up to 90 % have been observed (Mörner 1992; Lindström et al. 1994). In remnant or isolated populations, such severe mange outbreaks can have a detrimental effect and cause extinction of

local populations, as recorded in red foxes on a Danish island (Henriksen et al. 1993). Thus, sarcoptic mange may be the limiting factor for some carnivore species, which has replaced rabies (due to the oral vaccination program). Because mange, as shown by our and other studies, affects the most abundant or invasive canid species, such as red fox and raccoon dog, no mange control is needed. The increased mortality of common carnivores due to mange may lead to recovery of other wildlife persecuted by these species, as has been observed in Scandinavia (Smedschaug et al. 1999).

We observed two possible outbreaks of sarcoptic mange during the 20 year study period. The percentage of infected animals during these outbreaks did not exceed 25 %. This indicates that, in natural conditions, carnivores living at relatively low densities are less vulnerable to mange epizootic than high-density populations. We observed peaks of mange prevalence, as well as single cases, suggesting that this infection has persisted in these carnivore populations. The second reservoir species of sarcoptic mange seems to be the raccoon dog-one of the invasive species in Poland. Isolated cases of infected raccoon dogs were observed in BPF between outbreaks, which confirms the continued presence of scabies among individuals of this species. Raccoon dogs are already recognized as a reservoir of rabies (Holmala and Kauhala 2006).

It is known that high population density is a major contributing factor to epizootics. In this study area, densities of the three species of medium-sized denning carnivores were low and varied between 2 and 7 individuals per 10 km² (Jędrzejewska and Jędrzejewski 1998; Kowalczyk et al. 2000, 2003), which may explain mild epidemics of sarcoptic mange among carnivores in BPF. However, as suggested by Holmala and Kauhala (2006), the pooled density of medium-sized carnivores showing high space use overlap and increased potential contact

 Table 4
 Review of sarcoptic

 mange infections in carnivores

Species	Country, locality	% of infected animals ^a	References
Red fox	Italy, Western Alps	25	Balestrieri et al. 2006
	Norway	30	Davidson et al. 2008
	Norway	7	Davidson et al. 2008
	Slovakia	24	Kočišová et al. 2006
	Spain, Asturias,	+	Oleaga et al. 2012
	Spain, Central Ebro Valley	23	Gortázar et al. 1998
	Sweden	32	Mörner 1992
	Sweden, Norrbotten and Västerbotten	50 to > 75	Danell and Hörnfeldt 1987
	Poland, Białowieża Forest	19	This study
Arctic fox	Sweden	19	Mörner 1992
Badger	England	+	Collins et al. 2010
	Italy, Western Alps	0	Balestrieri et al. 2006
	Norway	+	Holt and Berg 1990
	Sweden	0	Mörner 1992
	Poland, Białowieża Forest	9	This study
Raccoon dog	Finland	+	Mörner 1992
	Japan, Kanagawa Prefecture	+	Takahashi et al. 2001
	Japan, Kanagawa Prefecture	+	Ninomiya and Ogata 2005
	Korea	+	Eo et al. 2008
	Poland, Białowieża Forest	6	This study
Wolf	Poland, Białowieża Forest	3	Jędrzejewska et al. 1996
	Poland, Carpatian Mountains	6	Nowak et al. 2008
	Spain, Asturias	19	Oleaga et al. 2011
	Sweden	+	Mörner 1992
	USA, Yellowstone National Park	+	Almberg et al. 2012
_	Poland, Białowieża Forest	7	This study
Raccoon	USA, Michigan	75	Fitzerald et al. 2004
Coyots	USA, South Dakota	12–56	Chronert et al. 2007
	USA, Texas	Up to 70	Pence and Windberg 1994
Lynx	Norway	+	Holt and Berg 1990
	Sweden	+	Mörner 1992
	Switzerland, Alps	+	Ryser-Degiorgis et al. 2002
~	Poland, Białowieża Forest	2	This study
Black bear	USA, Michigan	+	Schmitt et al. 1987
	USA, Michigan	+	Fitzerald et al. 2008
Pine marten	Norway	+	Holt and Berg 1990
	Sweden	+	Mörner 1992
a	Poland, Białowieża Forest	0	This study
Stone marten	Italy, Western Alps	6	Balestrieri et al. 2006
	Poland, Białowieża Forest	5	This study
Ferret	Australia and New Zealand	+	Philips et al. 1987; Tenquist
Stoat	Russia	+	and Charleston 2001 Lavrov 1956; McDonald
			and Lariviére 2001
Polecat	Poland, Białowieża Forest	0	This study
American mink	Poland, Białowieża Forest	0	This study
Weasel	Poland, Białowieża Forest	0	This study

