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Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: History of colonization, features behind its success, and threats to native fauna

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Abstract We aimed to review the history of the introduction and colonization of the raccoon dog *Nyctereutes procyonoides* in Europe, the features behind its successful expansion and its impact on native fauna. The raccoon dog quickly colonized new areas after being introduced to the European part of the former Soviet Union. Today it is widespread in Northern and Eastern Europe and is still spreading in Central Europe. Features behind its success include its adaptability, high reproductive potential, omnivory, hibernation in northern areas, multiple introductions with > 9000 individuals from different localities, and tendency to wander enabling gene flow between populations. Firm evidence of the raccoon dog's negative impact on native fauna, such as a reduction in bird populations, is still scarce. Raccoon dogs may destroy waterfowl nests, although a nest predation study in Latvia did not confirm this. Predator removal studies in Finland suggested that the raccoon dog's impact on game birds is smaller than expected. However, raccoon dogs may have caused local extinction of frog populations, especially on islands. Raccoon dogs may compete with other carnivores for food, for example for carrion in winter, or for the best habitat patches. In northern Europe potential competitors include the red fox *Vulpes vulpes* and the badger *Meles meles,* but studies of their diets or habitat preferences do not indicate severe competition. The raccoon dog is an important vector of diseases and parasites, such as rabies, *Echinococcus multilocularis* and *Trichinella* spp. and this is no doubt the most severe consequence arising from the spread of this alien species in Europe [*Current Zoology* 57 (5): 584–598, 2011].

Keywords *Nyctereutes procyonoides*, Competition, Introduction, Predation, Vector of diseases and parasites

1 Introduction

Invasive species have many ecological effects and may threaten biological diversity (e.g., Ebenhard, 1988; Hulme, 2007; Vilà et al., 2010). Alien species may alter habitat, and predate on or compete with native fauna or be important vectors of diseases and parasites. They may also hybridize with native species and thus affect their genetic variability. Besides ecological effects, they may have considerable economic impacts on invaded areas (Vilà et al., 2010).

There are 44 alien mammal species in Europe, 33 of which are considered established, i.e. they form self-sustaining populations (Genovesi et al., 2009). These include several carnivore species, such as the American mink *Neovison vison*, raccoon *Procyon lotor* and raccoon dog *Nyctereutes procyonoides*. They were brought to Europe because of their valuable fur or as pets and either escaped or were intentionally introduced into the wild (Genovesi et al., 2009). These carnivores are widespread in Europe, occurring in over 10 European counties.

The raccoon dog is one of the most successful alien carnivores in Europe. It has spread rapidly into many European countries after being introduced by Russians during the first half of the 20th century (e.g., Lavrov, 1971; Lever, 1985; Helle and Kauhala, 1991). The raccoon dog has been suspected of causing damage to native fauna through predation, but firm evidence of this is scarce (Lavrov, 1971; Nasimovič and Isakov, 1985; Kauhala, 2004). Raccoon dogs may also compete with native medium-sized carnivores, such as the Eurasian badger *Meles meles* and the red fox *Vulpes vulpes* (Jędrzejewska and Jędrzejewski, 1998; Kowalczyk et al., 2008). Furthermore, the raccoon dog is an important vector of zoonoses and parasites, such as rabies *Echinococcus multilocularis* and *Trichinella* spp (e.g., Oivanen et al., 2002; Deplazes et al., 2004; Holmala and

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Kauhala, 2006; Romig et al., 2006). Its role as a vector of diseases and parasites is likely to cause considerable ecological and economic impacts and may also cause health problems to humans.

Our aim was to review the published literature on the history of the introduction and colonization of the raccoon dog, the features behind its success and its ecological effects in Europe.

2 Original Distribution and Subspecies

The raccoon dog originates from the Far East. Six subspecies are usually distinguished: *N. p. procyonoides* (Gray, 1834) in most of China and northern Vietnam, *N. p. orestes* (Thomas, 1923) in the mountainous region of Yunnan in China, *N. p. koreensis* (Mori, 1922) in Korea, *N. p. ussuriensis* (Matschie, 1907) in the Amur and Ussuri regions of Siberia and eastern China, *N. p. viverrinus* (Temminck, 1838) in Japan (except Hokkaido) and *N. p. albus* (Beard, 1904) in Hokkaido (Ellerman and Morrison-Scott, 1951; Ward and Wurster-Hill, 1990).

The climate in the original distribution area varies from the subtropical regions of Japan, northern Vietnam and southern China to a harsh continental climate with cold winters in Mongolia and southeast Siberia. Accordingly, raccoon dogs in different areas have adapted to different climates, habitats and diets, which can be seen in their body size, fat reserves, thickness of fur, and their behavioral and dental characteristics (Kauhala and Saeki, 2004a).

3 Introductions to Europe

A total of about 9100 individuals of the Ussuri raccoon dog *N. p. ussuriensis* were introduced, mainly to European parts of the former Soviet Union, between 1929 and 1955 (Lavrov, 1971). This subspecies is now widespread in northern and Eastern Europe (Mitchell-Jones et al., 1999; Kauhala and Saeki, 2004b). Its original range in south-east Siberia covers the valleys of the Amur and Ussuri rivers and the Khankai lowland, the shores of the Sea of Japan and also areas as far inland as Komsomol'sk (Novikov, 1962). In its native range the winters are cold with thick snow cover, and raccoon dogs are forced to hibernate. It has thick winter fur and accumulates large fat deposits in autumn to survive through the harsh winter (Stroganov, 1969). The Ussuri raccoon dog was thus pre-adapted to survive in areas with long winters in northeast Europe. Its thick fur was the reason that Russians introduced it into the western parts of their country.

Russians first bred the animals in fur farms and then released them deliberately so as to have a new valuable fur animal in the wild. The first introductions in 1928 or 1929 (415 pregnant females) were made to Transcaucasia, Abkhazia, southern Ossetia and Karatalinia (Lever, 1985). In many areas, especially on the Asian side of the Caucasus, the populations did not flourish but remained small or vanished completely.

