A review of the ecology of the raccoon dog (*Nyctereutes procyonoides*) in Europe

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Abstract: The raccoon dog (*Nyctereutes procyonoides*) was introduced from East Asia into the former USSR between 1928 and 1957. Since then it has colonised a large part of Europe and is considered an invasive alien species. This paper reviews the current knowledge on the ecology of the raccoon dog in Europe, undertaken as a basis for a risk assessment. The raccoon dog is about the size of a red fox (*Vulpes vulpes*). In autumn it accumulates fat and, in areas with cold winters, it may stay underground for weeks. It does not dig and often uses badger (*Meles meles*) setts and fox earths for reproduction. Raccoon dogs are monogamous. Each pair occupies a fixed home range the periphery of which often overlaps with that of neighbours. Pre-breeding population density usually is between 0.5 and 1.0 adults/km^2. Habitat use is characterised by a preference for shores, wet habitats and deciduous forests. Foraging raccoon dogs move quite slowly, mostly staying in cover. They are omnivorous gatherers rather than hunters. Their diet is variable, with amphibians, small mammals, carrion, maize and fruits being important components. There is no proof of a negative effect on their prey populations. Raccoon dogs produce a relatively large litter of usually 6 to 9 cubs. After six weeks the den is left and the whole family roams around. From July onwards the cubs, still only half grown, start to disperse. Most cubs stay within 5 to 30 km of their place of birth, but occasionally travel more than 100 km.

Keywords: raccoon dog, *Nyctereutes procyonoides*, ecology, Europe, wasbeerhond.

Introduction

Since the Russians started to introduce the raccoon dog (*Nyctereutes procyonoides* Gray, 1834) in the former USSR, from 1928 onwards, the species has successfully colonised large parts of north and central Europe. This invasive canine, which is a potential predator of, and competitor with, native species, has been the object of many research projects in a number of European countries in recent decades. Despite the accumulated knowledge about its ecology, inaccurate information is still being published regularly in the popular press. A sound risk analysis of its possible impact on native species should be based upon a thorough knowledge of the results of scientific research. The risk analysis of the raccoon dog in the Netherlands has been published in an extensive report (Mulder 2011). This paper reviews and summarises all the available European research on the ecology of the raccoon dog. It especially focuses on recent research with radio-collars and other techniques, and may be regarded as an addition to the older reviews on the raccoon dog by Duchêne & Artois (1988) and Nowak (1993), and an extension of the recent work of Kauhala & Kowalczyk (2011). The present situation of the raccoon dog in the Netherlands, as well as the risk analysis itself, will be dealt with in a separate paper (Mulder, in prep).

Biology and introduction history in Europe

The species

The raccoon dog is called 'wasbeerhond' in Dutch and 'Marderhund' in German. It is taxonomically quite an isolated species in the Canidae, the dog family. The nearest relatives would be the members of the genus *Dusicyon*, a group of South-American fox like canids (Clutton-Brock et al. 1976). However, more recent DNA-analysis showed that the African bat-eared fox (*Otocyon megalotis*) may be its nearest relative (Wayne et al. 1997). On the continent of Asia a total of seven different subspecies have been described in the raccoon dog (Nowak 1993). Corbet, however, lumped all seven continental subspecies into one subspecies: *N. p. procyonoides* Gray, 1834. Two other subspecies occur on different Japanese islands: *N. p. viverrinus* Temminck, 1844 on Honshu, Shikoku and Kyushu, and *N. p. albus* Beard, 1904 on Hokkaido (Corbet 1978).

The raccoon dog has its original distribution in the far east of Asia (figure 1), running from south-eastern Siberia to northern Vietnam in the woodland zone, as well as on the Japanese islands (Nowak 1984). 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 south-east Siberia. Accordingly, raccoon dogs in different areas have adapted to different climates, habitats and diets, which resulted in differences in body size, fat reserves, thickness of fur, and behavioural and dental characteristics (Kauhala & Kowalczyk 2011). The raccoon dogs which have been introduced into Europe originate from the Amursk-Ussuria region, north of Wladiwostok; they belong to the (former) subspecies *N. p. ussuriensis* (Nowak 1993) and are adapted to a cold climate with severe winters (Kauhala & Kowalczyk 2011).

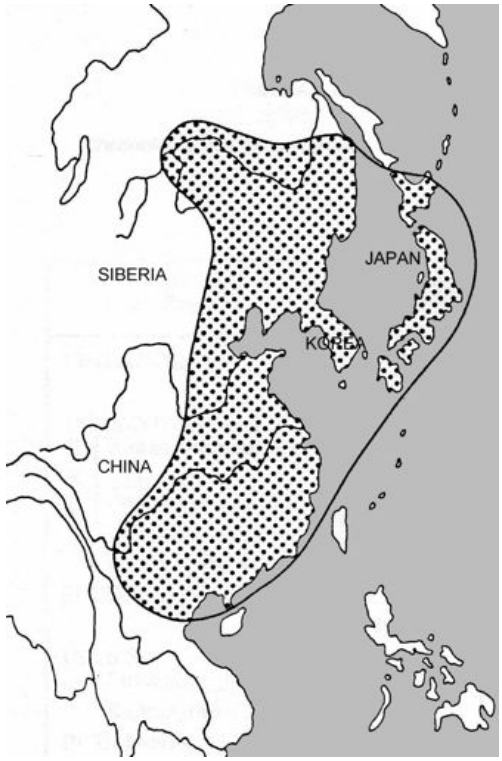

Figure 1. The original range of the raccoon dog in East Asia. After Nowak (1984).

Introduction history in Europe

The history of the introduction of the raccoon dog in Europe has been dealt with in detail by Kauhala & Kowalczyk (2011). Between 1928 and 1957 approximately 9,100 animals, mostly from captive bred stock, were released in more than 70 areas of the former USSR, mainly in the European part (Lavrov 1971, Helle & Kauhala 1995). The aim of the Russians was to enrich the fauna with a valuable fur animal. The raccoon dog spread rapidly, although introductions in very cold climates and in mountainous areas failed. In a later stage, raccoon dogs were captured and translocated from successfully settled populations to new areas.

In Germany the first raccoon dogs were observed in 1964 in the north-east, in Mecklenburg-Vorpommern, but may have been ani-

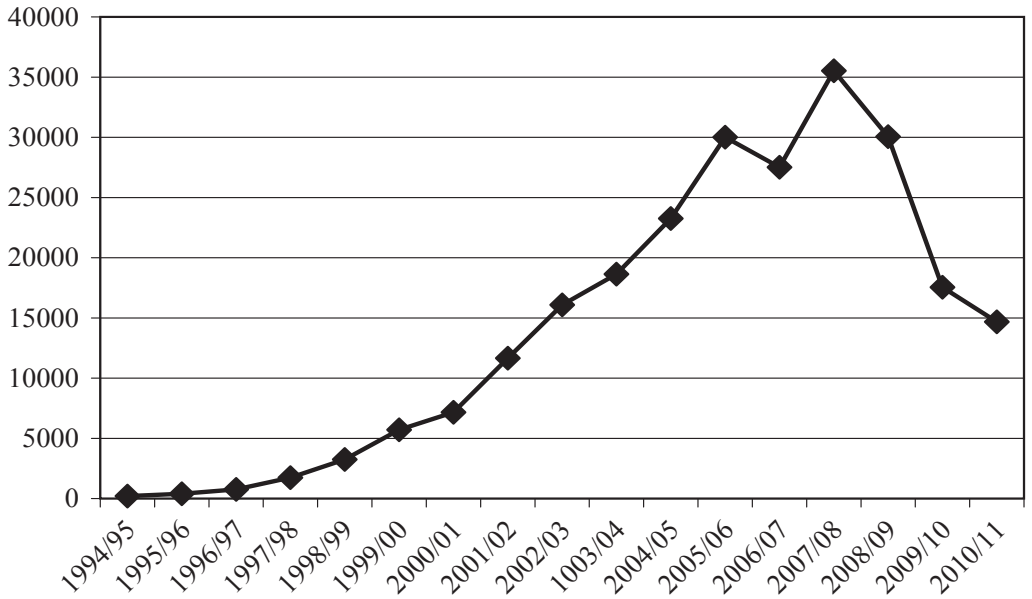

Figure 2. Hunting bag of raccoon dogs in Germany. The low numbers shot in the last two hunting seasons are caused by epizootics of mange and canine distemper in northeastern Germany. Source: http://www.jagdnetz.de/datenundfakten/jahresstrecken?meta_id=257.

mals escaped from captivity (Bruchholz 1968). It was expected that central Europe would be invaded rapidly (Ansorge 1998), but the speed of colonisation was not as rapid as expected. The first raccoon dogs reaching the Dutch border, 480 km distant from north-east Germany, were observed around 2001 (Mulder, in prep). Thus, the speed of their expansion through the north of Germany was about 13 km/year. Until the early 1990s the number of raccoon dog observations in Germany remained low, but from then on the hunting bag (number of animals killed) increased exponentially. Since the hunting season of 2005/2006 between 27,500 and 35,000 animals were shot each year in the whole of Germany; however, in recent years the population has declined as a result of diseases in the north-east of the country (figure 2).