^a + presence of infection

rate, may exceed the threshold density needed for disease spread. It is worth noting that, because *S. scabiei* may cause mortality of individuals, the source of assessed individuals needs to be taken into account. In our study, samples of dead animals for several species showed significantly higher prevalence of mange than samples of culled and trapped animals. When only "found dead" animals are investigated, the prevalence of infection can be overestimated.

Our studies have revealed mild epizootics of sarcoptic mange in carnivore communities of the BPF. We did not investigate the influence of mange outbreaks on the population dynamics of infected species as significant declines of their densities were not observed. Furthermore, our studies have shown that a combination of different factors, mainly sociality and shared use of dens, may significantly increase the risk of infection. Social carnivores are more susceptible to mange than solitary ones due to a high overlap of space and habitat use and denning behavior, including the shared use of den sites (Kauhala and Holmala 2006; Kowalczyk et al. 2008). These traits increase the contact rate between individuals of the same and different species. It seems that, in carnivore communities such as in the BPF, numerous species may serve as a reservoir of the pathogen and increase its persistence in the environment. Sociality and den site use are important factors of sarcoptic mange spread and prevalence in wild population of carnivores worldwide.

Acknowledgments We are grateful to Drs. K. Zub, and K. Schmidt for providing the data. The study was financed by grants KBN 6 P04C 057 12 and NCN 2012/05/B/NZ8/01247. We thank Miss Delyth Williams for kindly correcting the English.

Open Access This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and the source are credited.