More raccoon dogs were released in the mid-1930s e.g., in Leningrad, Novgorod and Kalinin Provinces, in North Caucasus, Ryazan Province south of Moscow, Kirgizia and Ukraine (Fig. 1; Lavrov, 1971). Raccoon dogs were introduced to Astrakhan between 1936 and 1939 and to Moldavia between 1949 and 1954 (Lever, 1985). They were also released in Estonia in the 1950s, in Pskov in 1947 and in the Karelian Isthmus near Finland in 1953 (Lavrov, 1971). One hundred raccoon dogs were released in Belarus in 1963 (Lever, 1985). Some individuals were also introduced further north, to the Kola Peninsula in 1936 and to Archangel in 1950-1953 (Lavrov, 1971).

4 Spreading in Europe

Many introductions made to the European part of the Soviet Union were successful and the populations started to increase rapidly. Populations spread at a rate of 40 km per year (and even up to 120 km per year) from the introduction sites (Lavrov, 1971).

The first wandering raccoon dogs were seen in Finland in the 1930s and 1940s (Siivonen, 1958; Suomalainen, 1950; Fig. 1). The raccoon dog started to truly colonize Finland in the mid-1950s, but there was a time-lag of about 10 years until rapid population increase started in the mid-1960s. The phase of rapid population growth lasted for another decade and by the mid-1970s most of southern and central Finland was inhabited (Helle and Kauhala, 1991). After this phase of increase the population growth seemingly ceased and numbers fluctuated for 10–15 years until they started to increase again. The raccoon dog population is still increasing, and today the raccoon dog is the most common medium-sized carnivore in Finland (Kauhala, 2007). The hunting bag increased from 818 in 1970/71 to 172,000 in 2009 (Finnish Game and Fisheries Research Institute, 2010[1]).

Raccoon dogs were found all over Estonia in the 1950s (Lavrov, 1971). Their numbers remained low,

[1] Finnish Game and Fisheries Research Institute, 2010. Hunting 2009. Official Statistics of Finland – Agriculture, Forestry and Fishery 6/2010, 1–34.

however, because of numerous wolves *Canis lupus* and lynx *Lynx lynx*, the natural enemies of raccoon dogs in Estonia. In contrast, wolves and lynx were very scarce in Finland in the 1960s and 1970s (Ermala, 2003), which may have contributed to the rapid spread of raccoon dogs in the country. Raccoon dogs were found all over Lithuania in the late-1950s and thus colonized the country in about 10 years (Lavrov, 1971; Fig. 1). In Latvia 1000 raccoon dogs were observed or hunted as early as 1951.

The first raccoon dogs were seen in Sweden in 1945 (Notini, 1948) but after that raccoon dogs were observed only occasionally in Norrbotten, until they started to spread a few years ago (P.-A. Åhlèn, pers. com.). The reason for this long time-lag between the first observations and the rapid population increase in Sweden is not known. In Norway (Finnmark) the first records of raccoon dogs are from 1983 (Wikan, 1983). There were no other observations in Norway until winter 2007/2008 when a few raccoon dogs were shot in central Norway (R. Andersen, pers. com.). They most probably invaded central Norway via Sweden.

Raccoon dogs were first noticed in Poland in 1955 and in East Germany in 1961/1962 (Dehnel, 1956; Nowak and Pielowski, 1964; Nowak, 1984). Fifteen years later, i.e. by the end of the 1960s, almost all of Poland, with the exception of higher parts of the mountains in the south, was occupied by the species (Fig. 2). Nowadays the raccoon dog is among the most common carnivores in some areas of the country (Jędrzejewska and Jędrzejewski, 1998). Over 11,000 raccoon dogs are caught in Poland annually, and the hunting bag increases from year to year. In Germany, the raccoon dog population remained sparse until it started to increase in the 1990s, thirty years after the first observations, especially in eastern parts of the country (Ansorge and Stiebling, 2001). The hunting bag has increased exponentially since the early 1990s in Germany (Drygala et al., 2008a, b), and in Brandenburg (eastern Germany) alone the hunting bag increased from 398 in 1995/1996 to

