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Contact rate and risk of rabies spread between medium-sized carnivores in southeast Finland

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Spatial and temporal interaction between medium-sized carnivores (raccoon dog *Nyctereutes procyonoides*, red fox *Vulpes vulpes*, European badger *Meles meles* and domestic cat *Felis silvestris catus*) was studied in southeast Finland using radiotelemetry to estimate the risk of contact and contact rate (number of contacts) between individuals. There was a high level of overlap between home ranges both within and between species and individuals had frequent contact. The risk of contact was high for members of raccoon dog pairs, individual cats and badgers, but also for raccoon dogs and badgers and for raccoon dogs and cats. The lowest risk of contact was for neighbouring raccoon dogs and for male foxes. In this carnivore community the transmission of disease, such as rabies, both within and between species is likely. The role of the badger as a vector of rabies is probably much greater than previously assumed.

Introduction

The role of the raccoon dog (*Nyctereutes procyonoides*) as a vector of rabies has grown in recent years in northeast Europe, especially in the Baltic States (WHO 2004). The raccoon dog is one of the most common carnivores in southern Finland too, and it was the main victim of rabies during an epizootic in the late 1980s (Westerling 1991, Nyberg *et al*. 1992). Red foxes (*Vulpes vulpes*), European badgers (*Meles meles*) and semi-feral domestic cats (*Felis silvestris catus*) are other potential vectors of rabies in northern Europe. The fox has been the main vector of rabies in central and western Europe since World War II (Wandeler *et al*. 1974, Chautan *et al*. 2000), and many foxes also died of rabies during the Finnish epizootic. In Russia, where the number of wildlife rabies case increased sharply in 2005, the fox remains the main vector species (WHO 2005). Badgers are fairly susceptible to the rabies infection and they can transmit the virus easily (Wandeler *et al*. 1974, Smith 2002, Smith & Wilkinson 2002). Domestic cats are also frequently infected (WHO 2004). In order to control rabies and create a model for the disease, it is essential to study the interactions and probability of contact between medium-sized carnivores because contact (bites) between individuals determine the rate of rabies spread (White *et al*. 1995). We need knowledge of both the spatial and temporal interactions between individuals to estimate the risk of contact and rate of transmission of the disease.

The aim of the present study was to examine the risk of contact and contact rate (number of contacts) between medium-sized carnivores in a community with a quite high (pooled) density of several potential vector species (*see* Kauhala *et al*. 2006). We conducted both spatial and temporal interaction analyses. We will discuss how the interactions and risk of contact may affect the transmission of diseases, such as rabies.

Material and methods

Study area

The study area (approx. 54 km^2) was located in Virolahti (60°32´N, 27°41´E), southeast Finland, close to the Russian border. The area consists of managed coniferous and mixed forests (64%), fields bordered by large ditches (18%), seashore with reed beds and other wetlands (12%) and small patches of deciduous forests, clear-cuts and bogs. There is a small village in the middle of the area. The mean temperature during the year was 4.8 °C, the mean being –6.3 °C in January and 18.8 °C in July. The ground was covered with snow from late November or December, depending on the year, until mid-April. Raccoon dogs, foxes and badgers were regularly hunted in the area.

Radio tracking

The risk of contact between individuals was studied using VHF-radio-telemetry. The animals were captured mainly with wired traps, anaesthetized (by a veterinarian) with ketamine hydrochloride, weighed, their sex was determined and they were fitted with radio-collars (model TW-3, 138–138.5 MHz, Biotrack, Dorset, UK) and plastic ear-tags (sheep tags, Dalton, UK). The age (young/adult) of the animals was estimated from body weight, teeth and by palpation of the prominence of the ulna (Kauhala & Helle 1990). Only adults were fitted with radio-collars.