Appearance, size and tracks

The raccoon dog is a small and stocky medium-sized predator. It has a characteristically long fur with guard hairs up to 12 cm, in a mixture of black, grey, brown and white. Its face is striking, especially in the long winter coat: black eye-pads, a whitish nose in between (the most important difference with the face of the raccoon, *Procyon lotor*) and long whitish side-whiskers. The tail is short (15-22 cm), not reaching the ground, mostly light coloured with a blackish tip. From nose to tail base the raccoon dog measures 50 to 85 cm. The legs are short and black. Its footprints are small and more rounded than those of the red fox (*Vulpes vulpes*), which leaves more elongated footprints. As with the fox, the nails are always visible in the prints. Raccoon dog footprints may be exactly the same as those of small dogs. Because of its broad body and short legs, the raccoon dog does not place its footprints in one (almost) straight line as the fox does: the prints of left and right legs are quite widely spaced apart. The short legs, broad body and long hair sometimes give the animal the appearance of a badger (*Meles meles*), especially in winter. Its height is only

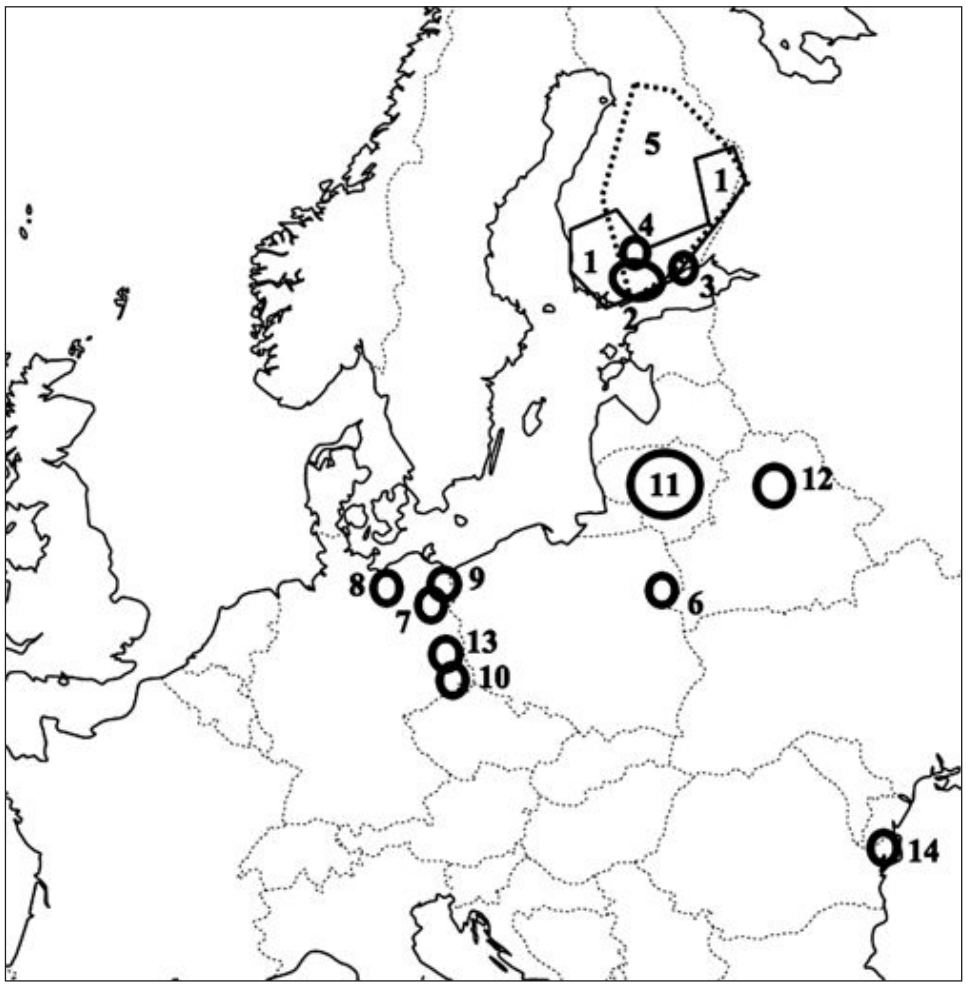

Figure 3. Location of raccoon dog research areas in Europe. Associated literature:

1. Southwestern, southern and northwestern Finland: Kauhala (1993), Helle & Kauhala (1995)
2. Southern Finland: Helle & Kauhala (1993), Kauhala et al. (1998b)
3. Virolahti, southeastern Finland: Kauhala & Holmala (2006), Kauhala et al. (2006)
4. Evo, central-south Finland: Kauhala (1996c), Kauhala et al. (1998c)
5. Central, east and south Finland: Helle & Kauhala (1995)
6. Białowieża Primeval Forest: Reig & Jedrzejewski (1988), Selva et al. (2003), Kowalczyk et al. (2008), Kowalczyk et al. (2009)
7. Ueckermark: Stiebling et al. (1999), Ansorge & Stiebling (2001)
8. Lewitz: Stier, personal communication
9. Mecklenburg-Vorpommern: Stier (2006), Drygala et al. (2008), Drygala et al. (2009), Drygala et al. (2010)
10. Oberlausitz: Ansorge (1998), Ansorge & Stiebling (2001)
11. Lithuania: Baltrunaite (2005), Baltrunaite (2006), Baltrunaite (2010)
12. Vitebsk, northern Belarus: Sidorovich et al. (2000), Sidorovich et al. (2008)
13. Brandenburg: Sutor (2008), Sutor et al. (2010), Sutor & Schwarz (2011)
14. Danube-delta: Barbu (1972)

Raccoon dogs. *Photo: J.L. Mulder*.

about 37 to 39 cm (Nowak 1993). In Finland females tend to be somewhat smaller and weigh less (except when pregnant) on average than males; however, the differences are not statistically significant (Kauhala 1993).

In regions with severe winters, body weight of raccoon dogs fluctuates considerably throughout the year. In late autumn it may be 50-70% higher than in spring (Kauhala 1993). Weight decreases during winter, and starts to increase in March or April, reaching maximum values in August to November (Nowak 1993). However, in areas with mild winters the weight fluctuations throughout the year are much less pronounced. In the Danube delta male raccoon dogs weighed about 6.5 kg in autumn and winter, and about 6.0 kg in spring, and females 5.5 and 5.6 kg respectively, without stomach contents (Barbu 1972).

General biology

Present knowledge about the biology and the ecology of the raccoon dog, has been accumulated through several studies, mainly in the east and north of Europe (figure 3). Important research has been done in Finland (Kauhala and co-workers), Poland (Kowalczyk and co-workers) and East Germany (Stier, Drygala, Sutor and others).

The raccoon dog is the only member of the canid family showing winter lethargy in areas where winters are harsh (Kauhala & Saeki 2004). If snow depth exceeds 20 cm, raccoon dogs usually stay in their hiding place (Heller 1959). During winter and when rearing pups raccoon dogs prefer to use dens. At other times of the year a den is used only occasionally (Kauhala et al. 1998c). When active, raccoon dogs like to stay under cover as much as possible. During the day they usually rest in cover as well.

Raccoon dogs move relatively slowly, they walk with a quiet gait and are not fast runners. When disturbed, they seek cover in a fast trot, or take to water to swim away. Raccoon dogs often keep very still when approached and may pretend to be dead when in danger. They rarely climb, but sometimes ascend easily accessible trees to reach nests in bird colonies (Nowak 1993). A simple one metre high

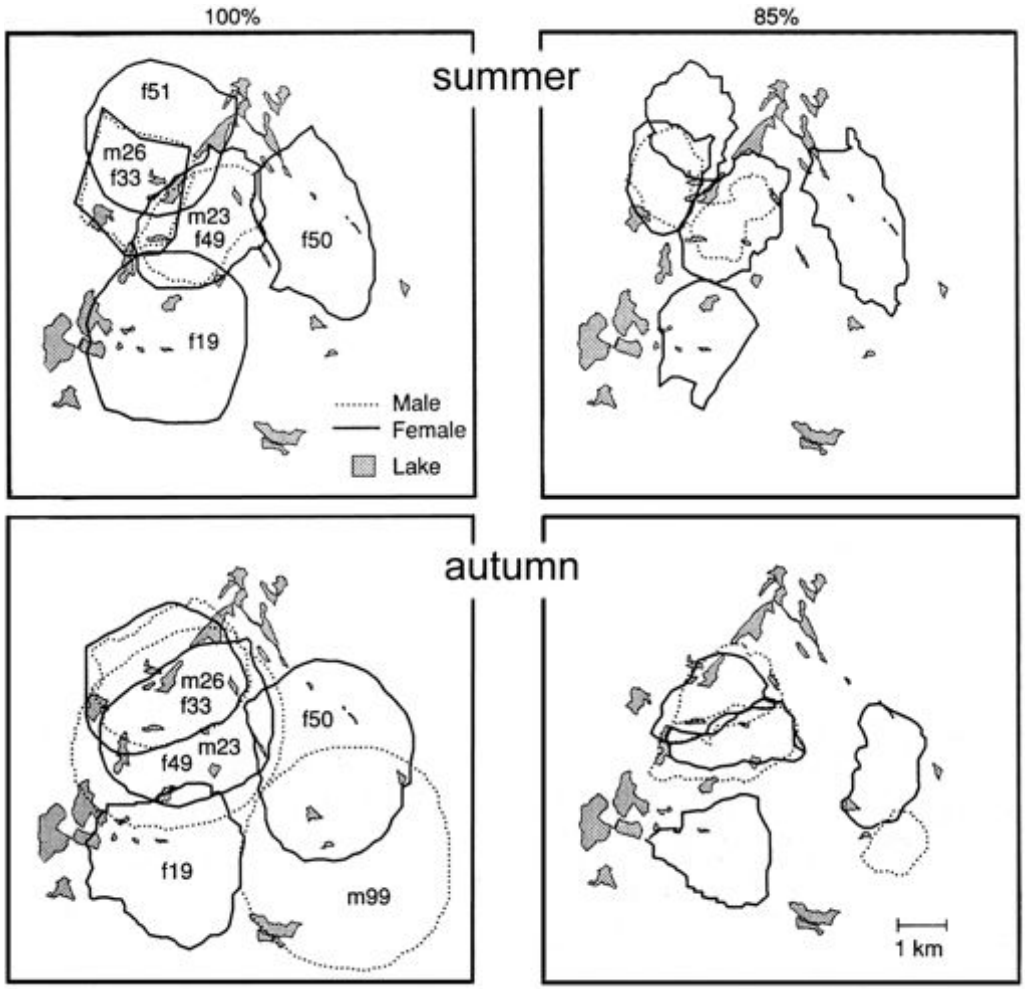

Figure 4. Home ranges of raccoon dogs in southern Finland, according to the harmonic mean distribution of radio-locations, in summer and autumn. To the left 100% of all locations included, to the right 85% of locations included (core areas). After Kauhala et al. (1993a).

fence is enough to keep them in captivity (Stier 2006b). In contrast to foxes and especially badgers, raccoon dogs have little tendency to dig burrows; although they may dig small pits while foraging for small prey (Nowak 1993).