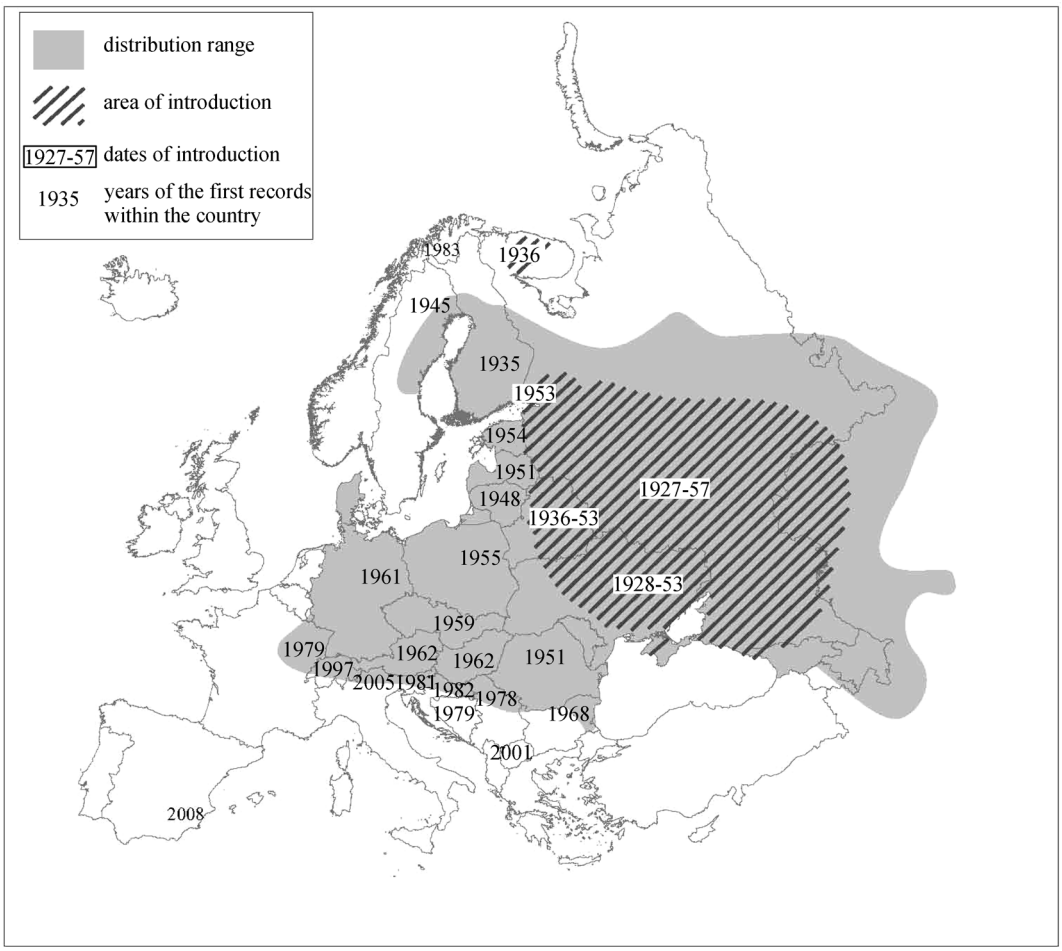

Fig. 1 Area of raccoon dog introductions, the first observations of the species in different countries and its present distribution in Europe

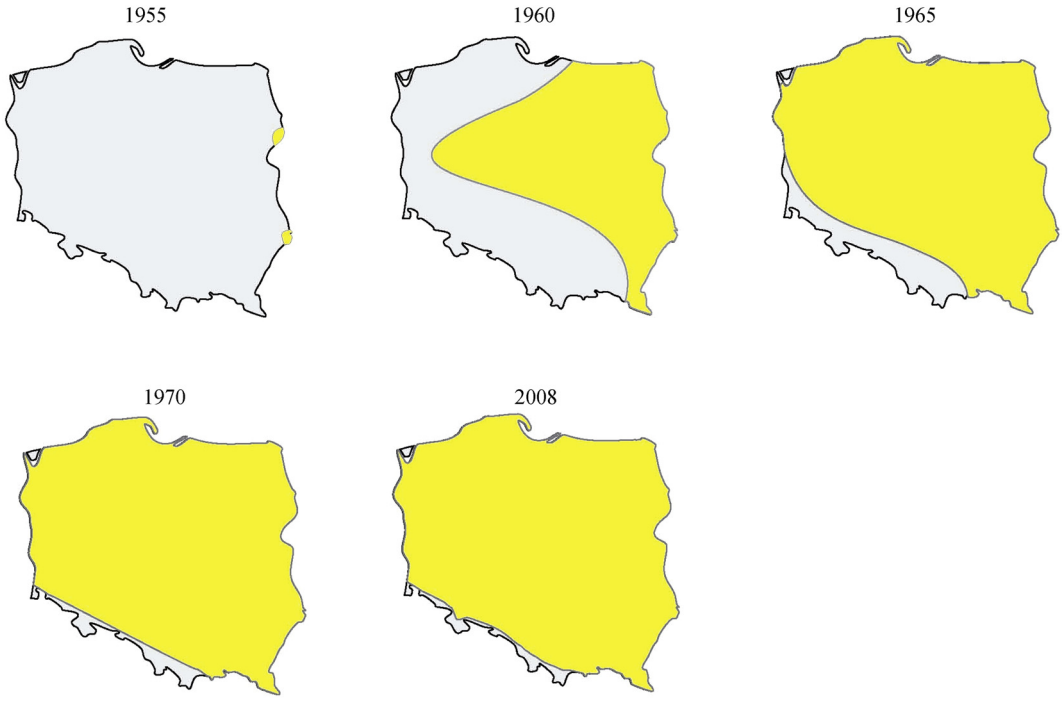

Fig. 2 Expanding of the frontier of raccoon dog distribution across Poland, based on Nowak and Pielowski (1964), Pielowski et al. (1993), and Kamieniarz and Panek (2008)

11,659 in 2001/2002 (Anon, 1997[1, 2]). In the 2008/2009 hunting season, official figures show 30,000 animals were shot in Germany (Anon, 2009[3]). The raccoon dog has also spread to Denmark (Jutland and Fyn) where 25 observations of the species were made between 1995 and 2003 (Baagøe and Jensen, 2007).

The first observations of raccoon dogs were made in Eastern and Central Europe between 1951 and 2002 (Nowak and Pielowski, 1964; Artois and Duchêne, 1982; Nowak, 1984; Lever, 1985; Weber et al., 2004; Fig. 1). For instance, in France the first observation of the species was made in 1975 or 1979 and the first case of reproduction was observed in 1988 (Léger and Ruette, 2005). In northern Italy raccoon dogs were seen and photographed in 2005 (P. Genovesi, in litt.), showing that the species has managed to cross the Alps. Today the raccoon dog is also found occasionally in the Netherlands, Moldova, Slovenia, Croatia, Bosnia-Herzegovina, and Serbia. It has also been seen once in Macedonia (Ćirović and Milenković, 1999; Mitchell-Jones et al., 1999; Ćirović, 2006). One raccoon dog was run over by car in SE Spain in 2008 (Anon, 2008[4]).

The northern limit of the raccoon dog's distribution is determined by climate. It can live in areas where the mean annual temperature is above 0°C, the thickness of snow cover is < 80 cm, the snow cover lasts < 175 days and the length of the growing season for plants is at least 135 days (Lavrov, 1971). Today the northern limit of its permanent distribution lies at the Arctic Circle (Helle and Kauhala, 1991). Raccoon dogs will possibly widen their distribution area northwards due to climate change. Increased spring precipitation in the form of snow at higher latitudes may, however, compensate for the effect of global warming (Melis et al., 2010).