References

- Almberg ES, Cross PC, Dobson AP, Smith DW, Hudson PJ (2012)
 Parasite invasion following host reintroduction: a case study of
 Yellowstone's wolves. Phil Trans R Soc B 367:2840–2851. doi: 10.1098/rstb.2011.0369
- Arlian LG (1989) Biology, host relations, and epidemiology of *Sarcoptes scabiei*. Annu Rev Entomol 34:139–161. doi: 10.1146/annurev.en.34.010189.001035
- Arlian LG, Vyszenski-Moher DL (1988) Life cycle of *S. scabiei* var. *canis*. J Parasitol 74:427–430
- Arlian LG, Bruner RH, Stuhlman RA, Ahmed M, Vyszenski-Moher DL (1990) Histopathology of hosts parasitized by S. scabiei. J Parasitol 76:889–894
- Arlian LG, Morgan MS, Rapp CM, Vyszenski-Moher DL (1996) The development of protective immunity in canine scabies. Vet Parasitol 62:133–142. doi:10.1016/0304-4017(95)00854-3
- Arlian LG, Rapp CM, Stemmer BL, Morgan MS, Moore PF (1997) Characterization of lymphocyte subtypes in scabietic skin lesions of naive and sensitized dogs. Vet Parasitol 68:347–358. doi:10.1016/S0304-4017(96)01093-X
- Balestrieri A, Remonti L, Ferrari N, Ferrari A, Valvo TL, Robetto S, Orusa R (2006) Sarcoptic mange in wild carnivores and its cooccurrence with parasitic helminthes in the Western Italian Alps. Eur J Wildl Res 52:196–201. doi:10.1007/s10344-006-0036-4
- Bartoń K, Zalewski A (2007) Winter severity limits red fox populations in Eurasia. Glob Ecol Biogeogr 16:281–289. doi: 10.1111/j.1466-8238.2007.00299.x
- Bornstein S, Mörner T, Samuel WM (2001) Sarcoptes scabiei and sarcoptic mange. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames, pp 107–119
- Bornstein S, Gidlund K, Karlstam E, Bergström K, Zakrisson G, Nikkilä T, Bergvall K, Renström L, Mattsson JG (2004) Sarcoptic mange epidemic in a cat population (FC-42). Vet Dermatol 15(Suppl. 1):20–40. doi:10.1111/j.1365-3164.2004.411_42.x
- Bunevich AN, Dackevich VA (1985) Spatial distribution and food of the raccoon dog in Białowieża Forest (in Russian). Zapovedniki Belorussii 9:114–120
- Burgess I (1994) Sarcoptes scabiei and scabies. Adv Parasitol 33:235–274
- Chronert JM, Jenks JA, Roddy DE, Wild MA, Powers JG (2007) Effect of sarcoptic mange at wind cave national park. J Wildl Manage 71:1987–1992. doi:10.2193/2006-225
- Collins R, Wessels ME, Wood R, Couper D, Swift A (2010) Sarcoptic mange in badgers in the UK. Vet Rec 167:668. doi: 10.1136/vr.c5672
- Danell K, Hörnfeldt B (1987) Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. Oecologia 73:533–536
- Davidson RK, Bornstein S, Handeland K (2008) Long-term study of *S. scabiei* infection in Norwegian red fox (*Vulpes vulpes*) indicating host/parasite adaptation. Vet Parasitol 156:277–283. doi:10.1016/j.vetpar.2008.05.019
- Eo K-Y, Kwon O-D, Shin N-S, Shin T, Kwak D (2008) Sarcoptic mange in wild raccoon dogs (*Nyctereutes procyonoides*) in Korea. J Zoo Wildl Med 39:671–673. doi:10.1638/2008-0034.1
- Fernandez-Moran J, Gomez S, Ballesteros F, Quiros P, Benito JL, Feliu C, Nieto JM (1997) Epizootiology of sarcoptic mange in a population of cantabrian chamois (*Rupicapra pyrenaica parva*)