Radio tracking was carried out from a truck with a Yagi-type antenna. Bearings were taken from at least two points usually within five minutes. The mean distance between the tracker and the animal was 563 m (290–910 m) in a random sample of 30 locations. We located the animals once every 15 minutes during the hours of darkness. When possible, two animals with overlapping home ranges were located simultaneously by two persons. The mean length of the tracking sessions was 5.0 ± 1.19 hrs. The mean location error was 150 m (*see* Kauhala & Tiilikainen 2002).

We gained data for 19 raccoon dogs, 5 red foxes, 8 badgers and 13 cats between autumn 2000 and summer 2004. The total number of locations was > 8800. We studied the relationships between individuals both within and between species, including the comparisons with enough data. We considered a male and a female raccoon dog as a pair, if the core areas of their home ranges (Kernel 50%) overlapped greatly, because raccoon dogs are known to be monogamous (Kauhala *et al*. 1993). In this study the yearly core areas of pair members overlapped by 60% (S.D. = 29.5) and those of 'neighbouring' raccoon dogs by 9% (S.D. = 10.5).

Interactions between individuals

We first calculated home ranges (95% fixed Kernel, Worton 1989) and performed overlap analyses using the software Ranges 6 (Kenward *et al*. 2003) to see which home ranges overlapped (*see* also Kauhala *et al*. 2006), and included in further analyses only animals sharing at least part of their home ranges. We used the fixed Kernel method (Kernel 95%), because Seaman *et al*. (1999) reported that fixed Kernel estimates were least biased in the outer contours (*see* also Kernohan *et al*. 2001).

Spatial analysis

Spatial analyses measure spatial interactions of animals throughout a time interval of interest (Kernohan *et al*. 2001). We calculated the proportion (%) of an animal's home range that was overlapped by another individual's home range (P_{area}), and the proportion of an animal's locations (%) in the shared area (P_{fix}). The ratio P_{fix}/P_{area} indicates spatial attraction to or avoidance of the shared area. The ratio > 1 indicates attraction, the ratio < 1 means avoidance, and the value close to 1 indicates ignorance. We used the Wilcoxon one sample test to see whether the medians of the indices (within species) differed from unity.

Temporal analysis

Temporal interaction analyses compare the relationship between animals at a particular point in time, which requires simultaneous locations for each pair of animals (Minta 1992). We first calculated distances between simultaneous locations for each pair of animals. We then calculated Jacob's index of avoidance or cohesion, using the software Ranges 6 to see whether the animals avoided, ignored or were attracted by one another (Jacobs 1974, Brown *et al*. 2000, Kenward *et al*. 2003). The distances between n observed pairs of same-time locations for the two animals and $n \times n$ possible distances between the animals (expected values) were compared. Jacob's index rises towards 1 if two animals favour each other's company (i.e. are closer to each other than by chance alone), is close to 0 if the animals ignore each other, and falls towards –1 if the animals avoid each other. This analysis was based on the geometric mean distances, as recommended by Walls and Kenward (2001).

We also examined the nightly routes of each pair of animals using the same-time locations, and counted the number of times their paths crossed.

Estimating the risk of contact and contact rate

We assumed that two animals were likely to come into contact during a tracking session if > 10% of the same-time locations were within 100 m or > 20% were within 200 m or > 30% were within 300 m from each other. We selected these limits because we wanted to take into account both the distance between the animals and the proportion of time they spent near each other. We consider this more reliable than the single discriminating value, e.g. 100 m, used by Cortenay *et al*. (2001). We then calculated the proportion of tracking sessions with contact risk (= contact risk per tracking session) for each pair of animals.

Although we did not track the animals all night, we estimated that the risk of contact per tracking session equals that of one night (therefore we use 'night' instead of 'tracking session' in the following). Contact risk per night should thus be considered as the minimum value. We also estimated 'the risk of contact between two animals during the infective period of three nights' (CR), using the formula:

$$\mathrm{CR} = 1 - (1 - c)^3 \qquad (1)$$

where c = contact risk per night (S. Emet in litt.). We used the time period of three nights, because the infective period for foxes and badgers is known to last about three days (Smith & Wilkinson 2002) and no data are available for raccoon dogs. We also divided the data into three seasons: breeding season (April–mid-July), late summer and autumn (mid-July–October) and winter (November–March, data only for foxes and cats) but found that the risk of contact did not differ between the seasons (χ^2-test: $p > 0.10$ in all cases). Therefore, we pooled the data for all seasons.