5 Features behind the Raccoon Dog's Success

5.1 Population genetics

One of the main factors responsible for the successful expansion of raccoon dogs in Europe was mass introduction over a wide area coupled with a large amount of genetic variation. Together with their natural tendency to disperse and high migratory ability this allowed

[1] Anon., 1997. German Hunter's Union, Union of the German regional hunting association ed. Bonn: DJV–Handbücher (In German).
[2] Anon., 2003. German Hunter's Union, Union of the German regional hunting association ed. Bonn: DJV–Handbücher (In German).
[3] Anon., 2009. German Hunter's Union, Union of the German regional hunting association ed. Bonn: DJV–Handbücher (In German).
[4] Anon., 2008. http://anseblog.blogspot.com/2008/06/perro-mapache-en-murcia.html.

raccoon dogs to invade neighboring areas in a relatively short time. More research on the colonization process should be done, because the exact details are still poorly known.

Genetic data on raccoon dogs is still scarce. So far, populations from several locations in Finland and Germany have been investigated by Pitra et al. (2010). Reconstructed phylogenies reveal two major clades in European raccoon dogs, which diverged approximately 457,800 years ago. In total, nine haplotypes were found in raccoon dogs in Europe with a sequence divergence of 0.2%–3.2% (mean 1.3%).

As suggested by Pitra et al. (2010), a combination of factors including multiple translocations with use of individuals from different geographical areas, secondary contact and admixture of two co-occurring separate maternal lineages with divergent evolutionary histories are probably the main determinants of the genetic variability of raccoon dogs in Europe. It was probably a sequential, two-step process that included reduction in genetic variation due to the founder effect and population bottlenecks during initial introductions in the European part of the former Soviet Union in 1929–1955, followed by an increase in genetic variation by hybridization of individuals from multiple native-range sources representing divergent haplogroups (Pitra et al., 2010). However, according to Ansorge et al. (2009) there was no indication of the founder effect or inbreeding in the European populations, indicated by the same level of variability that can be seen in the native Amursk population. Additionally, phylogenetic analysis indicates different invasion corridors of the species in the western range of raccoon dog distribution in Central Europe, as earlier suggested by Ansorge et al. (2009), with the secondary contact zone between previously geographically and genetically different source populations in Germany (Pitra et al., 2010).

5.2 Adaptability of raccoon dogs

An important factor behind the raccoon dog's success is the very high plasticity of the species. They are true omnivores and eat anything they can catch (reviewed in Sutor et al., 2010). In Białowieża Forest, the index of food niche breadth for raccoon dogs was 6.25, nearly twice as high as in the next species with the widest niche – the red fox (3.77; Jędrzejewska and Jędrzejewski, 1998). The diet of raccoon dogs varies between areas and seasons, according to the availability of different food sources (e.g., Ivanova, 1962; Nasimovič and Isakov, 1985; Sutor et al., 2010).

In many areas, small mammals form the bulk of their diet in all seasons (Bannikov, 1964; Nasimovič and Isakov, 1985; Kauhala et al., 1998a; Bao et al., 2005; Sutor et al., 2010). Carrion may reach up to 76% of biomass consumed during harsh winters (Jędrzejewska and Jędrzejewski, 1998; Sidorovich et al., 2000). Frogs, lizards, invertebrates and birds are also frequently consumed (e.g., Barbu, 1972; Jędrzejewska and Jędrzejewski, 1998; Sutor et al., 2010). Raccoon dogs eat berries and fruit, especially in late summer and autumn because they serve as an important food source when raccoon dogs fatten themselves before entering winter dormancy (e.g., Nasimovič and Isakov, 1985; Kauhala et al., 1993a; Kauhala, 2009; Sutor et al., 2010).

The preferred habitats of raccoon dogs are wet open habitats: damp meadows and forests with sparse canopy but abundant undergrowth, marshlands, river valleys and gardens. However, they may occupy various habitats from continuous forests to open agricultural landscapes and suburban areas (Jędrzejewska and Jędrzejewski, 1998; Kauhala and Auttila, 2010; Drygala et al., 2008c). However, habitat preferences at the western and southern edge of the distribution area are poorly known.

5.3 Life history

The raccoon dog has a high reproductive capacity; higher than expected for a medium-sized carnivore species (Kauhala 1996a). This has also contributed to its success. Mean litter size is 8–10 in areas with favourable conditions, both in native and introduced ranges (Judin, 1977; Helle and Kauhala, 1995; Kowalczyk et al., 2009). The maximum litter size at birth in a sample of 203 adult females from southern Finland was 16. The maximum number of embryos was 18, and that of *corpora lutea* was 23 (Helle and Kauhala, 1995). Raccoon dogs are monogamous and the male participates in pup-rearing by warming and guarding the pups when the female is foraging (Ikeda, 1983; Yamamoto, 1987; Kauhala et al., 1998b; Drygala et al., 2008a). Females can thus spend a lot of time foraging and produce enough milk for a large litter.

The raccoon dog's opportunistic diet further contributes to the large litters and also survival rate of juveniles. The survival rate is highest when the crop of berries is good (Kauhala and Helle, 1995). The mean annual mortality rate of juveniles during their first year of life is as high as 88% – 89% in southern Finland (Helle and Kauhala, 1993). Raccoon dogs thus produce many pups, but most of them die early in their life, and the mortality rate of juveniles is the major mortality factor of the species. The mortality rate is lowest (ca. 43%) among middle-aged (2–4 year old) raccoon dogs and increases

after 5 years of age. Only one per cent of individuals reach the age of 5 years, with the maximum life span being about 8 years (Kauhala and Helle, 1995). Raccoon dogs generally reach sexual maturity at the age of 10 months, but the reproductive value is highest among 2-3-year old females which thus produce most of the pups in the population (Helle and Kauhala, 1995).

5.4 Hibernation

In Europe, raccoon dogs are found from the warmer conditions of Hungary and the Balkans to the much harsher conditions of northern Europe (Kauhala and Saeki, 2004b). In cold climates raccoon dogs hibernate during winter. During hibernation their body temperature is 1.4 – 2.1 °C lower than during summer. This habit is unique among canids, and may also have contributed to the successful spread of raccoon dogs in northern Europe (Mustonen et al., 2007).

In winter, raccoon dogs settle in shelters which protect them against cold and predation (Kowalczyk and Zalewski, 2011). In Poland, active badger setts are most often selected by raccoon dogs. Badger setts can also be used as breeding dens (Kowalczyk et al., 2008).

