Dispersal of the raccoon dog Nyctereutes procyonoides into a newly invaded area in Central Europe

Authors: Drygala, Frank, Zoller, Hinrich, Stier, Norman, and Roth, Mechthild

Source: Wildlife Biology, 16(2) : 150-161

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/08-076

Wildl. Biol. 16: 150-161 (2010)
DOI: 10.2981/08-076

www.wildlifebiology.com

Original article

Dispersal of the raccoon dog *Nyctereutes procyonoides* into a newly invaded area in Central Europe

Frank Drygala, Hinrich Zoller, Norman Stier & Mechthild Roth

In order to understand dispersal behaviour and its population consequences, we captured 136 raccoon dog *Nyctereutes procyonoides* pups (i.e. < 1 year old) in northeastern Germany (Mecklenburg-Western Pomerania). We ear-tagged all animals and additionally fitted 48 of them with radio-collars. There were findings of 59 (43.4%) animals and the mean distance from the marking point was 13.5 km ± 20.1 (SD). Dispersal mortality rate was 69.5% among young raccoon dogs. Most animals (55.9%) were recovered < 5 km from the marking place, whereas only 8.5% of the records were > 50 km from the marking point. The distances of the dispersal did not differ between sexes. Most (53.7%) records of ear-tagged young raccoon dogs were made in August and September, and only 34.1% were recorded during October-April. Hunting (55%) and traffic (27%) were the major mortality criteria. Most radio-collared young raccoon dogs dispersed between July and September. The mean natal home-range size (MCP 100) with and without excursion was 502.6 ha ± 66.4 (SD; N = 9) and 92.1 ha ± 66.4 (N = 17). There were no differences between males and females in the month of dispersal. Raccoon dogs dispersed into all directions with distances varying between 0.5 km and 91.2 km. Radio-collared, dispersing animals showed a variety of movement patterns and the impression of flexible migration behaviour was confirmed. The fact that males and females showed equal dispersing behaviour is supposed to be one of the factors contributing to the high expansion and the success of the species.

Key words: northeastern Germany, dispersal, ear-tagging, Nyctereutes procyonoides, raccoon dog, telemetry

Frank Drygala, Norman Stier & Mechthild Roth, Dresden University of Technology, Chair of Forest Zoology, Piennerstraße 7, D-01735 Tharandt, Germany - e-mail addresses: drygala@gmx.net (Frank Drygala); stier@forst.tu-dresden.de (Norman Stier); mroth@forst.tu-dresden.de (Mechthild Roth)*
Hinrich Zoller, University of Rostock, Universitätsplatz 2, D-18055 Rostock, Germany - e-mail: hinrichzoller@aol.de

**Present address: Sonnenburgerstraße 54, D-10437 Berlin, Germany*

Corresponding author: Frank Drygala

Received 5 November 2008, accepted 24 November 2009

Associate Editor: Xavier Lambin

During 1929-1955, the raccoon dog *Nyctereutes procyonoides* was introduced into Europe. Approximately 9,100 animals were released, mainly into the western parts of the former Soviet Union, expanding their range at an average annual speed of about 40 km (Lavrov 1971). Within 50 years (1935-1984), a territory of 1.4 million km^2 was colonised (Nowak 1993). The first raccoon dog sighted in Poland was in 1955, and in 1964, sightings were recorded in eastern Germany (Mecklenburg-Western Pomerania; Nowak & Pielowski 1964, Nowak 1973). Until the early 1990s, only a few animals were recorded in Germany, but shortly thereafter, an exponential increase of game kills became evident (Drygala et al. 2002), and during the hunting season of 2008/09, 30,053 raccoon dogs were shot (Deutscher Jagdschutz Verband 2009). The rapidly increasing size of the raccoon dog population is of conservational and wildlife management interest, because of the impact that these animals may have on indigenous prey species and competing predators (Sidorovich et al. 2000, Kauhala & Saeki 2004, Sidorovich et al. 2008).

Furthermore, predators and pests are of significant conservational concern, and to forecast their expansion, advances in the management of these populations also require a detailed understanding of dispersal behaviour. Since field studies are rare, there is an almost complete absence of empirical data on dispersal and other relevant behavioural parameters in recent studies of the raccoon dog populations in Central Europe. To fill this gap and to specify and forecast the species population dynamic, the aim of our field study was to provide current detailed information on dispersal direction, relocation distances, month of dispersal, date of relocations and the mortality of dispersing animals. This could help us understand the invasion process and the ecological implications of the species in its new living area.

Today, the raccoon dog has become a permanent member of the fauna in Germany and the increasing bag numbers indicate that the population has not yet reached the carrying capacity of the environment. Furthermore, besides close-to-nature habitats (e.g. reed beds, swamps and mixed forests), intensively used agricultural habitats with low forest cover are colonised (Drygala et al. 2008b).

Apart from its role as a new predator, long-distance dispersal of the raccoon dog can accelerate the spread of rabies and other diseases, and of parasites. During a rabies epizootic in Finland at the end of the 1980s, the raccoon dog was the main vector and victim of the disease (Westerling 1991, Nyberg et al. 1992). Furthermore, raccoon dogs are potential vectors of the fox tapeworm *Echinococcus multilocularis*, and some infections of this dangerous parasite have recently been reported from eastern Germany (Thiess 2004, Tackmann et al. 2005).