- in northwestern Spain. Vet Parasitol 73:163–171. doi:10.1016/S0304-4017(97)00061-7
- Fitzerald SD, Cooley TM, Murphy A, Cosgrove MK, King BA (2004) Sarcoptic mange in raccoons in Michigan. J Wildl Dis 40:347–350
- Fitzerald SD, Cooley TM, Cosgrove MK (2008) Sarcoptic mange and *Pelodera dermatitis* in an American black bear (*Ursus americanus*). J Zoo Wildl Med 39:257–259. doi:10.1638/2007-0071R.1
- Gerasimov Y (1958) Mange in wild foxes. Translation of Russian game reports. Canadian Department of Northern Affairs National Resources, Ottawa, pp 1–5
- Gortázar C, Villafuerte R, Blanco JC, Fernandez de Luco D (1998) Enzootic sarcoptic mange in red foxes in Spain. Z Jagd 44:251–256
- Goszczyński J, Wójtowicz I (2001) Annual dynamics of den use by red foxes *Vulpes vulpes* and badgers *Meles meles* in central Poland. Acta Theriol 46:407–417
- Hawkins JA, McDonald RK, Woody BJ (1987) Sarcoptes scabiei infestation in a cat. J Am Vet Med Assoc 190:1572–1573
- Hendrickson ChJ, Samelius G, Alisauskas RT, Lariviere S (2005) Simultaneous den use by Arctic foxes and wolves at a den site in Nunavut, Canada. Arctic 58:418–420
- Henriksen P, Dietz HH, Henriksen SA, Gjelstrup P (1993) Sarcoptic mange in red fox in Denmark. A short report. Dansk Vettidsskr 76:12–13
- Herr J (2008) Ecology and behavior of urban stone martens (*Martes foina*) in Luxembourg. PhD Thesis. University of Sussex, UK
- Holmala K, Kauhala K (2006) Ecology of wildlife rabies in Europe. Mammal Rev 36:17–36. doi:10.1111/j.1365-2907.2006.00078.x
- Holt G, Berg C (1990) Sarcoptic mange in red fox and other wild carnivores in Norway. Nor Veterinaertidsskr 102:427–432
- Jędrzejewska B, Jędrzejewski W (1998) Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Ecological studies 135. Springer, Berlin
- Jędrzejewska B, Jędrzejewski W, Bunevich AN, Miłkowski L (1996) Population Dynamics of Wolves Canis lapus in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. Mammal Rev 26:103–126. doi: 10.1111/j.1365-2907.1996.tb00149.x
- Jędrzejewski W, Jędrzejewska B, Zub K, Nowakowski WK (2000) Activity patterns of radio-tracked weasels *Mustela nivalis* in Białowieża National Park (E Poland). Ann Zool Fenn 37:161–168
- Kalema-Zikusoka G, Koch RA, Macfie EJ (2002) Scabies in freeranging mountain gorillas (*Gorilla berengei berengei*) in Bwindi Impenetrable National Park, Uganda. Vet Rec 150:12–15
- Kauhala K, Holmala K (2006) Contact rate and risk of rabies spread between medium-sized carnivores in southeast Finland. Ann Zool Fennici 43:348–357
- Kočišová A, Lazar P, Letková V, Čurlík J (2006) Ectoparasitic species from red foxes (*Vulpes vulpes*) in East Slovakia. Vet Archiv 76:S59–S63
- Kowalczyk R, Zalewski A (2011) Adaptation to cold and predation—shelter use by invasive raccoon dogs Nyctereutes procyonides in Białowieża Primeval Forest (Poland). Eur J Wildl Res 57:133–142. doi:10.1007/s10344-010-0406-9
- Kowalczyk R, Bunevich AN, Jędrzejewska B (2000) Badger density and distribution of setts in Białowieża Primeval Forest (Poland and Belarus) compared to other Eurasian populations. Acta Theriol 45:395–400
- Kowalczyk R, Zalewski A, Jędrzejewska B, Jędrzejewski W (2003) Spatial organization and demography of badgers (*Meles meles*) in Białowieża Primeval Forest, Poland, and the influence of earthworms on badger densities in Europe. Can J Zool 81:74–87. doi:10.1139/Z02-233
- Kowalczyk R, Jędrzejewska B, Zalewski A, Jędrzejewski W (2008) Facilitative interactions between the Eurasian badger (*Meles meles*), the red fox (*Vulpes vulpes*), and the invasive raccoon dog (*Nyctereutes procyonoides*) in Białowieża Primeval Forest, Poland. Can J Zool 86:1389–1396. doi:10.1139/Z08-127