We also estimated the number of different animals each individual might contact during the 3-day period (contact rate), by combining the data for the number of overlapping home ranges and CR. The number of overlapping home ranges was estimated from our data for Virolahti, using the number of home ranges in the middle of the study area and data for population density (*see* Kauhala *et al*. 2006: fig. 2).

$$\text{Contact rate} = N \times \mathrm{CR} \qquad (2)$$

where N = the number of animals sharing at least part of an individual's home range. Here, contact events are supposed to be independent of each other (S. Emet in litt.).

The estimated contact rate between foxes is based on the data of only three foxes (one male and two females) sharing a home range and should thus be interpreted with caution. Two male foxes were also living in bordering home ranges. The data for raccoon dog–fox comparisons were insufficient for reliable conclusions to be drawn. A large number of cats populated the study area, so the number of possible cat contacts is also an underestimate.

Den use

We also examined the use of dens by badgers and raccoon dogs both during their active period (April–October) and during their winter lethargy (November–March). We calculated the proportion of daytime (6:00–22:00) locations in the same den for each pair of animals during the active period, and the proportion of all locations in the same winter den.

Results

Spatial interactions

The overlap of home ranges within species was greatest between members of raccoon dog pairs and lowest between neighbouring raccoon dogs (Table 1, *see* also Kauhala *et al*. 2006). Members of raccoon dog pairs favoured the common area, whereas badgers, foxes and cats seemed to use the common area independently of conspecifics. Neighbouring raccoon dogs avoided the area they shared, as did the two male foxes living in bordering home ranges (P_{fix}/P_{area} = 0.61) (differences in the ratios (P_{fix}/P_{area}) between the groups: Kruskal-Wallis test statistic = 12.3, d.f. = 4, p = 0.015).

Badger home ranges, which were larger than those of raccoon dogs (Kauhala *et al*. 2006), tended to cover a large proportion of raccoon dog home ranges, and both raccoon dogs and badgers tended to favour the common area (Table 2). Badger and raccoon dog home ranges largely overlapped with cat home ranges, but only raccoon dogs favoured the shared area. Foxes seemed to favour the area they shared with raccoon dogs.

Table 1. Spatial interaction analysis within species, including the percentage of overlap (mean ± S.D.) between yearly Kernel 95% home ranges (P_{area}), percentage of fixes in the shared area (P_{fix}) and median of the ratio P_{fix}/P_{area}. n = the number of cases studied. [1)] Including foxes (one male and two females) within one home range. * $p < 0.05$.

Pair-wise comparisons	P_{area}	P_{fix}	P_{fix}/P_{area}	n
Raccoon dogs				
pair members	84 ± 13.4	95 ± 2.9	1.13*	6
neighbours	32 ± 17.6	30 ± 19.0	0.84*	22
Badgers	42 ± 24.2	44 ± 25.8	1.03	16
Foxes[1)]	65 ± 31.5	70 ± 23.1	1.19	6
Cats	47 ± 21.4	53 ± 25.8	1.12	20

Table 2. Spatial interaction analysis between medium-sized carnivores, including the percentage of overlap (mean ± S.D.) between yearly Kernel 95% home ranges (P_{area}), percentage of fixes in the shared area (P_{fix}) and median of the ratio P_{fix}/P_{area}. n = the number of cases studied.