The mechanisms that determine dispersal behaviour in canids are unclear (White & Harris 1994). Previous studies showed that e.g. in wolves *Canis lupus* both sexes disperse, although a slight male bias has been demonstrated in a few studies (Ballard et al. 1987, 1997, Fuller 1989, Gese & Mech 1991, Wabakken et al. 2001), and in red foxes *Vulpes vulpes,* males disperse longer distances than females (Harris & Baker 2001). Prior to our study, it was only known about the raccoon dog that most pups start to move with their parents, usually in late June or early July in Germany (Drygala et al. 2008c) and that dispersal of juveniles in Finland starts in August. Thereafter, most raccoon dogs leave their natal home range in September or October (Kauhala et al. 1993, 1998).

However, more knowledge on dispersal behaviour and patterns is crucial for Central Europe. If the sex ratio of short- and long-distance dispersers is equal among young raccoon dogs, this will guarantee pair bonding and hence ensure reproduction in newly invaded areas. Therefore, one main concern of our investigation was to specify the sex ratio among dispersing juveniles, and relate this to potential expansion of the species in Central and Western Europe.

Material and methods

Study areas

Our main study area 'Galenbeck' (located at 53°37'N, 13°42'E; situated at 1-113 m a.s.l. and covering 250 km^2) is located in eastern Mecklenburg-Western Pomerania, approximately 50 km west of the German-Polish border. The area is characterised by a temperate climate. The average annual temperature between 1999 and 2003 was 9.7°C, and the average temperature was 0.8°C in January and 18.2°C in July. The total annual precipitation averaged 431 mm and the mean annual relative humidity was 75% for the same time period (German Weather Service/Neubrandenburg 2003).

Typical of the area are close-to-nature habitats like reed beds, swamps, streams, ditches and a large lake (575 ha). Of the total area, 27.5% was covered with mainly deciduous forest, and meadows (32.9% of the area) for cattle and farmland (28.4% of the area) made up the largest parts of the region. Although the human population is sparse in the study area (49 inhabitants/km^2 in the Uecker-Randow-District; Residents' Registration Office 2003), the area is dissected by many dirt roads, which facilitate radio-tracking in the area.

The other study area (covering 150 km^2) is located close to 'Penzin' in the northwestern part of the state (53°55'N, 11°56'E and situated at 4-89 m a.s.l.). The average annual temperature was 9.3°C between 2004 and 2006, and ranged from a mean of -0.2°C in January to a mean of 15.5°C in July. The mean annual relative humidity was 80.3% (German Weather Service/Laage 2008). The human population density is 51 inhabitants/km^2 (in the Güstrow-District; Residents' Registration Office 2007) and settlements covered 3.4% of the study area. Vast agricultural landscape with meadows (21.3%) and farmland (48.8%) make up the major land used in

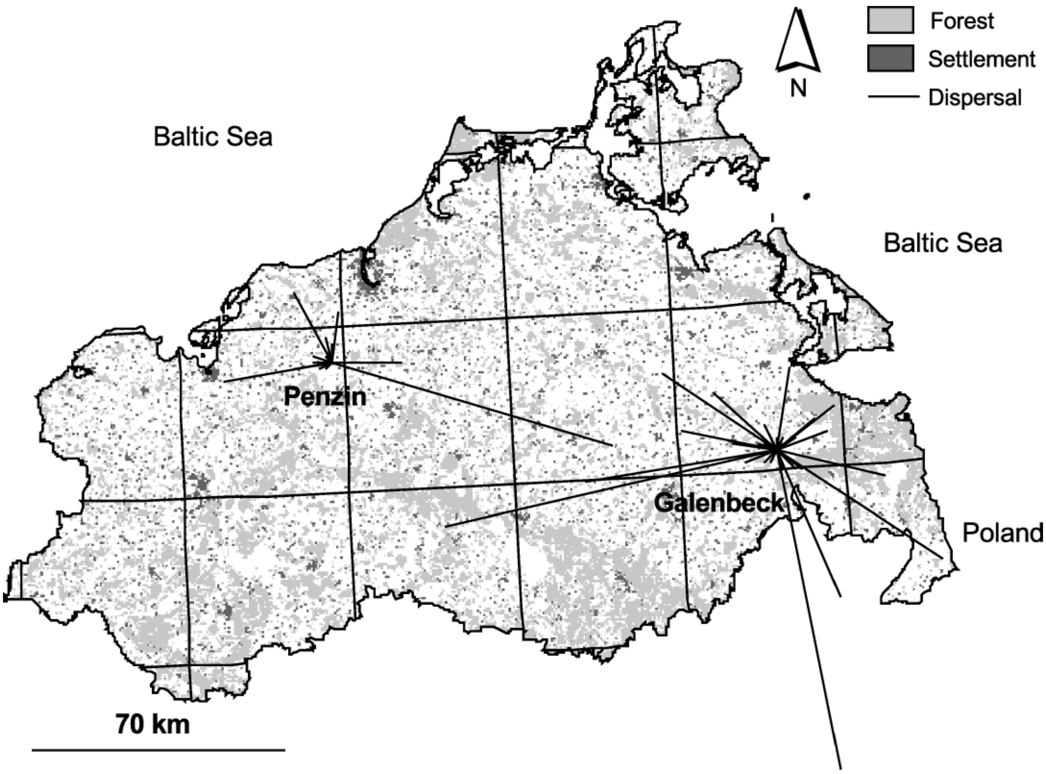

Figure 1. Location of the study areas Penzin and Galenbeck in Mecklenburg-Western Pomerania (northeastern Germany) and dispersal distance and direction of raccoon dogs (N = 59). For simplification, all marking points of each study area were standardised to one location.

the region. There are no forests, only small woods covering 2.7% of the area.