Raccoon dogs live in pairs in home ranges, of which only the core areas seem to be avoided by neighbours (see below). Except when they have small cubs in a den, the partners rarely stray far from each other and criss-cross their territory together to forage (Kauhala et al. 1993a, Kauhala & Holmala 2006, Drygala et al. 2008a). Members of a pair tend to hibernate together (in 84% of 106 cases); in summer they spend less days sleeping together in a den, although still a considerable proportion (67% of 106 cases - Kauhala & Holmala 2006). The raccoon dog is the only canid with this behaviour and such a tight pair bond. Raccoon dogs have large litters which are born relatively late in the year; however, the pups quickly become independent and start to disperse early, before they are even fully grown (see below).

Raccoon dogs are predominantly active at

night. However, they may be quite active during daylight hours, but usually only in the cover of thick vegetation (Kauhala et al. 2007, Drygala et al. 2000). In Poland, where winters are severe, raccoon dogs prefer unoccupied badger setts to fox earths for winter dormancy (Jędrzejewska & Jędrzejewski 1998). From October onwards they clean out the burrows and refurbish them with dry grass and leafs. Dormancy starts when the temperature drops below -8 to -10 °C. In large badger setts only two or three entrances are used, the rest are closed up (Wlodek & Krzywinski 1986). Generally two raccoon dogs (a pair) share an earth during winter dormancy, sometimes small groups of juveniles (Judin 1977). Sometimes other, more open, places are used for winter dormancy, especially in milder winters: reed beds, piles of branches, open holes under the roots of fallen trees and wild boar's (*Sus scrofa*) 'nests'. In Germany, with milder winters and less snow, raccoon dogs are known to be active throughout the winter (Stier 2006a).

Ecology

Home range

In southern Finland, Kauhala et al. (1993a) were the first to study the home range and behaviour of raccoon dogs in Europe (figure 3: no. 2). In an area with coniferous forests interspersed with clear cuts, small streams and pine swamps, 23 raccoon dogs were radio-tracked for periods of between a few months to three years. The average maximum home range was 950 ha, the 85% utilisation core area was 340 ha, and the 60% core area only 130 ha (Harmonic mean method, Dixon & Chapman 1980). Maximum home ranges were larger in autumn than in summer, but the core areas were similar in size between seasons. The core areas (85%) of adjacent pairs did not overlap in the pup-rearing season (summer) and only partially in the autumn; the peripheral areas of the maximum home ranges, however, overlapped considerably (figure 4). The home ranges of the male and the female within a pair were almost identical.

In a later study in southeastern Finland Kauhala et al. (2006) followed 17 raccoon dogs with radio-collars (figure 3: no. 3). The average total individual home range (± sd) (over all years and seasons, 95% fixed kernel, Worton 1989) was 390 ± 142 ha, the 50% core area 80 ± 0.51 ha. Seasonal home ranges (n=32; three seasons a year, no winter data) were smaller and covered on average 260 ± 135 ha (95%) and 40 ± 26 ha (50%). This study area consisted mainly of managed coniferous forests (68%), fields (18%),and seashore, reedbeds and other wetlands (together 12%). In summer the core areas of the members of a pair overlapped by 75 ± 3.5% (n=2 pairs), whereas the core areas for adjacent pairs overlapped by only 1 ± 3% (n=7) in summer.

Drygala et al. (2008a) radio-collared 74 raccoon dogs in an area in north-eastern Germany (Mecklenburg-Vorpommern), about 50 km from the Polish border (figure 3: no. 9). This research was done about ten years after the start of the rapid increase in raccoon dog sightings in the area, and the population was supposed to not yet be saturated. From 12 males and 14 females sufficient data were obtained to calculate home range sizes. From these animals, 62 stable seasonal home ranges were obtained, some for the same animals over several successive years. Four seasons were distinguished: oestrus and gestation (March-April), parturition and cub rearing (May-July), intensive foraging and fat accumulation (August-October) and reduced and winter burrow associated activity (November-February). Home ranges were calculated from the 95% kernel distribution of locations and are thus comparable to the data of Kauhala et al. (2006) described above. Home range size fluctuated through the year. During oestrus and gestation the home ranges were small, around 160 ha, during fat accumulation they were much larger, around 540 ha. The overall year averages were 382 ± 297

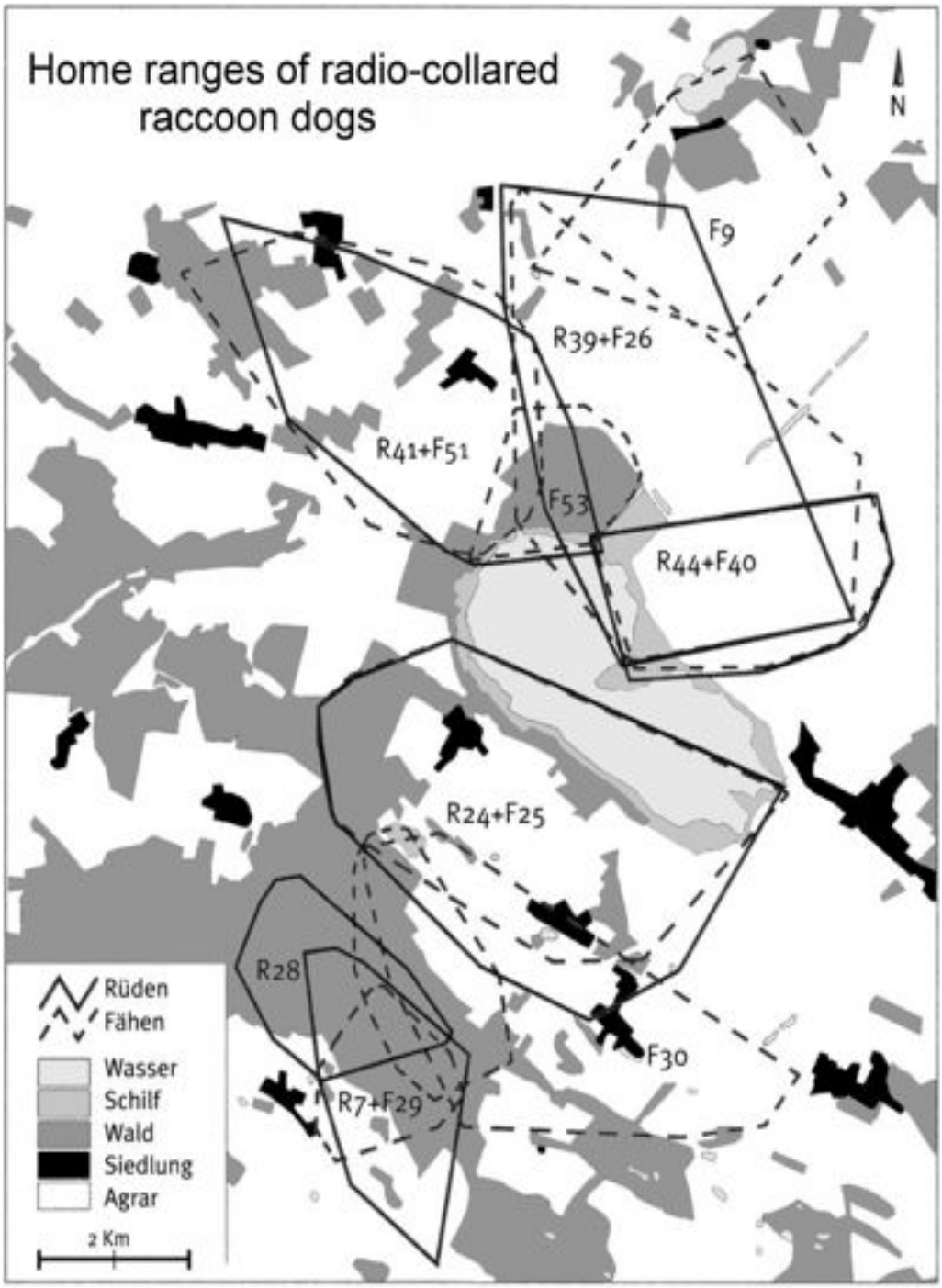

Figure 5. Home ranges of raccoon dogs in the study site in Mecklenburg-Vorpommern, Germany. R=male, F=female, Wasser=water, Schilf=reeds, Wald=woodland, Siedlung=village, Agrar=fields and meadows. After Stier (2006a).

ha for 30 seasonal ranges of females, and 352 ± 313 ha for 32 seasonal ranges of males. The large standard deviation indicates huge differences between pairs, some having small, and others very large, home ranges. There were no clear differences between males and females since the male and female of a pair stay closely together during foraging: the overlap between the home ranges of members of a pair was 85-93%. Only when having small cubs do the parents split up, with one of them staying with the cubs; as a result the overlap during this period was less, 69% on average. Home ranges were smaller in agricultural landscapes (239 ± 214 ha) than in forest landscapes (313 ± 440 ha) (see below).

Although the raccoon dog's home ranges appeared to be quite evenly spread over the research area (figure 5), the raccoon dogs did not exhibit very territorial behaviour. Adjacent home ranges overlapped to a considerable extent, with a maximum in the August-October period of about 30% on average, and a minimum of about 3% during winter. In March-April the average overlap was 16%, and 12% during cub rearing. The overlap in the core area (85% kernel distribution) was least during cub rearing, suggesting at least avoidance if not territoriality and defence of the breeding den. Similar results were obtained by Kauhala et al. (1993a); adjacent radio-collared adults never visited the vicinity of the breeding dens of their neighbours.