Hibernation usually lasts from November until March (in Finland), but when the winter is mild raccoon dogs may be active even in mid-winter. They usually sleep when the air temperature is < –10 °C, snow depth > 35 cm and day length < 7 h (Kauhala et al., 2007). Most raccoon dogs are active when the temperature is above zero, there is no snow and day length is > 10 h. For instance, in Germany raccoon dogs do not usually hibernate (Drygala et al., 2008b).

Raccoon dogs are very well adapted to a long period of food deprivation in winter (Asikainen et al., 2002). They fatten themselves during autumn and almost double their body weight between early summer and late autumn (Korhonen, 1988a, b; Kauhala, 1993; Mustonen et al., 2007). Fattening in autumn and sleeping in winter are regulated by hormonal changes (Nieminen et al., 2002). Thyroid hormone levels are low during winter and the animal thus adapts its general metabolism to the availability and requirements of energy (Korhonen, 1987[1]). In fur farms, raccoon dogs lose their appetite when air temperature decreases to –5 °C, which indicates an endogenous behavioural pattern: when it is too cold raccoon dogs stop eating and hibernate.

5.5 Dispersal

Another feature behind the success of raccoon dogs is their tendency to wander (Nasimovič and Isakov, 1985). After introduction in Europe, raccoon dogs wandered as far as 300 km in a year (Nasimovič and Isakov, 1985) or 500 km within three years (Nowak, 1973). Adults may disperse in a colonizing population (Sutor, 2008) whereas in stable populations only juveniles usually disperse (Nasimovič and Isakov, 1985; Kauhala et al., 1993b; Kauhala and Helle, 1994). The mean dispersal distances, estimated on the basis of home range sizes, were 14 km for females and 19 km for males in south-east Finland, with the mean maximum distances being 48 km and 71 km respectively (Kauhala et al., 2006). The maximum straight line distance in a couple of months was 145 km in southern Finland (Kauhala and Helle, 1994). In north-east Germany, the mean and maximum dispersal distances of both sexes were 13.5 km and 91 km respectively (Drygala et al., 2010). Very little is still known about dispersal routes and more research on the subject is required.

The successful expansion of raccoon dogs in Europe was also possible due to the secretiveness of the species and low persecution at the beginning of invasion. Raccoon dogs are nocturnal animals, utilising mainly wet habitats covered with dense vegetation and showing inactivity in winter. These facts decrease their vulnerability to persecution (Kauhala et al., 2007; Kowalczyk et al., 2008). In many countries the species was only persecuted once it had successfully established its population. In some areas hunters are not very interested in hunting raccoon dogs because the fur of wild animals has low value.

6 Density in Different Landscapes

Population density varies according to the structure of the landscape. In Finland, Kauhala et al. (2010) described an inverse relationship between home range size and the proportions of meadows and gardens in the home range. Habitat richness (number of habitat patches per ha) also affected home range size: home ranges were small in areas where the landscape was a small-scale mosaic consisting of meadows with abundant undergrowth, gardens where raccoon dogs could find fruit and berries and small patches of mixed forests (Kauhala et al., 2010).

Because home range size and population density tend to be negatively correlated in monogamous canids with exclusive home ranges (Trewhella et al., 1988; Contesse

[2] Korhonen H, 1987. Energy metabolism of raccoon dog (*Nyctereutes procyonoides*, Gray 1834): Applied perspective to common farming practices. Publications of the University of Kuopio. Original Reports 1/1987, 1– 69.

et al., 2004; Woodroffe et al., 2004), population density can be estimated from home range size. The maximum density is then two adults in each home range in pup-rearing season when overlap of home ranges is smallest (Kauhala et al., 1993b). For instance, in the 'best' areas of southern Finland home ranges are only 100 ha and raccoon dog density can be up to two adults per km^2, whereas in poorer areas with large spruce forests pup rearing home ranges are about 260 ha and the corresponding density is < 0.8 adults per km^2 (Kauhala et al., 2010).

In northern Germany pup rearing home ranges are about 200 ha (Drygala et al., 2008b) and the density would thus be up to one adult per km^2. The area is a mosaic of mixed forests, wetlands and maize fields. As the raccoon dog population in Germany is still increasing and spreading, population density may also increase. In forests of Suwałki Landscape Park, NW Poland, raccoon dog density was estimated to be only 0.37 individuals per km^2 (Goszczyński, 1999). In Białowieża Primeval Forest (Poland) density was 0.5 – 0.7 ind./km^2, and mean home range size 5.0 km^2 (Jędrzejewska and Jędrzejewski, 1998; Kowalczyk et al. unpublished).

7 Predation on Native Fauna

Hunters in particular have suspected that raccoon dogs destroy the nests of game birds (Lavrov, 1971). According to Naaber (1971, 1984), raccoon dogs robbed 85% of waterfowl nests in some areas of Estonia. Ivanova (1962) found remains of birds (mainly water birds) in 45% of raccoon dog scats collected in a river valley in Voronez. When the raccoon dog population increased rapidly in Russia, it was thought to be very harmful but, according to Lavrov (1971), this was not based on fact. Raccoon dogs were accused of causing the decline of grouse populations even in areas where raccoon dogs did not occur (Lavrov, 1971). Even today robust scientific studies clearly demonstrating that raccoon dogs cause damage to native birds are scarce.

7.1 Diet studies

Birds eaten by raccoon dogs are mainly passerines (Kauhala, 2009; Sutor et al., 2010). They are more important for raccoon dogs when voles are scarce than during vole peak population times (Ivanova, 1962; Judin, 1977; Kobylińska, 1996). It is not known whether raccoon dogs have caused a decline in passerine populations. The occurrence of birds in the diet increases with latitude, i.e. birds are consumed especially in northern Europe (Sutor et al., 2010). The increase of carnivory with increasing latitude has also been detected among other omnivorous mammals (Vulla et al., 2009).