Possible predators to raccoon dogs, especially to juveniles, are red fox, white-tailed eagle *Haliaeetus albicilla*, domestic dog *Canis familiaris* and badger *Meles meles* (Sidorovich et al. 2000, Drygala et al. 2008a, Kowalczyk et al. 2009). Raccoon dogs were regularly hunted in both study areas (Fig. 1).

Ear-tagging

We captured 82 (39 males and 43 females) young (< 1 year) raccoon dogs in 'Galenbeck' during June 1999 - October 2003 and 54 (33 males and 21 females) young raccoon dogs in 'Penzin' during August 2004 - August 2006. The total of 136 young raccoon dogs were captured and released at the point of capture during approximately 600 trapping nights for both study areas (see Fig. 1 and Table 1). Because the whole State of Mecklenburg-Western Pomerania (as is supposed for the entire Central Europe) is suitable as raccoon dog habitat (Drygala et al. 2008b) and the straight line distance between the two study areas is only 123 km, we pooled data on animals for both study areas for further analysis.

Table 1. Capture and returned information for ear-tagged (N = 88) and radio-collared and ear-tagged (N = 48) raccoon dogs. Returned information and mean dispersal distances (in km) are given for animals reported before (N = 41) and after (N = 18) one year of age.

	Captured raccoon dog < 1 year old	Returned information < 1 year after parturition (dispersal)	Returned information > 1 year after parturition (resident adult)	Total returned information
Ear-tagged only	88 (64.7%)	15 (36.6%)	9 (50.0%)[1]	24 (40.7%)
Radio-collared and ear-tagged	48 (35.3%)	26 (63.4%)	9 (50.0%)	35 (59.3%)
All	136	41	18	59
Mean dispersal distance (km)	-	11.6 ± 18.4	17.8 ± 23.4	13.5 ± 20.1

[1] Of the nine animals, three were recaptured and radio-collared outside their natal home range.

Raccoon dogs were captured alive using wire-box traps and fish bait. They were easy to handle and did not need to be immobilised. Adults were distinguished from juveniles by means of body weight, fur and attrition of teeth, especially of incisors. Individuals captured in their first year of living (before 1 May) were classified as juveniles. All animals were sexed, weighed and fitted with numbered plastic ear-tags (Rototags©).

We defined dispersal as the movement of an animal from its birthplace to where it might reproduce (Howard 1960). In our study, we measured the distance between the marking place and the place where the animal was reported, as the straight line distance. Published dispersal distances are biased towards short-distance movements and must be regarded as conservative minimums of both the frequency and distances, moved by long-distance dispersers (Linnell et al. 2005). Thus, to improve reliability of our data, we recorded the date (month) of the received returned information and classified raccoon dogs in 41 young (< 1 year) animals, who probably died while dispersing, in their first year of age, and 18 relocations for individuals who survived for > 1 year (adults). Almost all ear-tagged raccoon dogs were hunted or found dead when registered, and only three animals were trapped again outside their natal home range (see Table 1). To specify the age of dispersing juveniles, we set 1 May as the date of parturition (Nowak 1993, Kauhala et al. 1998, Boge 2006, Drygala et al. 2008c). The date (month) of dispersal was estimated using telemetry or the returned information data for juveniles that were hunted or found dead. We collected returned information during the entire study period for both study areas.

We have presented elsewhere the mean home-range sizes of resident adult raccoon dogs in the study area 'Galenbeck' (Drygala et al. 2008a). Mean home-range size for adults was used to estimate the dispersal distance for raccoon dogs, using the two formulas of Trewhella et al. (1988):

$$\text{Mean dispersal distance for males} = 2.778 + 4.038 \times \text{home-range size};$$

$$\text{mean dispersal distance for females} = 3.853 + 2.659 \times \text{home-range size}.$$

To compare our data with those obtained in a study from Finland, we used the formulas, originally calculated for red fox, for raccoon dogs, because both species live in pairs (see Kauhala & Holmala 2006). We compared the formula calculation with the mean relocation distance for young male and female raccoon dogs.

To assess the invasion pattern of the species in general, we displayed the dispersal direction (direction of relocation from release site) and distance. Furthermore, we recorded whether the animals were hunted, road-killed or killed by domestic dog, and we also analysed the percentage allocation of mortality factors.

Radio-tracking

In our main study area of 'Galenbeck', we fitted 48 young (< 1 year) animals (25 females and 23 males) with expandable radio-collars (Wagener, Cologne). Each transmitter weighed 56 g and lasted about one year. Raccoon dogs were monitored between June 1999 and October 2003. We located the animals using a handheld H antenna (HB9CV) or a three-element Yagi-antenna and TRX-1000s receivers (Wildlife Materials, USA) at different times of the day, i.e. at night and day (point method) as often as possible (a total of 2,877 locations). To record the month of dispersal, we were mainly interested in estimating whether the animal was captured in its natal home range, in its new/temporary home range, or whether it was trapped on dispersal.