In southern Brandenburg, also in northeast Germany (figure 3: nr 13), Sutor & Schwarz (2012) followed 9 raccoon dogs with radio-collars in a mixed agricultural landscape, and obtained similar results. The yearly average home range sizes were 183 ± 154 ha (95% kernel). Core areas (50% kernel) measured 50 ± 49 ha. The authors distinguished the same four seasons as Drygala et al. (2008a), see above, and also found the ranges to be largest in autumn and smallest in winter. Again, only during the pup-rearing season was there no overlap in the core areas of adjacent home ranges.

In conclusion, the raccoon dog is monogamous, with a probable lifelong pair bond. It does not defend an exclusive territory but respects and avoids neighbouring core home ranges.

Habitat use

The raccoon dog mainly lives in landscapes with moist or wet habitats, such as moors and wet grasslands with clumps of trees, and reed beds along lakes and streams, and in deciduous and mixed forests with dense undergrowth. Large scale agricultural areas and large scale coniferous forests are less preferred. In eastern and central Europe it prefers lower elevations; it is hardly found above 800 m (Nowak 1993).

In Europe two extensive studies of habitat use of radio-collared raccoon dogs have been published. Kauhala (1996c) studied the activities of twelve adult raccoon dogs in the boreal zone of central southern Finland (figure 3: no. 4). The study area was characterised by industrial forests, small pine swamps and many small lakes and streams. The habitat choice of raccoon dogs in the snow-free time of the year was determined for three seasons: early summer (May-June; pup-rearing), midsummer (July; pups begin to forage with their parents) and autumn (August-October; young disperse, adults prepare for winter). The distribution of radio-fixes (except those surrounding the dens) was compared to a large sample of random locations in the study area. Raccoon dogs preferred shore areas (7% of the available habitat) in all seasons, more so during early summer (30% of fixes) than during midsummer (19%) or autumn (17%). Along shores and in shallow water frogs are abundant and easily caught in early summer. During midsummer and autumn the dense undergrowth along the shores of lakes and streams provides shelter. Safety may also play a role: raccoon dogs tend to escape into water when chased or attacked. Moist heathlands were favoured in autumn, probably because of their abundant supply of berries: raccoon dogs fatten up on berries before their winter dormancy. In Japan,

berries and fruits have also been found to be important elements of the racoon dog's diet in autumn (Ikeda 1985) and raccoon dogs have sometimes been observed migrating to areas with abundant fruits and berries (Nasimovic & Isakov 1985, cited by Kauhala 1996c). Kauhala (1996c) concludes that the raccoon dog's use of habitats is affected by the availability of food, shelter and suitable den sites. In Europe it lives in habitats which are not found in its original distribution area, such as coniferous forests, steppe and semi-deserts. In the Russian far-east the raccoon dog favours open landscapes, especially damp meadows and agricultural land and avoids dark forests (Judin 1977; Nasimovic & Isakov 1985, as cited by Kauhala 1996c). In all areas, however, the raccoon dog is very often found near water, and forages on fruits and berries in autumn.

The second large study on habitat use was conducted by Drygala et al. (2008b) in north-eastern Germany (figure 3: no. 9). The study area was part of a vast agricultural landscape, more or less similar to the general landscape in the east and south of the Netherlands, with many maize fields, interspersed with reed beds, swamps, mixed forests, streams, ditches and lakes. The three main habitats were meadows (33%), arable land (28%) and forests (27%). A total of 12 males and 14 females, all residents, were tracked for a period of between one month and four years. Four seasons were distinguished: oestrus and gestation (March-April) - parturition and pup rearing (May-July) - intensive foraging and fat accumulation (August-October) - reduced activity and winter-burrowing (November-February). Winter lethargy is less pronounced than in Finland and depends on the severity of the winter. In total 62 individual seasonal home ranges with at least 29 locations each (average 65 ± 23) were available for analysis.

Of the available radio locations 43% were in deciduous forest, 31% in meadows or pastures and only 10% in arable land. The home ranges of the animals could be divided into two types: an agrarian type with 82% of the area in agricultural land and less than 5% in forest, and a forest type with at least 50% and an average of 68% forest. Both contained less than 14% of other habitats. The raccoon dogs did not show any preference for forests (except in autumn), reeds, small woods or hedges; they used them according to availability. However, they did tend to avoid open farmland (except during the pup-rearing period), meadows and settlements (villages and farms).

Population density

Estimating the population density of raccoon dogs is difficult because of their secretive behaviour. The two main methods are using the results of radio-telemetry research, and the distribution and number of litters (Stiebling et al. 1999). On the basis of a large telemetry study Drygala et al. (2008a) calculated the pre-breeding population density in north eastern Germany to be 0.95 adults/km². In Brandenburg, East Germany, Sutor & Schwarz (2012) estimated the pre-breeding population density as 1.1 adults/km². In south-eastern Finland the maximum population density was estimated to be about 0.77 adults/km² (Kauhala et al. 2006). In Białowieża Primeval Forest (Poland) raccoon dog density was 0.17-0.5 adults/km², compared to 0.25-0.35 foxes and 0.13-0.21 badgers (Kowalczyk et al. 2008). According to Jędrzejewska & Jędrzejewski (1998) and Kowalczyk et al. (2003) raccoon dogs in Białowieża reached densities of 0.7 adults/km². In Suwałki Landscape Park in northeastern Poland raccoon dog density was estimated to be 0.37 adults/km² (Goszczynski 1999). From these data we may conclude that in central and western Europe pre-breeding population density is generally between 0.5 and 1.0 adults/km².

Reproduction

Raccoon dogs reach sexual maturity at the age of 8-10 months. Pairs are formed in autumn.

Females come into oestrus after awakening from winter lethargy. Therefore, the timing of the mating season fluctuates with the length of winter; in Russia and in Finland it lasts from the end of February to the beginning of April, in the Danube delta from mid February to mid March (Barbu 1972, Nowak 1993, Helle & Kauhala 1995). Older females breed earlier than younger ones (Helle & Kauhala 1995). In northeastern Germany the mating season is at the end of February and the beginning of March. Females are in oestrus for about 4 days and pregnancy lasts 59-64 days (Valtonen et al. 1977), so the pups in northeastern Germany are born at the end of April or the beginning of May (Stier 2006a) and in Finland in May or the first half of June (Kauhala 1993). In Białowieża Forest the average date of birth is 25 April (Kowalczyk et al. 2009). Raccoon dogs bring dry grassy vegetation into the den, sometimes as early as mid October, to make a nest (Wlodek & Krzywinski 1986, Stiebling et al. 1999). Pups remain in the den for about six weeks. They start to take solid food from week 3 or 4 onwards and are weaned after 40 to 50 days (Nowak 1993). In the Danube delta the sex ratio at birth was slightly in favour of males: 1.1 males for every female; among pups of several weeks old it was 1.2. However, among adults the sex ratio was 0.91 (Barbu 1972).

The raccoon dog produces a relatively large litter, larger than expected for a medium-sized carnivore species (Kauhala 1996b). It usually consists of 6 to 9 pups but can range from 2 to 12 pups; the recorded maximum was 19 pups (Nowak 1993). Litter size was also recorded in Białowieża at, or shortly after birth in 21 litters. It ranged from 4 to 12, with an average of 8.4 (Kowalczyk et al. 2009). In Finland average (± sd) litter size at birth was 9.5 ± 3.2 in the south-west and 7.0 ± 2.6 in the north-east (combined n=371). Litter size was positively correlated with the body condition of the mother (Kauhala & Saeki 2004). Maximum average pup weight in a Finnish litter was 139 grams (Kauhala 1993). The mean total litter weight was 21% of the mean weight of the female. Investment in reproduction thus is relatively high in the raccoon dog; the weight of a fox litter is only 10-13% of the mean weight of the female (Kauhala 1996b).

Kauhala et al. (1998c) and Drygala et al. (2008c) studied the behaviour of raccoon dogs intensively, during parturition and subsequent care for the pups, by radio-tracking (both studies) and video-surveillance (Drygala et al. 2008c). The video observations at a breeding den showed, that in the two weeks before parturition the male and female always arrived and went together, spending about 33% of each 24 hour period away from the den (Drygala et al. 2008c). Also in Finland the parents were at the den simultaneously, for 37% of daylight hours and 23% of the night (Kauhala et al. 1998c). Drygala et al (2008c) found that on the day of parturition the female and the male left for 3.18 and 0.33 hours respectively. The time away from the den increased for both parents in the following weeks, but the female was always absent for considerably longer than the male. Shortly after parturition, the ranges of both the male and female were very small. The daily range of the female increased from week to week, to about 150 ha in the sixth week, but the range of the male continued to be small (about 15 ha) and centred around the den. Its average distance (± sd) to the den was only 94 ± 17 metres during the first five weeks. The pups were seldom left alone during their first month of life; on average 2.6 ± 1.6% of the time only in northeastern Germany, and in Finland 15% (range 7-34%) of the night and 7% (range 2-12%) of the day. Video recordings showed that the attending parent often left as soon as the other parent returned from a foraging trip. In the fifth week both parents were absent for 13.5 ± 12.0% of the time, and in the sixth week as much as 71.2 ± 39.6%. Males spent more time alone at the den (40%) than females (16%). The male plays an important part the in guarding the pups, enabling the female to spend much time foraging, both during the day and dur-

ing the night. In this way she can compensate for the high energy demands of milk production (Kauhala et al. 1998c). In the sixth week after parturition the den was abandoned and the pups started to rest above ground and to travel around; the male's daily range started to increase from then on (Drygala et al. 2008c).