According to diet studies (84 data sets from different parts of native and introduced ranges) it is unlikely that raccoon dogs affect game bird populations in general. This is because, excluding some Finnish data, there were remains of waterfowl or grouse in only 0–5% of the feces or stomachs of raccoon dogs (Kauhala, 2009).

Although raccoon dogs may prey on ground-nesting birds such as waterfowl (Barbu, 1972; Włodek and Krzywiński, 1986; Schwan, 2003; Sutor et al., 2010), they probably consumed many of the non-passerine birds as carcasses (Novikov, 1962; Barbu, 1972; Woloch and Rozenko, 2007; Kauhala and Auniola, 2001). Waterfowl, especially female eiders *Somateria mollissima,* occurred commonly in the feces of raccoon dogs in the SW archipelago of Finland (Kauhala and Auniola, 2001). However, a viral disease killed many brooding eiders during the years (1998–1999) when the data were collected and raccoon dogs probably found most of the eiders as carcasses. Raccoon dogs also catch sick or injured birds left behind by hunters (Samusenko and Goloduško, 1961; Pavlov and Kiris, 1963; Barbu, 1972; Naaber, 1974; Viro and Mikkola, 1981; Kauhala et al., 1993a).

Remains of egg shells, including those of domestic poultry, occurred in 0 – 41% of the samples (Kauhala, 2009). In most studies, they are not mentioned at all. It is thus hard to know the extent of egg consumption by racoon dogs. Opermanis et al. (2001) found, however, that raccoon dogs destroyed only 0.3% of waterfowl nests in a wetland area of Latvia.

Amphibians (e.g., *Rana* spp., *Bufo* spp., *Bombina* spp. and *Triturus cristatus*) commonly occur in the diet of raccoon dogs in spring and summer (e.g., Ivanova, 1962; Lavrov, 1971; Barbu, 1972; Viro and Mikkola, 1981; Kauhala et al., 1993a, 1998a; Jędrzejewska and Jędrzejewski, 1998; Sutor et al., 2010). Both adult frogs and tadpoles are easy prey for raccoon dogs and this may cause a decline in frog populations, especially on islands and in other fragmented or isolated areas (Kauhala and Auniola, 2001; Sutor et al., 2010). Frogs were scarce in the diet of raccoon dogs in the outer archipelago in southern Finland, although they occurred commonly in the diet on the mainland (Kauhala and Auniola, 2001). It is possible that raccoon dogs had already caused a decline in the frog populations of the archipelago.

7.2 Predator removal studies

Predator removal studies do not provide firm evidence of the harmfulness of raccoon dogs to game bird

populations. Studies in Finland indicated that the breeding success of ducks improved in only one study area in northern Finland where raccoon dogs occurred only occasionally even at the beginning of the experiment (Kauhala, 2004). The most frequently removed predators in the area were red foxes and pine martens *Martes martes*. In southern Finland where raccoon dogs are common, the breeding success of dabbling ducks was positively correlated with a raccoon dog index. Furthermore, the breeding success of ducks improved in the predator protection area of southern Finland during the experiment (Kauhala, 2004). In the predator removal area chick production declined at the end of the study with a simultaneously increasing fox population. The most frequently removed predators in this area were raccoon dogs, which may have resulted in an increase in fox populations which, in turn, may have affected the breeding success of ducks. The raccoon dog index also correlated positively with the reproductive success of black grouse in southern Finland (Kauhala et al., 2000).

Another predator removal study in Finland indicated, however, that raccoon dog removal might have had some effect on the breeding success of ducks (Väänänen et al., 2007), but the change was not significant. Furthermore, chick production of, for example, mallards *Anas platyrhynchos* and coots *Fulica atra,* increased at first but then declined after the second year of raccoon dog removal. This happened simultaneously with the decline in the raccoon dog index. These results resemble those of the predator removal study described above and probably relate to the interactions between different predators. On the other hand, when different areas were compared there was a negative relationship between the breeding success of mallards and raccoon dog abundance index, so more research is needed on this topic in order to understand these contradictory outcomes.

8 Competition with Native Carnivores

Raccoon dogs consume carrion during all seasons if available, but carcasses are especially important for them in winter when other food sources are scarce (Jędrzejewska and Jędrzejewski, 1998; Sidorovich et al., 2000, 2008). Raccoon dog scavenging was recorded on 47% of carcasses available in Białowieża Forest (Poland; Selva et al., 2005). According to Sidorovich et al. (2000) raccoon dogs compete with native carnivores for carcasses in Belarus in late winter. This competition can be so severe that the increasing raccoon dog population appears to have caused a decline in native carnivore populations, including the red fox, brown bear *Ursus arctos* and pine marten. The polecat *Mustela putorius* has probably suffered most from competition with raccoon dogs (Sidorovich et al., 2000). This information is, however, based only on correlative data and firm evidence is lacking. However, in Białowieża Forest, the rate of food niche overlap was very high (59%) among raccoon dogs and polecats in spring and autumn (Jędrzejewska and Jędrzejewski, 1998). The polecat population has also decreased in Finland during recent decades. The probable reasons for this include habitat changes and competition with other carnivores (Liukko et al., 2010).

In northern Europe, the red fox and the badger might compete directly or indirectly with raccoon dogs for food, habitats or den sites. Correlative data from Finland showed that when raccoon dogs were heavily hunted and their population decreased, the fox population started to increase (Kauhala, 2004). This may be a coincidence, but it can also indicate that raccoon dogs and red foxes compete for some resources in Finland. In southern Finland, there was some overlap in the diet of raccoon dogs, badgers and foxes but differences also existed: the badger consumed more invertebrates and the fox more mammals and birds than the raccoon dog (Kauhala et al., 1998a). Furthermore, female foxes in Finland have become more carnivorous after the arrival of the raccoon dog, as revealed by a study on dental morphology (Viranta and Kauhala, 2011). This case of character displacement points to the conclusion that foxes and raccoon dogs have competed for food resources in Finland. However, in winter when food is scarcest both raccoon dogs and badgers hibernate and, hence, no competition for food between the raccoon dog and other carnivores exists in this season in northern areas.