The mean distance between observer and animal was usually < 1 km. As recommended by Garrott et al. (1986), we used multiple triangulations with at least three bearings per localisation to eliminate reflected signal errors.

We estimated the mean tracking accuracy at 91.6 m ± 50.0 (SD; N = 52) by locating hidden transmitters. In addition, we made visual observations of radio-collared animals on short-cut meadows using binoculars and night vision (distance < 300 m) as often as possible to improve the accuracy of the fixes. For tracking using a 2-3 element Yagi antenna, a 1-in-10 rule is acceptable (Kenward 2001). Thus, our tracking resolution (100 m) and observer-animal distance (< 1,000 m) were in a ratio of 1:10. We analysed telemetry data using ArcView GIS 3.2a. Because all animals showed home-range shift after being fitted with a radio-collar, we did neither analyse stability of short-term home ranges nor autocorrelation of locations.

We managed to track continuous dispersal movements of juveniles in different years, usually starting before dawn. By doing so, we tried to locate the animals every 15 minutes until they stopped roaming and rested over the day.

In a study on farmed raccoon dogs, the weight of the pups was between 2.5 kg and 3.6 kg on average in mid-July (Korhonen et al. 1982). If we assume 1 May as the date of parturition for raccoon dogs in Europe (Nowak 1993), these juveniles were 10-11 weeks of age. For home-range calculation, we used only data for juveniles which (N = 17) weighed < 2 kg, at the age of 7.9 weeks ± 1.1. Raccoon dog pups left the breeding den in the sixth week *post partum,* and thereafter, they roamed for another few weeks, guarded by their parents (Kauhala et al. 1998, Drygala et al. 2008c). Hence, we can be certain that the home-range sizes, estimated according to the minimum convex polygon method 100% (Mohr 1947) are for juveniles prior to dispersal. To estimate the area covered by excursions for young raccoon dogs, we calculated the natal home-range sizes (in ha) with and without excursions.

Statistical analysis

For statistical analysis (using SPSS 15.0.1), the Mann-Whitney U-test was used to compare differences in the distance of relocation between sexes. We tested significance of differences between month of relocation, month of dispersal and fate of ear-tagged raccoon dogs using a non-parametric χ^2-test. We tested differences between sexes in the month of dispersal using Pearson's χ^2-statistic. All values are presented as mean ± SD.

Results

Ear-tagging

From the total of 136 ear-tagged and additionally radio-collared young raccoon dogs, we received returned information on 59 individuals (43.4%), whereas from the 88 exclusively ear-tagged raccoon dogs, we received returned information of 24 animals (27.3 %) only. Fifteen animals died in their first year (mortality rate = 62.5%; see Table 1). Most juveniles were captured from June to September, but we did not capture young raccoon dogs from March to May. No animals were trapped again in their natal home range after dispersal (Fig. 2).

In only 18 out of 59 records of pups, the pups survived > 1 year of age. Hence, the dispersal mortality rate for young raccoon dogs was 69.5%. The mean distance of dispersal for all raccoon dogs was 13.5 km ± 20.1. The mean distance that young (< 1 year) raccoon dogs (N = 41) moved was 11.6 km ± 18.4, whereas the mean dispersal distance for animals who survived > 1 year of age and were recorded as resident adults (N = 18) was 17.8 km ± 23.4 (see Table 1). Of both males and females, 55.9% were recorded < 5 km from the marking place, whereas 8.5% moved > 50 km from the marking point. Raccoon dogs dispersed in all directions for distances of 0.5 km - 91.2 km. There was no difference in the dispersal distances between sexes (Mann-Whitney U-test: Z = -0.44, P = 0.66, N = 59; see Figs. 1 and 3). Littermates may occasionally disperse together or follow similar routes. The parallel progress of filling up the distribution area and expanding into new areas is well-founded by flexible dispersal distances and directions.

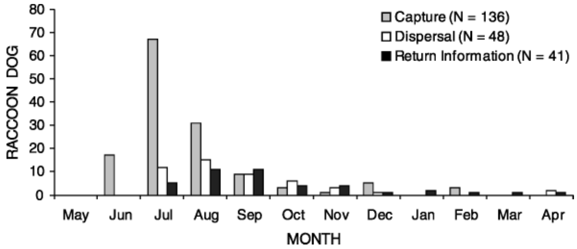

Figure 2. Month of capture (N = 136), dispersal (N = 48) and returned information (N = 41) for young (< 1 year) raccoon dogs. Month of dispersal was carried out using telemetry.