	Home range overlapped by		
	Badger	Fox	Cat
Raccoon dog			
P_{area}	73 ± 16.6	59 ± 36.8	33 ± 11.6
P_{fix}	79 ± 15.8	56 ± 43.1	42 ± 18.1
P_{fix}/P_{area}	1.10	0.98	1.22
n	6	2	7
	Raccoon dog	Cat	
Badger			
P_{area}	30 ± 12.1	16 ± 7.9	
P_{fix}	34 ± 22.1	16 ± 17.3	
P_{fix}/P_{area}	1.14	0.64	
n	6	6	
	Raccoon dog		
Fox			
P_{area}	21 ± 6.0		
P_{fix}	27 ± 13.4		
P_{fix}/P_{area}	1.99		
n	2		
	Raccoon dog	Badger	
Cat			
P_{area}	64 ± 18.1	69 ± 31.9	
P_{fix}	66 ± 19.0	68 ± 37.3	
P_{fix}/P_{area}	1.03	1.01	
n	7	6	

Temporal interactions

The mean minimum distance between members of raccoon dog pairs was shortest, but foxes sharing the territory, and individual cats were also often located near each other (Table 3). The minimum distance was largest (450 m) between the two male foxes living in bordering home ranges. Jacob's index was highest for members of raccoon dog pairs and for badgers, and lowest for neighbouring raccoon dogs and for a female raccoon dog and a male fox (–0.05) that shared their home range (fox home range covered 93% of raccoon dog home range).

The paths of members of raccoon dog pairs frequently crossed during the night, as did those of cats, whereas the routes of two foxes or neighbouring raccoon dogs crossed only rarely. The paths of the two neighbouring male foxes never crossed. The paths of raccoon dogs and those of other species also crossed frequently (differences between the groups: Kruskal-Wallis test statistic = 17.0, d.f. = 9, $p = 0.049$; Figs. 1 and 2).

Risk of contact and contact rate

The risk of contact was highest between members of raccoon dog pairs and between individual cats and lowest between neighbouring raccoon dogs and between the two neighbouring male foxes who had no contact during the period of radio tracking (Table 4). Badger–badger and raccoon dog–badger contacts were also frequent. CR between the female raccoon dog and male fox that shared most of their territory was 0.50.

A raccoon dog tended to share its home range with its mate and 4–6 neighbours. Thus a raccoon dog might have contact with its mate and one neighbour during the infectious period (Table 4). At least six badgers lived in the middle of the study area, and 8–12 raccoon dogs lived within their home ranges. It was, therefore, possible for a raccoon dog to have had contact with about four single badgers and a badger with 5–8 single raccoon dogs and about three other badgers during the 3-day infective period. The contact rate between cats and raccoon dogs was also high.

Den use

Members of raccoon dog pairs tended to hibernate together (84% shared locations, $n = 106$). In summer, they spent less time together in the den (67% of the 106 cases). Neighbouring raccoon

Table 3. Temporal interaction between medium-sized carnivores. The minimum distances (mean ± S.D.), as well as the observed and expected geometric mean distances between simultaneously-located pairs of animals are given. Jacob's index of avoidance or cohesion was calculated on the basis of the geometric means. Medians of Jacob's index are given in the table. n = the number of pairs of animals studied/the number of simultaneous locations. [1)] Including foxes (one male and two females) within one home range.

Pair-wise comparisons	Minimum distance (m)	Geometric mean		Jacob's index	n
		observed	expected		
Within species					
Raccoon dogs					
pair members	0	254 ± 75.4	803 ± 276.0	0.89	3/396
neighbours	300 ± 325.5	1133 ± 365.9	1185 ± 355.7	0.04	11/949
Badgers	153 ± 205.5	606 ± 261.9	1338 ± 383.5	0.66	9/334
Foxes[1)]	46 ± 39.9	952 ± 216.4	1165 ± 64.7	0.10	3/242
Cats	65 ± 112.4	371 ± 203.0	480 ± 177.7	0.19	10/356
Between species					
Rdogs–badgers	193 ± 208.1	637 ± 111.7	807 ± 196.0	0.24	6/278
Rdogs–cats	252 ± 237.5	609 ± 127.3	782 ± 212.5	0.17	9/195
Cats–badgers	325 ± 428.7	841 ± 438.4	973 ± 472.9	0.09	6/142
Kruskal-Wallis test statistic	14.8			15.4	
d.f.	7			7	
p	0.039			0.031	