In north-eastern Poland, the diet of raccoon dogs overlaps 41% with red foxes and 35% with badgers in spring and summer. In winter, diet overlap between raccoon dogs and red foxes increases to 62%, when both species utilize more carrion. Other species that raccoon dogs may compete with are semi-aquatic species (American mink – 38% and river otter *Lutra lutra* – 33%; Jędrzejewska and Jędrzejewski, 1998).

A habitat preference study from southern Finland indicated that the habitat preferences of raccoon dogs and badgers differed to some extent: raccoon dogs favored meadows (including clear-felled areas) and open woodlands with abundant and tall undergrowth as well as gardens, whereas badgers favored forests with a thick canopy but sparse undergrowth (Kauhala and Auttila,

2010). Management of forests using clear felling (common in Finland) may thus benefit raccoon dogs at the expense of native badgers. Both species were, however, flexible in their habitat use and when the most favored habitats were not available they used the same habitats, such as fields (Holmala and Kauhala, 2009; Kauhala and Auttila, 2010). Whether they compete in these circumstances for the best habitat patches is unknown and certainly requires further research. In north-eastern Poland the habitat niche of raccoon dogs overlapped 91% with that of the fox and 77% with that of the polecat (Jędrzejewska and Jędrzejewski, 1998).

Raccoon dogs commonly use badger setts (Kauhala and Holmala, 2006; Kowalczyk et al., 2008). Raccoon dogs thus benefit from the occurrence of badgers in the area. The habit of using badger setts has probably facilitated the invasion of raccoon dogs in Europe (Kowalczyk et al., 2008), because deep and complex badger setts might offer refuge against the cold and predation (Kowalczyk and Zalewski, 2011). Common use of burrows may lead also to intra-guild predation. In Białowieża Forest, the killing of raccoon dog pups by badgers was recorded. Raccoon dogs may also influence badger breeding success, as no concurrent breeding of badgers was recorded in badger setts in which raccoon dogs bred (Kowalczyk et al., 2008).

9 Raccoon Dogs as Vectors of Diseases and Parasites

9.1 Rabies

Although the red fox has been the main terrestrial wildlife rabies vector in Europe since the 2nd World War (e.g., Anderson et al., 1981), the significance of the raccoon dog as a vector of rabies has recently increased (Holmala and Kauhala, 2006; WHO, 2009). Seventy-three percent of the observed rabies cases were in raccoon dogs during an epizootic of sylvatic rabies in Finland in 1988-1989 (Nyberg et al., 1990; Westerling, 1991; Westerling et al., 2004). In the Baltic States as well, the raccoon dog is an important secondary host of rabies: the number of observed rabies cases in raccoon dogs in 2009 was 24 in Estonia and 28 in Lithuania (WHO, 2009). The corresponding figures for fox cases were 24 and 17. In Lithuania, the prevalence of rabies in raccoon dogs increased almost 2.5 times from 11.8% in 1994 to 28.9% in 2004 (Mačiulskis et al., 2006). In Russia, Belarus and Ukraine rabies also occurred in raccoon dogs in 2009 (WHO, 2009). In Poland, the raccoon dog is the second (after red fox) most important vector of rabies among wild animals. In 2001-2005, in north-eastern Poland (24,000 km^2), 131 cases of rabies were recorded in raccoon dogs (Siemionek et al., 2007). When oral vaccination was used, the number of rabies cases in raccoon dogs in Poland declined to 7–15 in the whole country (Smreczak et al., 2006, 2007, 2008; Smreczak and Żmudziński, 2009).

The role of the raccoon dog as a vector of rabies may further increase in Europe, because the raccoon dog population is still growing and spreading (Ansorge and Stiebling, 2001; Drygala et al., 2008a, b). The total number of reported wildlife rabies cases (excluding bats) in Europe in 2009 was 4114, 302 of which were in raccoon dogs (WHO, 2009).

Bait vaccinations against rabies have proved to be effective and have resulted in many rabies-free countries in Europe (Wandeler, 1988; Artois et al., 2001; Pastoret et al., 2004). The increasing raccoon dog population may, however, alter the situation: the current strategies to control wildlife rabies may not be effective enough in a community of two important vector species; the red fox and the raccoon dog (Holmala and Kauhala, 2006; Singer et al., 2009).The hibernation of the raccoon dog may further complicate the situation (Schneider et al., 1988). Indeed, a modelling study showed that epizootics in the community of two species were stronger than expected for single species (Singer et al., 2009). Rabies could persist in the community, even if the disease was not spreading in an individual vector species due to low density. In the community of two vector species raccoon dogs were usually the major rabies host, and the number of cases in fox populations depended on raccoon dog density. When raccoon dog density was high, invasive raccoon dogs could even outcompete native foxes (Singer et al., 2009). Additionally, badgers may act as a spill-over species and suffer from rabies epizootics.

Other viruses also dangerous to humans, including SARS (severe acute respiratory syndrome) and avian H5N1 viruses have been found in raccoon dogs in China (Guan et al., 2003; Changchun et al., 2004; Qi et al., 2009). Raccoon dogs have additionally fallen victim to canine distemper virus (CDV) in Japan (Machida et al., 1993; Aoyaki et al., 2000). CDV may have the most far-reaching consequences of all infectious agents for free-living carnivores (Deem et al., 2000). Data from Germany indicates the possible transmission of CDV between wild carnivores and the domestic dog *Canis familiaris* (Frölich et al., 2000). The prevalence of the virus was much higher in urban and suburban foxes than in rural ones. To our knowledge there is no data showing the role of the raccoon dog as a vector of CDV in

the carnivore community (including domestic dogs *Canis familiaris*), but this possibility cannot be ruled out.

9.2 Parasites

Alveolar echinococcosis caused by *Echinococcus multilocularis* is a dangerous emerging zoonosis in Europe. The parasite can even cause lethal diseases in humans (Eckert et al., 2000; Kern et al., 2003; Moks et al., 2005). The red fox has been the definite host in Central Europe, but recently cases have been detected in raccoon dogs too (Thiess et al., 2001; Machnicka-Rowinska et al., 2002; Deplazes et al., 2004; Kapel et al., 2005). Prevalence in foxes is high (35%–65%) in the core area of this zoonosis (Deplazes et al., 2004). Small mammals, mainly rodents, are the intermediate hosts of the parasite (Schantz et al., 1995).