By using the formulas of Trewhella et al. (1988) to estimate the relationship between dispersal distance and home-range size, females and males dispersed 14.0 km and 17.0 km, respectively. There were significant differences between the months of dispersal for 41 young raccoon dogs ($\chi^2 = 33.87$, df = 9, P < 0.0001). Most of the returned information (53.65%) was received in August and September, and only 34.1% were recorded during October-April. No raccoon dogs dispersed in May and June (see Table 1 and Fig. 2). We found significant differences between mortality criteria of

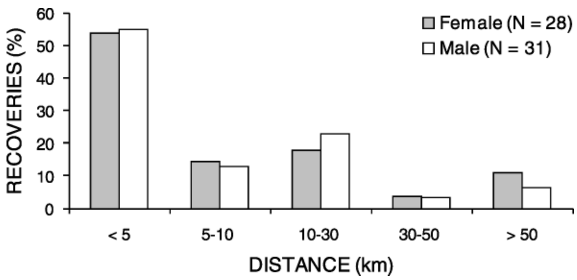

Figure 3. Distance of relocations for young female (N = 28) and male (N = 31) raccoon dogs from the points of capture.

raccoon dogs ($\chi^2 = 31.0$, df = 5, $P < 0.0001$). Of the 59 raccoon dogs reported, most animals were hunted (55%) and road-killed (27%), and of the hunted animals, 38% were shot as juveniles and 17% as adults. Domestic dogs killed 8%, and 2% were found dead with the cause of death unknown. For another 8%, the radio-collar had expired after approximately one year, and we could only estimate the distance and date of dispersal.

Radio-tracking

All 48 radio-collared raccoon dogs displayed exploratory behaviour and left their natal home range. Thus, we were able to identify the month when young raccoon dogs started dispersing. We received returned information (hunted or found dead) on 35 (72.9%) of the radio-collared raccoon dogs of which 26 animals died in their first year of living leading to a mortality rate of 74.3%.

Our telemetry data indicated that 14 individuals died during dispersal and that seven individuals established a post-dispersal home range. For five individuals, we were able to estimate the home-range size as a resident adult.

There were significant differences between the months of dispersal ($\chi^2 = 24.9$, df = 6, $P < 0.001$). Most animals dispersed between July and September. During winter, almost no dispersal was recorded, but in April, which is during the mating season, two males started to disperse again after they had established a temporary home range. During the early pup rearing period in May, no dispersal was recorded. There were no differences between sexes in the month when the dispersal started ($\chi^2 = 4.30$, df = 6, $P = 0.6$; see Table 1 and Fig. 2). The mean natal home-range size with and without excursions was 502.6 ha ± 66.4 (N = 9) and 92.1 ha ± 66.4 (N = 17), respectively.

Examples of four radio-collared young raccoon dogs showed a variety of dispersal patterns, and the impression of flexible behaviour was confirmed (Fig. 4 A-D).

A young male left his natal area and dispersed 28.5 km in a straight line (a total distance of ~ 58.1 km), in five days (a mean of ~ 11.6 km/day) in August, when he established his temporary home range in a suitable habitat. The male travelled westwards in an almost straight line, until the periphery of a larger city was met and he turned north (see Fig. 4A). Another male showed an extremely large home-range size (> 15,000 ha) while roaming solitarily in search of a suitable habitat and a pair mate in his first year of living (see Fig. 4B). The male lost his radio-collar at one year of age and was road killed, 1 km out of the displayed range on 2 September.

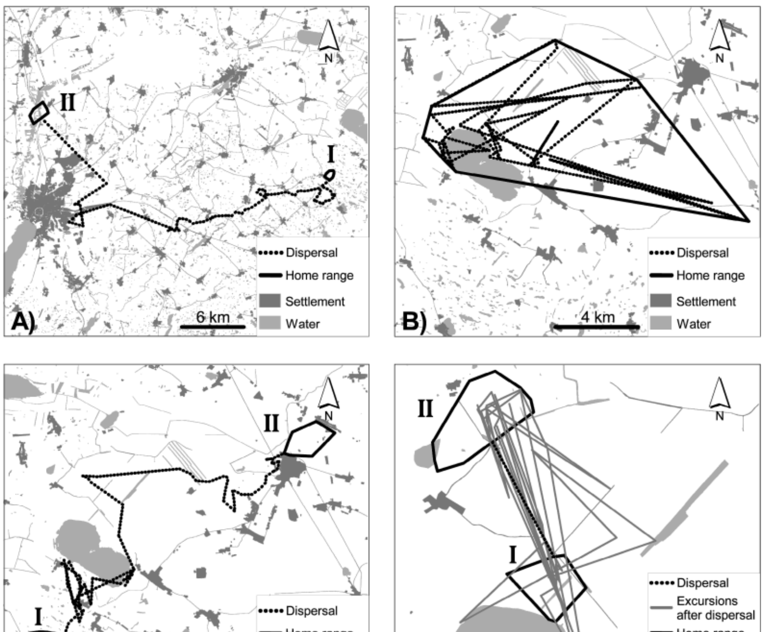

Figure 4. Examples of home ranges (Kernel 100%) for young male (A-B) and female (C-D) raccoon dogs (I indicates natal range, and II indicates the temporary range post dispersal), and dispersal patterns (line of consecutive locations).

A young female dispersed 16.3 km in a straight line (a total distance of ~ 47.9 km) in 10 days (in October-September), with a mean speed of 4.8 km/day from her natal home range. She was shot in January in her temporary post dispersal range in her first year of living (see Fig. 4C). A second female showed oscillating movements by gradually extending her activities into neighbouring areas, but kept returning to her natal home range until August. She became resident in close vicinity (3.05 km) with peripheral overlap to her parental home ranges. Pair mate and reproduction was recorded in her second year (see Fig. 4D).