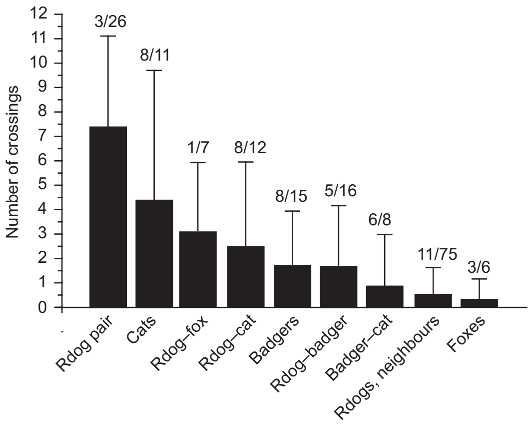

Fig. 1. Number (mean + S.D.) of crossings between the nightly routes of pairs of simultaneously-located individuals. Numbers of pairs/tracking sessions are given above the columns.

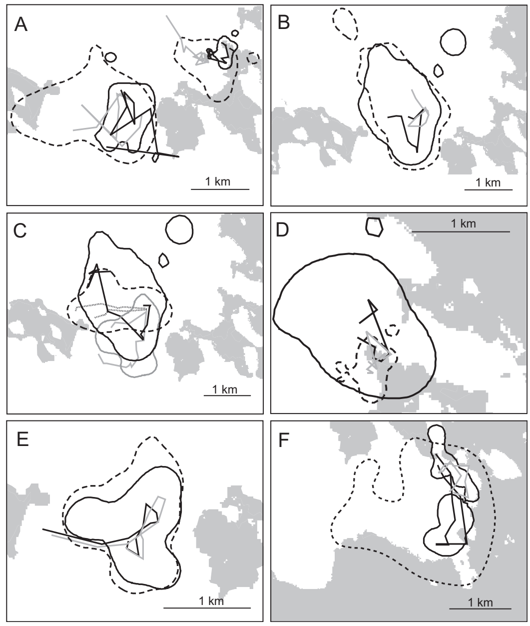

Fig. 2. Examples of the routes of simultaneously-located individuals in their home ranges (Kernel 95%). — **a**: Two cats: female (solid black lines) and male (dashed and solid grey lines), spring 2004 (right), a female cat (solid black lines) and a female raccoon dog (dashed and solid grey lines), spring 2003 (left). — **b**: Two badgers: male (solid black lines) and female (dashed and solid grey lines), summer 2002. — **c**: A male badger (solid black line) and two non-paired raccoon dogs: male (solid grey lines) and female (dashed and dotted lines), summer 2002. — **d**: A female badger (solid black lines) and a female cat (dashed and solid grey lines), summer 2004. — **e**: Raccoon dog pair members: male (dashed and grey lines) and female (black solid lines), autumn 2002. — **f**: A male red fox (dashed and grey lines) and a female raccoon dog (black solid lines), summer 2002.

dogs were occasionally found in the same den in winter (7%, $n = 214$), but very rarely in summer (0.6%, $n = 163$).

Badgers frequently hibernated together with other badgers (32%, $n = 131$), and occasionally rested together also in summer (17%, $n = 146$). Badgers and raccoon dogs also sometimes spent time in the same winter den (24%, $n = 135$). Twice we located two badgers and two raccoon dogs hibernating together, and on four occasions two badgers and three raccoon dogs were wintering in the same den. Badgers and raccoon dogs occasionally spent time in the same daytime resting site in summer (12.5%, $n = 124$).