Parents of raccoon dogs, like foxes, have never been observed to regurgitate food for their pups, either in the wild or in captivity (Drygala et al. 2008c, Yamamoto 1984). Since prey remains are rarely found at breeding dens, it was assumed that pups were entirely fed with milk. However, video recordings from a breeding den in northeastern Germany showed that the male carried prey to the den, to provide for the female as well as for the pups. The list of food items recorded at this particular den included 14 grass snakes, seven small mammals, four frogs or toads, two legs of a roe deer (*Capreolus capreolus*), two roe deer fawns, one passeriform bird, one chicken size egg, one mole (*Talpa europaea*) and twelve unidentified items. No prey remains were found at the den, except for the hooves and legs of the roe deer. Pups were recorded at the age of 19 days in the entrances of the den for the first time, chewing on solid food (Drygala et al. 2008c). In Białowieża it was observed that pups started to forage on their own rather quickly; by the end of May and the start of June some were already found at a distance of 800 metres from the den (Wlodek & Krzywinski 1986).

Usually the male guarded the litter inside the den, and the female slept outside, beside the entrance. Both parents carried the pups back to the breeding den during the first four weeks. From the fifth week onwards, the female only approached the pups for a couple of minutes to nurse them, until 45 days after parturition when the whole family left the den. The pups were not yet weaned at that time (Drygala et al. 2008c). These observations contrast with those of Kauhala & Saeki (2004) that pups are weaned at an age of four to five weeks.

Guarding the pups so closely during the first weeks of their life, may serve a dual purpose. First of all, predation by badgers and foxes is a real threat for the pups. A guarding raccoon dog was observed to successfully chase a badger away from a breeding den (Stier 2006a). Secondly, permanently attending the pups may be necessary to prevent hypothermia, especially in the colder regions of the raccoon dog's range (Drygala et al. 2008c).

Although usually born and raised in badger setts and fox earths, in Białowieża some pups are born in lairs in fallen hollow trees and in dense vegetation (Kowalczyk et al. 2009). Open lairs with pups are common in areas where no dens are available, for instance in moors; showers of rain and hail may in these situations lead to a high pup mortality (Barbu 1972).

Mortality and age

Within three months after birth 61% of the pups in Białowieża Forest disappeared, as deduced from the negative correlation between litter size and age of the pups (Kowalczyk et al. 2009). Mortality among young raccoon dogs during their first year amounted to 89% in Finland (Helle & Kauhala 1993), 82% in Białowieża Forest (Kowalczyk et al. 2009), and 69% in north-eastern Germany (Drygala et al. 2010). Pups may be killed by other predators, such as foxes and badgers, which raccoon dogs often share dens with, or die from diseases such as sarcoptic mange and rabies (Nowak 1993, Kowalczyk et al. 2009). In Poland golden and white-tailed eagles take raccoon dogs and their pups (Wlodek & Krzywinski 1986). In the Danube delta many pups in open lairs die as a result of rain and hail showers (Barbu 1972).

Life tables from southern Finland (where there is a high hunting pressure) indicate an annual average mortality rate of 52% for adults. Mortality rate was lowest among 2-4 year old raccoon dogs and increased after 5 years of age. The maximum life span seemed to be 7-8 years (Helle & Kauhala 1993). In Białowieża Forest in Poland the annual mor-

tality rate for raccoon dogs aged between 2 and 5 was 50-68% (Kowalczyk et al. 2009). In a sample of 328 raccoon dogs from eastern Germany (mostly shot), the oldest individuals were 6 years old; 70% were a maximum of 1 year old, 14% 2 years old and 9.5% 3 years old, while the older age classes comprised only 1-2% each (Ansorge & Stiebling 2001).

Of 82 adult dead raccoon dogs recorded in the Białowieża Forest, at least 55% died of natural causes: 27% by predation by wolves and dogs, often in the vicinity of predator kills, and 27% by diseases such as sarcoptic mange and rabies, mainly in August to November. (Today rabies has been eradicated from most of Poland, thus no longer constitutes a major mortality factor in raccoon dogs.) When killed by predators, raccoon dogs were rarely consumed. Forty percent of the recorded dead animals were killed by humans, the majority of them by cars; 18 out of 20 traffic victims were juveniles. Sixteen percent of the recorded deaths were due to hunting and poaching, although there is no hunting in the central reserve of the Białowieża Forest. A sample like this probably does not constitute a reliable representation of real mortality, because it is affected by observer bias, unlike studies with radio-collared animals (Kowalczyk et al. 2009).

In contrast to other carnivores, the sex ratio in samples of dead raccoon dogs always is equal (for instance Helle & Kauhala 1993). Males and females run the same risk of dying through being shot or killed on the road, for instance. This is most probably the result of their similar life style, activity, home range size and dispersal distance, which in other carnivore species generally differs considerably between the sexes (Ansorge & Stiebling 2001).

Raccoon dogs are vulnerable to predation for several reasons. Pups are easily accessed by badgers and foxes, which use the same (type of) burrows, and also by larger predators (wolf (*Canis lupus*), lynx (*Lynx lynx*) and brown bear (*Ursus arctos*)) when in more open lairs. Adult raccoon dogs may profit from carcasses left by larger predators; in some areas scavenged meat is a very important part of their diet (Jędrzejewska & Jędrzejewski 1998, Sidorovich et al. 2000, Sidorovich et al. 2008). However, feeding on such carcasses is risky because the raccoon dogs may become prey themselves when carcasses are revisited by wolves or lynx, or scavenged by large birds of prey (Kowalczyk et al. 2009).

Relations with native predators

Sidorovich et al. (2000) studied the dietary overlap between all the generalist predators in the natural forest landscape of northern Belarus: brown bear, lynx, pine marten, badger, red fox, raccoon dog and polecat. In the warm season (April - October) there seems to be little resource competition between the different predators, because of the wide food spectrum of most species. However, in the cold season food availability is much more limited, both in abundance and diversity: fruits, small mammals and especially carrion. Wild ungulate carrion (elk and wild boar) is intensively used by most species in winter; only badger and lynx use them to a lesser extent. In late winter, when snow conditions make it energetically costly to forage, carrion is often the only food available. In that period raccoon dogs are not active and remain dormant in their dens. However, in late autumn and early winter they feed extensively on the available carrion, depleting this resource substantially. During late winter this might severely affect the native predators in the area. The polecat seems to be particularly affected: track counts show a significant negative correlation between the abundance of raccoon dogs and polecats in two study areas over a 14-year period, from 1985 to 1998. During this period polecat numbers decreased while those of raccoon dog increased. In one of the two study areas a negative correlation was also found with red fox, pine marten, badger and brown bear. Deep

snow as well as poor soils with few masting trees - and therefore far fewer small mammals living under the snow - are factors that may increase late winter food competition in northern Belarus (Sidorovich et al. 2000) more than within the more southerly Białowieża Primeval Forest (Jędrzejewska & Jędrzejewski 1998), which has more fertile soils.

In Finland and in the Białowieża Forest (Poland) raccoon dogs have now become more common than foxes and badgers (Ansorge et al. 2009). Kowalczyk et al. (2008) postulate that badgers, and especially their setts, have a positive influence on raccoon dogs, facilitating their success. Burrows are an important resource for badgers, foxes and raccoon dogs, allowing for reproduction, winter rest (or lethargy) and daytime shelter. Use of badger setts by these other two medium-sized predators may lead to negative (predation, interference competition) and positive (facilitation) interactions among the three species. Communal denning has always been a common phenomenon between badgers and foxes in Europe, and now the raccoon dog also shares burrows with these two species. Kowalczyk et al. (2008) studied the three species in Białowieża Primeval Forest by radio-tracking and by badger sett monitoring, from 1997 to 2002. Cohabitation of setts was very common in winter: in 88% of 71 'sett-winters' badgers shared a sett with raccoon dogs, in 4% with foxes, in 4% with both species and in only 4% they were the sole species in the sett. In summer cohabitation was much less: in 80% of 49 'sett-summers' badgers lived alone in the setts, sharing with raccoon dogs or foxes in only 10% of 'sett-summers' (for each species). Occupation of badger setts by raccoon dogs or foxes never led to the departure of badgers. Different species sometimes used the same entrances to come and go, but used different parts of the sett to rest below ground. In all the years of research, only five times were raccoon dog pups found to be present in an active badger sett. In three of those cases there were no badger cubs present, in two cases it was not known if the badgers reproduced. Five cases of red fox reproduction were found in active badger setts, and in only one case was there also a badger litter. Foxes always used an entrance at the edge of the sett, an entrance which was not used by badgers. Once a fox cub was found dead at a sett, killed by a badger, and once two raccoon dog cubs were found dead. Several dead adult raccoon dogs and foxes were found in and around badger setts, and these may have been killed by badgers. In winter the raccoon dog may benefit from the use of badger setts, increasing their chances of winter survival. In summer however, the costs of sharing a sett may be higher than the benefits, due to predation of pups. No evidence of raccoon dogs or foxes being aggressive to badgers was found. However, the remains of a badger cub have been found in raccoon dog scats in Białowieża Primeval Forest (Jędrzejewska & Jędrzejewski 1998).

Studies in central Europe show that the 'invasion' of raccoon dogs has not resulted in a decrease of badger numbers (Kauhala 1995, Kowalczyk et al. 2000, Sidorovich et al. 2000, Baltrunaite 2010). It appears that these two species can coexist and utilise available resources with minimal competition (Jędrzejewska & Jędrzejewski 1998).

It has, however, been suggested that the number of foxes started to decline as soon as the raccoon dog appeared. Predator population size is usually assessed from the number of animals killed by hunters. In north-eastern Germany this 'bag record' did indeed decrease over about four years (2000-2004) after a rather long period of gradual increase; the decline coincided with the first part of the expansion of the raccoon dog population. However, since 2004 the bag record of the fox has been more or less stable again, although with strong fluctuations. So if the arrival of the raccoon dog has had some impact on fox numbers, it has not been very strong. In its original range, the raccoon dog has always coexisted with the red fox (Zoller 2006). In Lithuania the increase in the abundance of

the raccoon dog did not result in a distinct decline of native medium sized predators, also suggesting a weak or absent competition between them (Baltrunaite 2010).