Some young raccoon dogs literally got up and left one night or did excursions before dispersing, others changed between two areas before they eventually settled down permanently. Some roamed the landscape while others walked in a straight line before stopping.

Discussion

Reliability of the method used

Capture-mark-relocation data do not show whether any individual raccoon dog has completed its dispersal movement when it is relocated. Furthermore, the measured dispersal distance is a minimum estimate of distance travelled, as movements are often complex. E.g. the estimated straight-line distance of a male was 28.5% of the total distance travelled, and for a female, the straight-line distance was 34.0% shorter than the real distance roamed. The mean speed of 11.6 km/day for the male and 4.8 km/day for the female indicates that raccoon dogs are capable of reaching suitable habitats in a short time.

For the present analysis, the returned information received > 1 year after parturition (see Table 1) only includes the animals known to have settled as adult resident animals. Hence, we excluded dispersal distances from young raccoon dogs that were killed during dispersal. Therefore, we regard the mean distance roamed and recorded for resident adult raccoon dogs as the most reliable distance of dispersal. Using telemetry, we were able to record the month when juveniles (N=48) started dispersing from the point of capture. For animals that were showing temporary or stable home ranges after dispersal, the last bearing was always used to determine the month of dispersal. Because raccoon dogs can disperse in late April in the year after parturition, we can not rule out a bias towards late dispersers.

Dispersal

Our work represents the first quantified and comprehensive data on dispersal of the raccoon dog in Central Europe, and therefore, it is of great value to specify and forecast the species population dynamics. Previously, only a single study in Germany has examined dispersal in raccoon dogs, and the number of dispersal events recorded was rather small (N = 11; Sutor 2008). Therefore, information about dispersal distances and direction, relocation distances and date of dispersal, both for male and female raccoon dogs, is crucial to predict the ability of this invasive species to expand further. In a representative sample of dead animals, the causes of death for each animal shut have the same probability of being detected (Ciucci et al. 2007). In our study, the mortality factors for ear-tagged and radio-collared young raccoon dogs were comparable. In regard to the much higher returned information probability of radio-collared than of ear-tagged animals (72.9 vs 27.3%), mortality estimation using radio-collared raccoon dogs, seems to be more efficient.

In Japan, the Japanese raccoon dog *N. p. viverrinus* start to disperse in October and continue until February (Yashiki 1987, Yamamoto et al. 1994, Saeki 2001), and raccoon dogs disperse over shorter distances and disperse later than the raccoon dogs in Europe (M. Saeki, pers. comm.). In northeastern Germany, all marked young raccoon dogs dispersed from their natal areas and some (8.5%) travelled considerable distances (> 50 km) before settling. In a study from southern Finland, 17% of juveniles dispersed > 40 km (Kauhala & Helle 1994). In Europe 'long-distance runners' in western direction are responsible for the first records in the new distribution areas. E.g. a released raccoon dog, ear-tagged in western Ukraine was relocated in Poland after three years. The animal roamed approximately 500 km (Nowak 1973) while most probably trying to find a pair mate and thus continue to disperse. These data illustrate the ability of this medium-sized canid to reach areas far away in a comparatively short time, which contributes to the fast expansion of raccoon dogs.

However, in our study, most young raccoon dogs (55.9%) were reported close (< 5 km) to their natal home range. This is equivalent to the study conducted by Kauhala et al. (1993), who reported that 50% of juvenile raccoon dogs were recorded within a radius of 5 km from the marking point. Also in southern Brandenburg (eastern Germany), three raccoon dogs ear-tagged as juveniles were recorded quite near their marking place after one year (Sutor 2008).

The growth and expansion of the population is increasing in many parts of Central Europe and meanwhile, the whole area of northern and eastern Germany now belongs to the distribution area of the raccoon dog. Additionally, first records from Denmark, the Netherlands, France, Switzerland, Austria and Italy have been reported (Kauhala & Saeki 2004).

According to Knowlton et al. (1999), an increased mortality is often associated with dispersal when animals move into unfamiliar areas and low-security habitats. We assume that survival rate and reproduction success is highest for raccoon dogs with short dispersal distances because a higher dispersal mortality is more likely during long migrations.

Because of a high mortality rate (69.5%) among juveniles and a high reproduction potential (nine pups on average; Boge 2006) of raccoon dogs, they appear to be relatively r-selected in Central Europe which clearly is supporting the further expansion. Our results coincide with a study from Finland where: 1) the species spread through the southern and central parts in about two decades after the mid-1950s, 2) 88% of juveniles died in their first year, and 3) mean litter size was nine (Helle & Kauhala 1991, 1993, 1995, Kauhala 1992).

There are continuous observations since the beginning of the 1990s in eastern Germany, and the hunting bag is most probably still growing. Thus, considering the results from Finland, we believe that the population will continue to expand, and we expect an increase of the population in Germany.

In general, among canids, the time between emigrating and settling can be highly variable (Gese & Mech 1991). Possible motivation for dispersal of juveniles can be: search of own territory, prevention of inbreeding, search for pair mate, territoriality of parents, group-hierarchy and genetic disposition to migrate (Caughley & Sinclair 1994). Because of low territoriality in raccoon dogs (Drygala et al. 2008a), juveniles are most probably not pushed out of their natal range by parents, and their impulse to migrate is generically determined.