Discussion

Interaction of animals in the same species

Raccoon dogs are monogamous, the pair share their home range and move together throughout the year (Kauhala *et al*. 1993, Kauhala & Helle 1994, Kauhala & Saeki 2004). This study confirmed these facts: the home ranges of pair members overlapped largely, the distance between them was usually short, they favoured each other's company and were likely to have contact virtually every night. Pair members would definitely infect each other in a rabies epizootic. Neighbouring raccoon dogs avoided their shared area and would rarely have contact (contact rate about 1), and therefore the rate of rabies spread between territories would probably be rather low, if the diseased animals moved around in their home ranges like healthy animals do. However, if they change their behaviour, as some foxes are known to do (Andral *et al*. 1982, Artois & Aubert 1985), they may wander into neighbouring territories more often. On the other hand, raccoon dogs may contract the paralytic ('dump') form of rabies (Ševčenko & Ščerbak 1978), which may decrease the likelihood of rabies transmission between territories.

The social system of badgers in southeast Finland seems to be peculiar; population density is low (about one tenth of that in some areas of England; Cheeseman *et al*. 1981), badgers lived in large overlapping home ranges (about seven adult badgers in our study area) but did not use a communal den (Kauhala *et al*. 2006). It is not known whether these badgers formed a social group or just used the same area independently of each other. However, their paths frequently crossed and they visited the same sites, such as bird feeding places, concurrently. Moreover, two badgers would often rest in the same sett both in summer and winter. In summer, they frequently changed their resting place and companion. Thus their risk of contact was rather high. We lack direct observations of how they behaved towards one another, but in Britain badgers are known to sometimes fight and get bite wounds (Kruuk 1989). Facial licking during friendly encounters may also result in rabies transmission (Smith 2002). Rabies may thus spread easily between badgers. In other areas (e.g. Poland) with low badger density, badgers live in pairs with exclusive territories (Kowalczyk *et al*. 2003), which may decrease the risk of contact (Smith & Wilkinson 2002).

Most cats in the study area were pet cats or semi-feral farm cats (Kauhala *et al*. 2006). The relationships between individuals varied a lot, but most cats lived in overlapping home ranges in or near the village and had frequent contact. Cats often fight, which increases the risk of rabies transmission. Because of the dense cat population, the contact rate between cats is probably high.

The fox data were insufficient, because foxes were difficult to catch and an epizootic of sarcoptic mange killed many foxes in the area. One male fox and two female foxes shared their home range and had contact every now and then. Fox data were, however, gathered mainly in autumn. Male and female foxes probably had more contact during the breeding season. Although the two neighbouring male foxes never had any contact, rabid foxes may spend more time near the boundaries of their home ranges, which increases the probability of disease transmission between territories (Artois *et al*. 1991).

Table 4. Risk of contact between individuals per night and per 3-night period (CR) and the number of possible contacts (contact rate). Population density estimates and the number of additional individuals in the home ranges are based on Kauhala *et al.* (2006) and include only adult individuals. Comparisons between species: we calculated the number of contacts by the first mentioned animal with the latter. [1)] Including foxes (one male and two females) within one home range.

Pair-wise comparisons	Risk of contact per night	CR	Density adults/km^2	Number of additional individuals within the home range	Contact rate	*n*
Raccoon dogs						
pair members	0.88	0.998		1	1.0	3/31
neighbours	0.07	0.20		4–6	0.8–1.2	11/83
All raccoon dogs			0.38–0.77	5–7	1.8–2.2	
Badger–badger	0.30	0.66	0.21–0.26	5	3.3	9/26
Fox–fox[1)]	0.27	0.61	0.35–0.44	2	1.2	3/26
Cat–cat	0.55	0.91		> 10	> 9.1	10/26
Raccoon dog–badger	0.29	0.64		6	3.9	6/24
Badger–raccoon dog	0.29	0.64		8–12	5.1–7.7	6/24
Raccoon dog–cat	0.40	0.78		> 10	> 7.8	8/16
Cat–raccoon dog	0.40	0.78		8	6.3	8/16
Badger–cat	0.17	0.43		> 10	> 4.3	6/13
Cat–badger	0.17	0.43		6	2.6	6/13