Baltrunaite (2006) concluded that the impact of raccoon dog on red fox (and pine marten) in Lithuania was insignificant, as a result of differences in diet, hunting tactics, specific use of some habitats and its relatively low abundance. However, because fox and raccoon dog population indices correlated negatively during a five year predator removal experiment, Kauhala (2004) thinks that competition between these two species is possible and, if the hunting pressure on one of them is high, the other species may benefit and increase in numbers. Competition is possible, because foxes and raccoon dogs have a large overlap in diet (Kauhala et al. 1998b). Both species have been observed to kill cubs of the other species (Stier 2006b) but it is unlikely that adults of the two species kill each other; raccoon dogs do not seem to avoid foxes (Kauhala 2004) and the two species are more or less the same size and strength. A third process in the possible competition between raccoon dog and red fox may be an enhanced mortality in the red fox by sarcoptic mange after the arrival of the raccoon dog, due to a higher incidence of mange in this species than in the red fox (Mulder, in prep.).

Diet

Sutor et al. (2010) studied the diet of raccoon dogs in eastern Germany, and reviewed 81 other food studies from nine countries, both from Europe and from its native range in continental eastern Asia. Everywhere the raccoon dog can be typified as a 'gatherer' rather than a 'hunter', with a very broad spectrum of food items: an opportunistic omnivore. It profits from all available food sources, both temporary and permanent, which must have contributed to its successful colonisation of Europe. Important food items in virtually all studies were small mammals, insects, plants (cereals, maize, fruits and berries) and carrion. In wet habitats a large proportion of its diet consists of amphibians and fishes; in one German study area amphibians were found in about 50% of the stomachs and fish in 11% (Sutor et al. 2010).

In northern Belarus, in the transition zone of boreal coniferous forest and deciduous forest, the raccoon dog's diet varied with season and habitat, and not individually, i.e. between different pairs successively occupying the same home range. The diet reflects the availability of easy to get food categories. The main factors influencing the composition of the food consumed by raccoon dogs were: type of top soil (clay = rich or sand = poor), the proportion of lakes and marshes and the proportion of berry-rich pine stands, mostly on poor soils. On rich soils more reptiles, amphibians, small mammals and medium-sized mammals were eaten. More birds were consumed when there were many lakes and marshes in the area, fish and mollusc consumption increased with higher lake abundance and berry consumption increased with the abundance of berry rich pine stands. During periods of snow cover the consumption of small mammals decreased and the amount of carrion increased. In years with a good berry crop raccoon dogs ate many more berries than in years with a poor crop (Sidorovich et al. 2008). These results suggest that the raccoon dog is a generalist predator with opportunistic feeding behaviour. Baltrunaite (2005) came to the same conclusion after studying the diet of raccoon dogs in three different landscapes of Lithuania (figure 3: no. 11). In spring and summer the diet was more varied than in autumn and winter, and the availability of food determined diet composition.

There are many examples of the opportunistic feeding behaviour of the raccoon dog. It has been seen following a plough at twilight (to catch voles?); to turn over cow-dung to eat insects; to eat the scats of lynx; to follow the line of dredged sludge along a waterway, to eat

Table 1. Diet composition (%) in some relevant food studies. Several studies are listed two or three times, with a different method of calculating the importance of food-items, different seasons or different study areas. Methods: FO = Frequency of occurrence, i.e. percentage of stomachs in which the item occurred (sum of percentages >100%); PB = percentage of total biomass (adds up to 100%). Percentages within brackets form part of a more general category.

Author	Barbu 1972	Barbu 1972	Ansorge 1998	Ansorge 1998	Stier 2006a	Sutor et al. 2010	Sutor et al. 2010	Sutor et al. 2010
Area	Danube delta	Danube delta	SE-East-Germany, Saxony	SE-East-Germany, Saxony	NE-East-Germany	SE-East-Germany, Brandenburg	SE-East-Germany, Brandenburg	SE-East-Germany, Saxony
Main habitat	Marsh	Marsh	Agriculture	Agriculture	Agriculture	Agriculture	Agriculture	Agriculture
Season	Summer	Winter	Year	Year	Year	Summer	Winter	Year
n stomachs	85	40	27	27	306	232	58	37
Method	FO	FO	FO	PB	PB	FO	FO	FO
Invertebrates						69.4	29.3	95.0
Leeches	8.2	-			-			
Earthworms			7.4	2.1	2			
Molluscs	-	2.5			1			
Insects	50.6	-	59.3	0.8	2			
Fishes	3.5	2.5	7.4	10.9	13	1.7	0	10.8
Amphibians + reptiles						19.0	13.8	54.1
Amphibians	44.7	12.5	18.5	5.2	17			
Reptiles	15.3	5.0	7.4	4.0	1			
Birds	17.6	20.0	18.5	10.3	14	7.5*)	13.8*)	8.1*)
Bird eggs	8.2	-			-			
Small mammals			33.3	5.3	9	27.2	24.1	37.8
Rodents	21.2	35.0	(25.9)	(3.9)				
Insectivores	4.7	5.0	(7.4)	(0.2)				
Carrion	2.4	5.0	25.9	36.1	27	15.5	19.0	8.1
Compost						1.3	5.2	2.7
Plants	32.9	32.5	51.9	24.3	15			
Fruit/berries				(17.8)	(9)	25.4	22.4	43.2
Maize			(11.1)	(5.0)	(5)	18.1	32.8	21.0

*) including eggs

molluscs and other food items; to search the high water mark along the Baltic sea for fish and molluscs; to pick up potatoes after the harvest, to eat from carrots and beets in the field; to climb into fishermen's vessels to eat the discarded small fish; to visit campsites for edible waste and to walk long distances to orchards for the fallen fruit (Wlodek & Krzywinski 1986).

Raccoon dogs intensively use carrion (from wolf or lynx kills, hunting waste - entrails - or the natural death of ungulates) wherever it is available. Dead bison in the Białowieża Primeval Forest were revisited by raccoon dog pairs very often, especially when lying in cover; carcasses lying in the open were rarely visited (Selva et al. 2003). Scavenging on carcasses can be a risky business as raccoon dogs often become victims of large predators

(wolves) when visiting carcasses (Jędrzejewska & Jędrzejewski 1998). Raccoon dogs also profit from the food provided by hunters for wild boar (maize, offal, fruit, etc). However, many are shot at these feeding sites (Stiebling 2000). Other temporary and locally available abundant food sources are sometimes feasted upon: fish when fishponds dry up and eggs when a colony of black-headed gulls (*Chroicocephalus ridibundus*) is present (Nowak 1993).

Eggshell remains are rarely reported from studies of raccoon dog stomachs. Sometimes shells of domestic chickens are found, probably from feeding places for wild boar (Stier 2006a). In most such studies eggs are not mentioned at all (Kauhala 2009). The extent of egg consumption by raccoon dogs is not known but seems to be quite low.

A striking aspect in all diet studies is the lack of hares (*Lepus* spec.) and rabbits (*Oryctolagus cuniculus*). For the red fox, which is of similar size as the raccoon dog, these lagomorphs (when available) always make up an important part of the consumed food. This illustrates that raccoon dogs are not typical hunters, but subsist upon food items which do not require speed or agility.

Relevant diet studies

To get an impression of what raccoon dogs will eat in the Netherlands in the future, the most relevant diet studies were reviewed. These are the studies by Ansorge (1998), Stier (2006a) and Sutor et al. (2010), all three in eastern Germany (figure 3: nos. 10, 13 and 9 respectively) plus the only known wetland study, from the Danube delta (Barbu 1972; figure 3: no. 14). See table 1 for a list of the results of these studies. In addition to the results in table 1, some details of the different studies are listed here.

Barbu (1972). Summer. The 'summer' period here covered spring, summer and autumn, the warmer seasons of the year. Data are given in frequency of occurrence, so one small insect gives the same score as one bird or mammal. In 'summer' insects and amphibians were the most common prey, followed by rodents, birds and reptiles. The amphibians consisted of 32 individual newts, 55 toads, 5 tree frogs and 161 other frogs. The reptiles constituted of 11 lizards and 8 grass snakes. Bird-eggs were found in more than 8% of the stomachs, but considering only the period of April and the first half of May, bird eggs were present in 28.5% of the sample. Plants scored very high in the stomachs, but mostly represented accidentally (with other prey) ingested material. Fruit was found in only 4.8% of the stomachs and maize in 2.3%.

Barbu (1972). Winter. In winter (December to February) rodents (mostly water voles (*Arvicola terrestris*)) with 35% and birds (20%) predominated in the diet. The birds were mainly ducks, coots (*Fulica atra*) and moorhens (*Gallinula chloropus*). The author states that in winter many corpses of these species are available in the field. In mild winters the raccoon dog may to some extent (12.5% and 5% in different winters) feed on amphibians and reptiles.

Ansorge (1998) . A study of just 27 stomachs that found carrion and fruit to be the two main constituents in the diet. This study was repeated later as part of the study by Sutor et al., see below, with a slightly larger sample size (*n*=37).