It is supposed to be easy to find a suitable habitat for the ecological flexible (generalist, opportunist) raccoon dog (Drygala et al. 2008b, Sidorovich et al. 2008). For this reason, there is no need for long dispersal distances. However, the search for a partner is probably the main reason for the long dispersal distances of raccoon dogs in general.

There seems to be no consistent pattern in dispersal distance or direction, and young raccoon dogs of both sexes disperse over equal distances. A common behaviour was dispersal via one or more temporary home ranges until a definite home range was established. Others gradually extended their activities into neighbouring areas before settling in the vicinity of their natal home range. This is reflected in a small natal home-range size, but a large temporal home-range size including excursions into neighbouring areas. On the other hand, some juveniles suddenly left their natal home range and never returned. Another dispersal pattern shown by juveniles was roaming as pairs or alone in relatively large areas before settling.

Also in the red fox, a common pattern with dispersal through one or more temporary home ranges can be found. From these temporary ranges, foxes do exploratory trips, often progressively further and partly along routes taken earlier until a definite territory is established (Mulder 1985). Moreover, littermates sometimes disperse together or use the same routes (Pils & Martin 1978).

In raccoon dogs, most parturition occurs in May (varies from April to June) and sexual maturity is reached at 9-11 months of age (Kauhala & Saeki 2004). In our study, most relocations and month of dispersal for young raccoon dogs were recorded between July and September. Thus, raccoon dogs usually disperse at the age of 3-5 months before they reach sexual maturity in Central Europe.

The current population densities of 0.95 animals/km^2 (Drygala et al. 2008a) are most probably reached through 'short- and semi-distance runners' with a mean annual dispersal distance of 13.5 km. A longer (40 km) mean annual dispersal distance in the area of introduction (Lavrov 1971) was most probably recorded, because roaming animals tried to find a partner in raccoon dog free areas and thus did not settle.

Kauhala et al. (2006) estimated the mean dispersal distances at 19 km for males and 14 km for females in Finland. Using the same method (Trewhella et al. 1988), males (17.0 km) and females (14.0 km) dispersed almost identical distances in our study. All these data concur with the most reliable;

the mean dispersal distance (17.8 km) for raccoon dogs, recovered as resident adults in northeastern Germany (see Table 1).

Although individuals of most canid species disperse from their natal home range at sexual maturity, the motive for dispersal still remains obscure (Pulliainen 1985). Furthermore, the decision to disperse is likely to be influenced by a variety of factors acting either independently or synergistically, rather than caused by any single event (Dobson & Jones 1985).

Regarding the red fox, it can be claimed that because of their highly developed territoriality and exclusive home ranges, there is a close relation between population density, home-range size and distance of dispersal: the lower the fox population density, the further the foxes will move (Trewhella et al. 1988, Macdonald & Johnson 2000). Furthermore, male foxes typically disperse further than females do (e.g. males 13.7 km and females 2.3 km in Welsh hills; Lloyd 1980, Trewhella et al. 1988), whereas in our raccoon dog study, juveniles of both sexes disperse, and we recorded no bias towards males.

Raccoon dogs have a monogamous social system with bi-parental care, and a large home-range overlap without defending an exclusive territory (Kauhala et al. 1998, Drygala et al. 2008a,c). Furthermore, in contrast to the red fox, 'helpers' have not been observed in the raccoon dog (Kauhala & Saeki 2004). Young raccoon dogs most likely do not remain in their parental home ranges, because they would only use resources without supporting the reproduction success of the breeding pair. Consequently, we assume that in raccoon dogs, dispersal distance is strongly influenced by innate species traits that prompt the animals to travel a set distance before stopping, or by habitat features, or both.

During recent years, the role of the raccoon dog as a vector of rabies has increased in northeastern Europe, and today, it is a more common victim than the red fox, at least in Estonia (WHO 2004). Current studies of rabies in Europe indicate a high risk of distribution of this disease by dispersing juveniles, both of red foxes and raccoon dogs (Kauhala & Holmala 2006). In Finland, an annual peak in the occurrence of raccoon dog rabies has been found in autumn when juvenile raccoon dogs disperse (Westerling 1991). Because of oral vaccination there were no records of rabies for wildlife (excluding bats *Chiroptera* sp.) since 2005 in Germany (WHO-Rabies-Bulletin-Europe 2010). Regarding open borders and uncontrolled transmission of pets (e.g. of domestic dog), there remains a risk of a renewed outbreak in Central Europe. In this case, a further distribution of the zoonosis by migratory movements of young raccoon dogs is conceivable. Moreover, raccoon dogs are potential vectors of fox tapeworm, a parasite that also infects humans. Unlike rabies, which is transmitted by direct contact, the tapeworm spreads through eggs in carnivore faeces. As raccoon dogs typically deposit their scats in prominent latrines (Ikeda 1984, Goszszynski 1999), and have large home-range overlap among neighbours (Drygala et al. 2008a), intraspecific infection is likely. Thus, the raccoon dog is an important reservoir and vector of this dangerous zoonosis and an expansion of risk areas is probable.

We anticipate that raccoon dogs, as flexible dispersers in an anthropogenic landscape such as Central Europe, should do well in the next decades.