Interactions between species

Inter-specific contacts were frequent. Because badger home ranges were the largest (Kauhala *et al*. 2006), they covered a considerable number of raccoon dog home ranges. Raccoon dogs and badgers seemed to favour the common area, their paths frequently crossed, and their risk of contact was quite high (we observed them together several times in a bird feeding place). Badgers and raccoon dogs occasionally used the same dens, which further increases their contact risk. The estimated contact rate between raccoon dogs and badgers was so high that a diseased individual would definitely infect some individuals of the other species. If a raccoon dog infected some badgers, and each diseased badger in turn infected several conspecifics and a few raccoon dogs, badgers may spread the disease effectively. They might transmit the disease from one raccoon dog to another more often than raccoon dogs themselves do; when travelling across many raccoon dog territories badgers may have contact with many raccoon dogs, whereas contact with neighbouring raccoon dogs are infrequent. The significance of badgers as vectors of rabies has probably been underestimated.

The home ranges of raccoon dogs and badgers largely overlapped those of cats, and raccoon dogs seemed to favour the common area with cats. The contact rate between them was thus high. Nobody knew the total number of cats in the area, but it was high due to the large number of semi-feral farm cats in the village. Although badgers did not favour the area they shared with the cats, they also had contact with the cats now and then and disease transmission between them is possible.

Conclusions

The fox has been the main vector of rabies in central Europe since World War II (Wachendörfer & Frost 1980, Anderson *et al*. 1981, Wandeler 1988), but during recent years the role of the raccoon dog has increased in northeast Europe and today it is a more common victim than the fox, at least in Estonia (WHO 2004). In southern Finland, raccoon dogs are common and together with badgers, foxes and cats, they build up a dense community of medium-sized carnivores. Because the home ranges of all four species overlapped largely and no avoidance between individuals of different species was observed, contact between individuals, both within and between species, is frequent. Thus it is highly probable that a disease, such as rabies, would easily spread from one species to another. Although we do not know, whether the 'contacts' in this study would have resulted in bites and rabies transmission in every case, the estimated contact rate between raccoon dogs and badgers, and also between raccoon dogs and cats, was so high that disease transmission was likely. Moreover, the infectious period (for foxes) may sometimes last longer than three days (Macdonald & Voigt 1985).

The significance of badgers as secondary hosts and vectors of rabies is probably much greater than previously assumed. Since badger populations seem to be growing in Finland and elsewhere in Europe (Kauhala 1995, Smith 2002), their significance as rabies vectors may still increase. Because cats also frequently had contact with raccoon dogs and badgers, they may be infected and pose a risk to humans when they return home from their nightly trips. Cat bites have been the reason for many cases of post-exposure treatment of rabies in humans e.g. in Switzerland (Wachendörfer & Frost 1992).

Seasonal differences in the risk of contact could not be verified in this study (data for different seasons were insufficient). In the late 1980s, during an epizootic of sylvatic rabies in Finland, the first cases were observed in April (Westerling 1991), which may be due to dispersal of subadult foxes in late winter (Pastoret & Brochier 1999) and the increased movements of adult animals during the mating season. Another peak in the occurrence of rabies may be in autumn due to the dispersal of juvenile raccoon dogs (Cerkasskij 1980, Westerling 1991, Reinius 1992, WHO 2002, 2003, 2004). Dispersal of raccoon dogs and other vector species should be studied in northeast Europe, because very little is known about this important factor affecting rabies dynamics. In this study we radio tracked adults only and were able to examine the contacts within home ranges and neighbour-to-neighbour contacts but not inter-territorial movements of juveniles, which may effectively spread the disease.

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