Stier (2006a). This study is an extension of the work published earlier by Drygala et al. (2000, 2002). In 80% of the stomachs insects were present, but in terms of biomass they represented only 1.6% of the total stomach contents. Cultivated fruits (mainly plum, cherry, apple and pear) and maize represented 4% of the biomass eaten in winter, 15% in spring, 17% in summer and 23% in autumn. Maize was present in stomachs throughout the year, so most of it must have come from feeding sites for wild boar. Raccoon dogs had no problems (unlike foxes) with consuming shrews (Soricidae), moles and hedgehogs (*Erinaceus*

europaeus). These insectivores were the most common mammal category, followed by voles (Arvicolinae). The more agile species of mice (e.g. wood mouse (*Apodemus sylvaticus*), harvest mouse (*Micromys minutus*)) were the least consumed category of mammals. At least a portion of the birds in the stomachs must already have been dead when eaten by the raccoon dogs, because raccoon dogs do not climb and are too slow to surprise birds like buzzards (*Buteo buteo*) and thrushes (Turdidae). Radio-collared raccoon dogs were observed to search the verges of roads for hours on end, to eat traffic victims (insects, molluscs, amphibians, small mammals, birds). Carrion amounted to more than 40% of the biomass eaten in winter and was mostly hunting waste left in the field, such as the entrails of roe deer and wild boar. Although a large number of stomachs were collected in the spring season, bird eggs were found only twice; both were chicken eggs, probably eaten at a wild boar feeding place.

Sutor et al. (2010). In one of the study areas (the one in Saxony) there are many fish ponds, resulting in a larger proportion of amphibians and fish in the raccoon dog diet there, than in the other study area (in Brandenburg). Some stomachs in this study contained only one type of food: maize in winter, frogs or grasshoppers in summer. The category of small mammals mainly consisted of voles (*Microtus* spec.) and water vole, but also some shrews. About 10% of the invertebrate samples consisted of earthworms and molluscs. About 90% of the amphibian-reptile category consisted of amphibians (of these 18% were toads and 82% frogs) and 10% reptiles. Consumed fruits were mainly apples and pears. The birds in the stomachs were mostly (74%) small songbirds, mainly skylarks (*Alauda arvensis*) and their nestlings. Five stomachs contained thrushes, two contained parts of mallards (*Anas platyrhynchos*). Only in a negligible small number of stomachs were remains of bird eggs found. Carrion mainly consisted of hunting waste; this was abundantly available, especially in the Brandenburg study area from October to January.

Predation and impact on prey species

In southern Finland just 1% of raccoon dog faeces (n=206) collected in May and June (the breeding season for birds) contained remains of waterfowl, and none contained remains of gallinaceous birds (Kauhala et al. 1993b). The same study also examined 63 stomachs from southern and central Finland, dating from spring and summer. These stomachs contained no waterfowl remains, but a much higher (16%) occurrence was found of gallinaceous bird remains. Most of the gallinaceous birds were introduced pheasants (*Phasianus colchicus*), some black grouse (*Tetrao tetrix*), with hazel grouse (*Bonasia bonasia*) also occurring (Kauhala et al. 1993b). Grouse populations started to decline in south-west Finland as early as the 1960s, before the raccoon dog invaded the area (Helle & Kauhala 1991). In Poland, Reig & Jedrzejewski (1988) found that, while red foxes frequently prey on birds, raccoon dogs do so only occasionally. Naaber (1971) concluded that raccoon dogs have little impact on grouse or hare populations in Estonia. The raccoon dog is a rather slow and clumsy predator and most probably has great difficulties in catching fast prey such as adult birds or hares (Kauhala et al. 1993b).

A large scale predator removal experiment in southern Finland (removal in 55 km², control in 48 km²), during a five year period, found no evidence of the non-native raccoon dog having a negative impact on the breeding success of dabbling ducks (Anatinae) (Kauhala 2004). These results can either mean that the predator removal was not successful enough, or that the presence of raccoon dogs had no notable effect on the breeding success of waterfowl. The positive correlation between the raccoon dog index and the breeding success of dabbling ducks in this experiment suggests that the latter alternative is true. However, remov-

ing one predator (the raccoon dog), may not have the desired effect on the breeding success of birds, because the numeric and functional response of other predators, such as the fox, may increase and lead to compensatory predation (Kauhala 2004). In Latvia, of 1059 duck nests destroyed by predators on a eutrophic wetland, only 0.6% were attributed to raccoon dogs; the main predators were marsh harrier (*Circus aeruginosus*) (53.7%), corvids (14.7%) and American mink (*Neovison vison*) (9.0%); 13.6% of the predations could not be attributed to a specific predator (Opermanis et al. 2001).

In Germany much discussion, especially among hunters, has been devoted to the role of the raccoon dog in the predation of (the nests and chicks of) ground breeding birds. However, according to Langgemach & Bellebaum (2005), there is a lack of real data. The authors considered the impact of raccoon dogs on the breeding success of ground breeding birds to be rather small compared to that of foxes. Sutor et al. (2010) state: "Potentially predation pressure by the raccoon dog on widespread bird species is low, but a negative impact on small and isolated bird populations - for example the residual population of great bustard in Germany - cannot be excluded".

The trends in wetland breeding birds in Germany do not reveal a clear decrease in breeding populations since the arrival of the raccoon dog. Of all the duck species only the pochard (*Aythia ferina*) has declined in numbers (http://www.dda-web.de/index.php?cat=service&subcat=vid). Although there are indications that raccoon dogs do predate on nests of ground breeding birds there has, to date, been no sound research into the effect of this predation on population levels. Low reproduction and a population decline are two different things, which are not necessarily connected. Much of the reproductive effort of a species may get lost, to predation, without any effects on the population size.

Kauhala & Kowalczyk (2011) have reviewed the literature on all aspects of the invasion of raccoon dogs in Europe, including their impact on prey species. In this respect they state, based on expert judgement: "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 [500 km south of Moscow]. 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."

In island situations breeding bird populations are in general more vulnerable to predation by raccoon dogs, especially if mammalian predators were lacking before. If raccoon dogs reach such islands, their impact may be considerable (Kauhala 1996a). Kauhala & Auniola (2001) reported that 2-67% of raccoon dog faeces from the Finnish archipelago contained waterfowl (mainly eider (*Somateria mollissima*)) remains in different summers, but probably most of them had been found as carcasses. Raccoon dogs were estimated to kill only 1.2-3.5% of the nesting female eiders each year. Rather more scats (11-40%) contained eggshells. More eggshells were found in the scats in July (after eider chicks had hatched) than earlier in spring. The predatory impact may differ from area to area, depending on food availability and the local fauna composition (Kauhala & Auniola 2001).

Prey species other than breeding birds can be affected by the newly arrived raccoon dog. Especially on small islands, frog populations may become threatened. Frogs have indeed vanished from some islands off the south-west coast of Finland after raccoon dogs arrived

in the 1970s, and frog populations have not declined on the outer islands where raccoon dogs are not found (Nummelin, personal communication in Kauhala 1996a). Recently the remnant and reintroduced populations of the European pond turtle (*Emys orbicularis*) in north-east Germany have become endangered by non-native mammals. Raccoon dogs (and wild boar) eat eggs and newly hatched turtles in the nests, but more important for turtle population survival, raccoons catch young and adult turtles in shallow water (Schneeweiss & Wolf 2009). Sutor et al. (2010) also fear that the raccoon dog may have an impact upon the fire-bellied toad (*Bombina bombina*), which occurs in small isolated populations in Germany, but at present there are no data.

In conclusion: raccoon dogs can have an effect on the breeding success of ground nesting birds, mostly in wetland areas and especially in bird colonies. They eat the eggs and chicks, but only rarely the breeding adults. However, from population trends there is no evidence yet that they have an impact on the population size of ground breeding birds. There is still a lack of well-designed studies into predation on ground nesting birds. Raccoon dogs may pose a serious threat for small isolated populations of amphibians, and probably also for turtles.

Dispersal and colonisation capacity

Dispersal is defined as the movement of animals from their natal range to the place where they settle and (will) reproduce (Howard 1960). In field studies it is, however, usually unknown whether the marked animals, reported back by hunters for instance, have already settled and started to reproduce. The high dispersal capacity of the raccoon dog was already observed early in the history of the animal's introduction into Europe. In 1957 an ear-tagged animal was found in central Poland, which had been released in 1953 in western Ukraine; it had dispersed about 500 km (Nowak 1973). However, systematic dispersal studies have only been conducted in eastern Germany.

Drygala et al. (2010) fitted 48 young raccoon dogs in Mecklenburg-Vorpommern with radio-collars, and ear-tagged a further 88 pups. A total of 43% of the marked animals were reported back, at a mean distance from the marking point of 13.5 ± 20.1 km and a maximum of 91 km. Most animals were reported within 5 km of their marking point, only 8.5 % travelled more than 50 km. However, among individuals which were reported back at an age of >1 year, at which age it can safely be assumed that their dispersal process had been completed, dispersal distance was 17.8 ± 23.4 km (n=18). All of the 48 radio-collared young raccoon dogs left their natal range. However, in another dispersal study, in southern Brandenburg, 3 of the 11 ear-tagged juveniles, which were recovered after more than a year, were found in the vicinity of their marking place. The four longest distances covered by dispersing raccoon dogs in this study ranged from 58 to 108 km (Sutor 2008). The radio-collared individuals dispersed between July and September, in a variety of movement patterns. Some departed from one day to the next, others made several excursions before finally departing for good. Some travelled many times between their natal range and a second range, before eventually settling there. Some roamed the landscape, while others walked for days on end in the same direction (covering average daily distances of 5 - 12 km) before establishing a home range. Human settlements were avoided during dispersal. Almost no dispersal was apparent during winter. Two individuals (males) established a temporary home range during winter, but started to disperse again in April, the mating season. A striking characteristic was the lack of difference between males and females (this in contrast to most other canid species) in the average distance covered during dispersal and the time of dispersal. This implies, that reproduction can start quickly in newly invaded areas; in most other canids the males disperse