- Kowalczyk R, Zalewski A, Jędrzejewska B, Ansorge H, Bunevich AN (2009) Reproduction and mortality of invasive raccoon dogs *Nyctereutes procyonoides* in the Białowieża Primeval Forest (eastern Poland). Ann Zool Fennici 46:291–301
- Lavrov NP (1956) Characteristic and causes of the prolonged depression in numbers of the ermine in forest-steppe and steppe zones of USSR. In: King CM (ed) Biology of mustelids. Some Soviet research. British Library Lending Division, Boston Spa, Yorkshire, England, pp 170–187
- Lindquist WD, Cash WC (1973) Sarcoptic mange in a cat. J Am Vet Med Ass 162:639–640
- Lindström E (1992) Diet and demographics of the red fox (*Vulpes vulpes*) in relation to population density—the sarcoptic mange event in Scandinavia. In: McCullough DR, Barret RH (eds) Wildlife 2001: populations. Elsevier, London, pp 922–931
- Lindström ER, Andren H, Anglstam P, Cederlund G, Hörnfeld B, Jäderberg L, Lemnel PA, Martinsson B, Sköld K, Swensson JE (1994) Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology 75:1042–1049. doi: 10.2307/1939428
- Linnell JDC, Odden J, Pedersen V, Andersen R (1998) Records of intra-guild predation by Eurasian lynx. Can Field Nat 112:707-708
- Martin RW, Handasyde KA, Skerratt L (1998) Current distribution of sarcoptic mange in wombats. Aust Vet J 76:411–414. doi:10.1111/j.1751-0813.1998.tb12391.x
- McDonald RA, Lariviére S (2001) Diseases and pathogens of Mustela spp., with special reference to the biological control of introduced stoat Mustela erminea populations in New Zealand. J R Soc NZ 31:721–744
- Mörner T (1992) Sarcoptic mange in Swedish wildlife. In: Artois M (ed) Health and management of free-ranging mammals. Rev Sci Tech Off Int Epiz 11: 1115–1121
- Mörner T, Christensson D (1984) Experimental infection of red foxes (*Vulpes vulpes*) with *S. scabiei* var. *vulpes*. Vet Parasitol 15:159–164. doi:10.1016/0304-4017(84)90031-1
- Neal E, Cheeseman C (1996) Badgers. Poyser, London
- Newman TJ, Baker PJ, Harris S (2002) Nutritional condition and survival of red foxes with sarcoptic mange. Can J Zool 80:154–161. doi:10.1139/z01-216
- Ninomiya H, Ogata M (2005) Sarcoptic mange in free-ranging raccoon dogs (*Nyctereutes procyonoides*) in Japan. Vet Dermatol 16:177–182. doi:10.1111/j.1365-3164.2005.00439.x
- Nowak S, Mysłajek RW, Jędrzejewska B (2008) Density and demography of wolf, *Canis lupus* population in the westernmost part of the Polish Carpathian Mountains, 1996–2003. Folia Zool 57:392–402
- Oleaga A, Casais R, Balseiro A, Espí A, Llaneza L, Hartasánchez A, Gortázar Ch (2011) New techniques for an old disease: sarcoptic mange in the Iberian wolf. Vet Parasitol 181:255–266. doi:10.1016/j.vetpar.2011.04.036
- Oleaga A, Casais R, Prieto JM, Gortázar C, Balseiro A (2012) Comparative pathological and immunohistochemical features of sarcoptic mange in five sympatric wildlife species in Northern Spain. Eur J Wildl Res 58:997–1000. doi:10.1007/s10344-012-0662-y
- Pence DB, Ueckermann E (2002) Sarcoptic mange in wildlife. Rev Sci Tech Off Int Epiz 21:385–398
- Pence DB, Windberg (1994) Impact of a sarcoptic mange epizootic on a coyote population. J Wildl Manage 58:624–633
- Philips PH, O'Callaghan MG, Moore E, Baird RM (1987) Pedal S. scabiei infestation in ferrets (Mustela putorius furo). Aus Vet J 64:289–290
- Rossi L, Meneguz PG, de Martin P, Rodolfi M (1995) The epizootiology of sarcoptic mange in chamois, *Rupicapra rupicapra*, from the Italian Eastern Alps. Parassitologia 37:233–240