E. multilocularis is spreading in Europe and new endemic areas have been detected in recent years (Eckert et al., 2000). *E. multilocularis* has even invaded cities (Hofer et al., 2000; Deplazes et al., 2004). The parasite is found in Denmark, the Netherlands, Belgium, France, Germany, Poland, Czech Republic, Slovakia, Switzerland, Austria, northern Italy, Slovenia and Lithuania (Romig et al., 2006; Vergles Rataj et al., 2010). *E. multilocularis* has reached as far as Latvia and Estonia in the north: prevalence in foxes was 35.6% in Latvia and 29.4% in Estonia (Moks et al., 2005; Bagrade et al., 2008). The parasite is so far absent in Finland (Oksanen and Lavikainen, 2004).

The reason behind the spread of *E. multilocularis* in Europe is probably the growing fox and raccoon dog populations (Deplazes et al., 2004; Romig et al., 2006). The raccoon dog is highly susceptible to *E. multilocularis* infection and may provide an additional pool of definitive hosts in Europe (Romig et al., 2006). In Poland prevalence in raccoon dogs was 8% (Machnicka-Rowińska et al., 2002). Due to high densities of the species in some areas of the country, it is a serious source of infection. In northern Brandenburg, Germany, prevalence in raccoon dogs was 6.3%–12.0% (S. Schwarz et al., unpubl. data). The parasite is an increasing public health concern, because efficient control measures are not available (Eckert et al., 2000). However, baiting foxes in an urban area of Zurich using baits with praziquantel (an antihelminthic) has decreased the prevalence of *E. multilocularis* in the city (Hegglin et al., 2003, 2004).

Sarcoptic mange, a zoonosis caused by a parasite *Sarcoptes scabiei*, is an important mortality factor of raccoon dogs both in native and introduced ranges (Kauhala, 1996b; Shibata and Kawamichi, 1999; Kowalczyk et al., 2009). Raccoon dogs may also transmit the parasite to other animals including foxes, lynx and even brown bears (Mörner et al., 2005). Mange has caused significant declines in red fox populations in, for example, Sweden, in the city of Bristol, UK (Lindström et al., 1994; Harris and Baker, 2001) and also temporarily in Finland (K. Kauhala, pers. obs.). The occurrence of infected raccoon dogs in the area may increase the risk of serious epizootics among foxes, because both species may use badger setts as den sites (Kauhala et al., 2006; Kowalczyk et al., 2008). Also, badgers may be infected on rare occasions (Collins et al., 2010).

Trichinella spp. are parasitic nematodes that cause trichinellosis (Gottstein et al., 1997). The disease is common in carnivores, especially scavengers, all over the world. Foxes are the most common reservoirs of sylvatic trichinellosis in Europe, although in Finland the raccoon dog is another important reservoir (Pozio, 1998; Oivanen et al., 2002). Sylvatic trichinosis is more common in northern Europe than in central and southern parts of the continent, because the human impact on natural ecosystems is less intense in the north (Pozio, 1998). Domestic trichinellosis occurred only in two countries in the European Union, Finland and Spain, in the 1990s (Pozio, 1998).

The raccoon dog may be an important reservoir species in Finland, because it carries the most intense infections and is the only species that hosts all four *Trichinella* spp. (*T. spiralis, T. nativa, T. pseudospiralis and T. britovi*) that occur in Finland (Oivanen et al., 2002). The prevalence and risk of infection in wild animals (e.g., foxes) is lower in northern than in southern Finland, probably due to the sparse raccoon dog population in the north. The prevalence in foxes has increased simultaneously since the 1960s along with the increase in the raccoon dog population in Finland (Oivanen et al., 2002). Prevalence in foxes is much higher (44%) in Estonia where raccoon dogs are more common than in Sweden (10%) where raccoon dogs are sparse (Oivanen et al., 2002). These facts point to the conclusion that the role of the raccoon dog as a reservoir of *Trichinella* spp. is remarkable (Oksanen et al., 1998; Oivanen et al., 2002).

10 Conclusions

The raccoon dog is one of those invasive species which extended its range quickly after introductions and invaded neighboring areas. By the 1980s, raccoon dogs had colonized over 1.4 million km^2 of Europe (Nowak,

1973; Novak and Pielowski, 1964; Kauhala and Saeki, 2004b) and in many areas became the most numerous of carnivores (Jędrzejewska and Jędrzejewski, 1998; Sidorovich et al., 2000; Kauhala et al., 2006). The success of the raccoon dog invasion in Europe was enabled thanks to an exceptional combination of factors including: widely distributed and multiple introductions, great migratory ability and the high reproductive capacity of the species, plasticity of food habits, hibernation in areas where climate is harsh and its general adaptability to different climatic and environmental conditions, and the admixture of individuals from divergent matrilineages (e.g., Lavrov, 1971; Helle and Kauhala, 1995; Kauhala 1996a, 1996b; Kauhala et al., 2007, Kowalczyk et al. 2008, 2009; Pitra et al., 2010; Sutor et al., 2010).

Few projects have been conducted in Europe on the ecology of the species, so little is still known on the impact of raccoon dogs on native fauna. It seems that in many areas raccoon dogs fit very well into the local communities and successfully coexist with native medium-sized carnivores. Locally, the raccoon dog may be an important threat to populations of waterfowl and amphibians. In protected areas, intensive and long-term control should be conducted to preserve local fauna.

The raccoon dog is a very important vector of rabies, sarcoptic mange, trichinellosis and *Echinococcus multilocularis*. This is no doubt the most severe consequence of the colonization of this alien species in Europe. Since it is continuing its expansion as well as increasing in numbers in some areas where the population has been established, control measures against rabies must be reviewed. As cold climates with harsh winters are probably limiting raccoon dog distribution, they may benefit from global warming and disperse further north. As the species is widely distributed and numerous, it is impossible to eradicate.

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