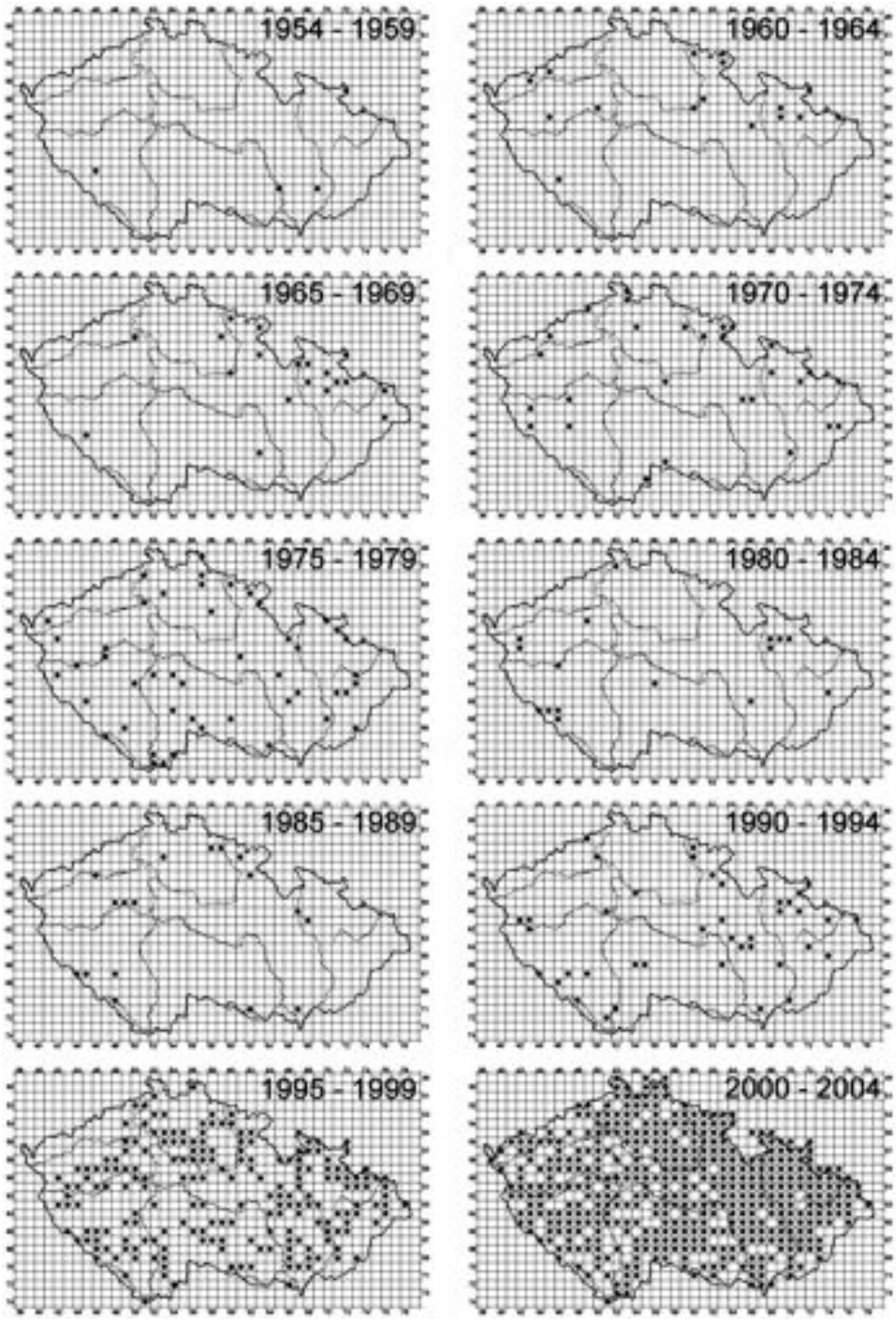

Figure 6. Records of the raccoon dog in the Czech Republic, in periods of five years, since 1954. Mrštný et al. (2007).

over much longer distances than the females and thus have difficulty in finding a mate in newly colonised areas (Drygala et al. 2010).

The population characteristics of the raccoon dog, in terms of reproduction and age structure, do not differ between populations in the original range and in the recently occupied European range. This suggests that the expansion in Europe is not the result of some kind of newly adopted 'expansion strategy' (Ansorge & Stiebling 2001). However, western Europe is ideally suited for further colonisation, because of the lack of rabies and large predators, the two main mortality factors among raccoon dogs (Kowalczyk et al. 2009). Its high rate of reproduction, even higher than expected given its body size, food habits and reproductive system, gives it a high colonisation potential. Other canids of a similar size usually have litters of 4 to 6 pups (Kauhala 1996b). The colonisation of Finland, as an example, proceeded very rapidly. The species spread through the southern and central parts of the country in two decades after the mid-1950s, although 88% of the juveniles died in their first year; litter size was nine (Helle & Kauhala 1991, Helle & Kauhala 1993, Helle & Kauhala 1995, Kauhala 1996b). Average life time production per adult female is about 15 young, which is relatively high for mammals. If adult mortality is low, the species has a high capacity for increase and dispersal (Helle & Kauhala 1995).

Dispersal is another factor contributing to a high colonisation capacity in raccoon dogs. All juveniles of both sexes disperse; there is no role (as 'helpers') for one-year-old individuals in the population, again in contrast to many other canid species. The relatively large average dispersal distance and the high reproduction have in the past resulted in a high rate of expansion, with an average speed of 40 km, and in some areas even 120 km per year (Lavrov 1971, Helle & Kauhala 1987). The raccoon dog's opportunistic use of habitat, as well as its adaptation to agricultural and forested areas, add to its success; food, water, daytime shelters and den sites are almost everywhere available and are important habitat components for the raccoon dog (Drygala 2009).

The pattern of colonisation of new territory has been similar in several European countries: a relatively long period with individual, more or less sporadic sightings and no indications of reproduction, followed by a relatively short phase of rapid (probably exponential) increase and population saturation. This has been elegantly documented for the Czech Republic by Mrštný et al. (2007). The first sightings in the country date from the mid 1950s. Until 1989 the sightings were sporadic. In the period 1990-1994 the raccoon dog was recorded in 7% of the area of the country, but permanent occurrence of this species was suspected in only 0.2% of the country. Then the increase really took off. Over the next five years the species was recorded in 32% of the country, with permanent occurrence in 1%. Between 2000 and 2004 the raccoon dog was recorded in 66% of the country, with permanent presence in 12% of the area. In conclusion, after a period of about 30 years with sporadic sightings, the Czech Republic was colonised by the raccoon dog in just 15 years (figure 6). A similar pattern was observed in Finland, with the first sightings in the 1930s and a rapid increase from 1965 onwards (Helle & Kauhala 1991), and in eastern Germany, with the first sightings in the 1960s and a rapid increase around 1990 (Drygala et al. 2002).

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Samenvatting

De ecologie van de wasbeerhond in Europa: een overzicht

De wasbeerhond (*Nyctereutes procyonoides*) is vanuit Oost-Azië in grote aantallen uitgezet in de voormalige Sovjet Unie, tussen 1928 en 1957. Van daaruit heeft de soort zich over Noord- en Midden-Europa verspreid. De soort wordt beschouwd als een invasieve exoot, omdat hij door mensen is geïntroduceerd, zich succesvol voortplant en zich verder verspreidt. Het beleid in Nederland met betrekking tot invasieve exoten is, om de risico's in te schatten voor de biodiversiteit met aandacht voor de impact op dier- en volksgezondheid en economie. Dit artikel bevat een uitgebreide samenvatting van de huidige kennis van de biologie en de ecologie van de wasbeerhond in Europa, die de basis kan vormen voor een goede inschatting van de te verwachten effecten van zijn komst naar Nederland (Mulder, in voorbereiding). De wasbeerhond (die door jagers ook wel marterhond genoemd wordt, naar het Duits) is ongeveer zo groot als een vos, maar heeft kortere poten en een kortere staart. In de herfst vet hij sterk op, en in koude winters gaat hij in winterrust. Bij het foerageren loopt hij langzaam en blijft hij meestal in dekking van vegetatie. Hij graaft en klimt nauwelijks. Voor de voortplanting gebruikt hij bij voorkeur de holen van das en vos, buiten die tijd slaapt hij bovengronds. Wasbeerhonden zijn monogaam en een paartje trekt gewoonlijk gezamenlijk op. Elk paar leeft in een vast activiteitsgebied, waarvan het centrum door de buren wordt gerespecteerd maar waarvan

de randen overlappen met die van de buren. In gemengde biotopen ligt de voorjaarsdichtheid gewoonlijk tussen de 0,5 en 1,0 individu/km^2. Wasbeerhonden hebben een voorkeur voor oevers, vochtige gebieden en loofbos, en mijden liever naaldbossen en open agrarisch gebied. Ze gebruiken echter wel degelijk alle biotopen in hun activiteitsgebied in zekere mate. De wasbeerhond is een alleseter en meer een 'verzamelaar' dan een 'jager'. In het brede voedselspectrum zijn vooral amfibieën, kleine zoogdieren, dode dieren, vruchten en maïs belangrijk. Hoewel hij ook eieren van grondbroeders kan eten, worden ze bij voedselstudies erg weinig aangetroffen. Tot nu toe is er geen goed opgezet onderzoek verricht naar de invloed van de wasbeerhond op de populaties van grondbroeders. Er zijn vooralsnog geen aanwijzingen dat soorten zijn achteruitgegaan in gebieden waar de wasbeerhond zich heeft gevestigd. Alleen op eilanden heeft de komst van de wasbeerhond geleid tot het lokaal uitsterven van amfibie-populaties, en tot predatie in broedvogelkolonies. Rond eind april vindt de geboorte plaats van relatief grote worpen, meestal bestaande uit 6 tot 9 jongen. De jongen worden vrijwel voortdurend bewaakt door tenminste één van de ouders. Al zes weken na de geboorte verlaat de hele familie het hol en gaat in het activiteitsgebied rondtrekken. Vanaf juli gaan de eerste jongen, nog slechts halfwas, op zoek naar een eigen leefgebied, waarbij ze meer dan 100 km kunnen overbruggen. De meeste blijven echter binnen 30 km van hun geboorteplek.

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