- Ruprecht AL, Buchalczyk T, Wójcik JM (1983) Występowanie norek (Mammalia: Mustelidae) w Polsce. Przegl Zool 27:87–99
- Ryser-Degiorgis MP, Ryser A, Bacciarini LN, Angst C, Gottstein B, Janovsky M, Breitenmoser U (2002) Notoedric and sarcoptic mange in free-ranging lynx from Switzerland. J Wildl Dis 38:228–232
- Schmidt K, Jędrzejewski W, Okarma H (1997) Spatial organization and social relations in the Eurasian lynx population in Białowieża Primeval Forest, Poland. Acta Theriol 42:289–312
- Schmidt K, Jędrzejewski W, Okarma H, Kowalczyk R (2009) Spatial interactions between grey wolves and Eurasian lynx in Białowieża Primeval Forest, Poland. Ecol Res 24:207–214. doi: 10.1007/s11284-008-0496-y
- Schmitt SM, Cooley TM, Friedrich PD (1987) Clinical Mange of the Black Bear (*Ursus americanus*) Caused by *S. scabiei* (Acarina, Sarcoptidae). J Wildl Dis 23:162–165
- Skerratt LF, Martin RW, Handasyde KA (1998) Sarcoptic mange in wombats. Aus Vet J 76:408–410
- Smedschaug ChA, Selås V, Lund SE, Sonerud GA (1999) The effects of a natural reduction of red fox (*Vulpes vulpes*) on small game hunting bags in Norway. Wildl Biol 5:157–166
- Soulsbury CD, Iossa G, Baker PJ, Cole NC, Funk SM, Harris S (2007) The impact of sarcoptic mange *S. scabiei* on the British fox *Vulpes vulpes* population. Mammal Rev 37:278–296. doi: 10.1111/j.1365-2907.2007.00101.x
- Storm GL, Andrews RD, Phillips RL, Bishop RA, Siniff DB, Tester JR (1976) Morphology, reproduction, dispersal, and mortality of Mild western red fox population. Wildl Monogr 49:1–82
- Sunde P, Overskaug K, Kvam T (1999) Intraguild predation of lynxes on foxes: evidence of interference competition? Ecography 22:521–523. doi:10.1111/j.1600-0587.1999.tb01281.x
- Takahashi M, Nogami S, Misumi H, Maruyama S, Shiibashi T, Yamamoto Y, Sakai T (2001) Mange Caused by *S. scabiei* (Acari: Sarcoptidae) in Wild Raccoon Dogs, *Nyctereutes procyonides*, in Kanagawa Prefecture, Japan. J Vet Med Sci 63:457–460. doi:10.1292/jvms.63.457
- Tenquist JD, Charleston WAG (2001) A revision of the annotated checklist of ectoparasites of terrestrial mammals in New Zealand. J R Soc NZ 31:481–542. doi:10.1080/03014223.2001. 9517666
- Theuerkauf J, Rouys S, Jędrzejewski W (2003) Selection of den, rendezvous, and resting sites by wolves in the Białowieża Primeval Forest, Poland. Can J Zool 81:163–167. doi:10.1139/ Z02-190
- Todd AW, Gunson JR, Samuel WM (1981) Sarcoptic mange: an important disease in coyotes and wolves of Albertya, Canada.
 Worldwide Furbearer Conference Proceedings, Frostburg, Maryland, pp 706–729
- Zalewski A (1997) Patterns of resting site use by pine marten Martes martes in Białowieża National Park (Poland). Acta Theriol 42:153–168
- Zalewski A (2007) Does size dimorphism reduce competition between sexes? The diet of male and female pine martens at local and wider geographical scales. Acta Theriol 52:237–250. doi: 10.1007/BF03194220
- Zalewski A, Jędrzejewski W (2006) Spatial organization and dynamics of the pine marten *Martes martes* in the Białowieża National Park, Poland. Ecography 29:31–43. doi:10.1111/ j.2005.0906-7590.04313.x
- Zub K, Sönnichsen L, Szafrańska PA (2008) Habitat requirements of weasels *Mustela nivalis* constrain their impact on prey populations in complex ecosystems of the temperate zone. Oecologia 157:571–582. doi:10.1007/s00442-008-1109-8