Acknowledgements - our research was funded by a graduate scholarship from the State of Saxony. We would like to thank the Forestry Administration of Mecklenburg-Western Pomerania for funding the study. We would also like to extend our gratitude to M. Saeki and O. Keuling for critical reviews of the manuscript. We thank M. Feidel for proofreading earlier versions of this paper. Lastly, we would like to thank all of our friends and aides involved with this project for their support in carrying out this study. GIS maps were provided by the Mecklenburg-Western Pomerania Office of Surveying.

References

Ballard, W.B., Whitman, J.S. & Gardner, C.L. 1987: Ecology of an exploited wolf population in south-central Alaska. - Wildlife Monographs 98: 1-54.

Ballard, W.B., Ayres, L.A., Krausman, P.R., Reed, D.J. & Fancy, S.G. 1997: Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. - Wildlife Monographs 135: 1-47.

Boge, A. 2006: Makroskopische und histologische Untersuchungen an den weiblichen und männlichen Fortpflanzungsorganen von wildlebenden Marderhunden unter besonderer Berücksichtigung des Alters und der Jahreszahl. (In German with an English summary: Macroscopic and histological investigation on female and male reproduction organs with special reference to age and year). - PhD thesis, University of Leipzig, Leipzig, Germany, 151 pp.

Caughley, G. & Sinclair, A.R.E. 1994: Wildlife Ecology and Management. - Blackwell Scientific Publications, Oxford, UK, 334 pp.

Ciucci, P., Chapron, G., Guberti, V. & Boitani, L. 2007: Estimation of mortality parameters from (biased) samples at death: are we getting the basics right in wildlife field studies? A response to Lovari et al. - Journal of Zoology 273: 125-127.

Deutscher Jagdschutzverband 2009: Marderhund und Waschbär in Deutschland. Jagdstatistik 1994-2009. - Available at: http://medienjagd.test.newsroom.de/grafik_neozoen08_09.pdf (Last accessed on 17 February 2010).

Dobson, F.S. & Jones, W.T. 1985: Multiple causes of dispersal. - American Naturalist 126: 855-858.

Drygala, F., Stier, N. & Roth, M. 2002: Erste Ergebnisse zur Nahrungsökologie, Home-Range und Habitatnutzung des Marderhundes (*Nyctereutes procyonoides*) - eines invasiven Caniden in Ostdeutschland. (In German with an English summary: Preliminary results from diet, home-range and habitat use of the raccoon dog (*Nyctereutes procyonoides*) - an invasive canid in Eastern Germany). - Artenschutzreport 12: 48-54.

Drygala, F., Stier, N., Zoller, H., Mix, H.M., Bögelsack, K. & Roth, M. 2008a: Spatial organisation and intra-specific relationship of the raccoon dog *Nyctereutes procyonoides* in Central Europe. - Wildlife Biology 14(4): 457-466.

Drygala, F., Stier, N., Zoller, H., Mix, H. & Roth, M. 2008b: Habitat use of the raccoon dog (*Nyctereutes procyonoides*) in north-eastern Germany. - Mammalian Biology 73: 371-378.

Drygala, F., Zoller, H., Stier, N., Mix, H. & Roth, M. 2008c: Ranging and parental care of the raccoon dog *Nyctereutes procyonoides* during pup rearing. - Acta Theriologica 53(2): 111-119.

Fuller, T.K. 1989: Population dynamics of wolves in north central Minnesota. - Wildlife Monographs 105: 1-41.

Garrott, R.A., White, G.C., Bartmann, R.M. & Weybright, D.L. 1986: Reflected signal bias in biotelemetry triangulation systems. - Journal of Wildlife Management 50: 747-752.

German Weather Service/Neubrandenburg 2003: Deutscher Wetterdienst, Referat Datenserien, Postfach 100465, 63004 Offenbach, Germany.

German Weather Service/Laage 2008: Deutscher Wetterdienst, Referat Datenserien, Postfach 100465, 63004 Offenbach, Germany.

Gese, E.M. & Mech, L.D. 1991: Dispersal of wolves (*Canis lupus*) in north-eastern Minnesota, 1969-1989. - Canadian Journal of Zoology 69: 2946-2955.

Goszszynski, J. 1999: Fox, raccoon dog and badger densities in north Eastern Poland. - Acta Theriologica 44(4): 413-420.

Harris, S. & Baker, P. 2001: Urban Foxes. British Natural History Series. - Whittet Books, Suffolk, UK, 152 pp.

Helle, E. & Kauhala, K. 1991: Distribution history and present status of the raccoon dog in Finland. - Holarctic Ecology 14: 278-286.

Helle, E. & Kauhala, K. 1993: Age structure, mortality, and sex ratio of the raccoon dog in Finland. - Journal of Mammalogy 74(4): 936-942.

Helle, E. & Kauhala, K. 1995: Reproduction in the raccoon dog in Finland. - Journal of Mammalogy 76: 1036-1046.

Howard, W.E. 1960: Innate and environmental dispersal of individual vertebrates. - American Midland Naturalist 63: 152-161.

Ikeda, H. 1984: Raccoon dog scent marking by scats and its significance in social behaviour. - Journal of Ethology 2: 77-84.

Kauhala, K. 1992: Ecological characteristics of the raccoon dog in Finland. - PhD thesis, University of Helsinki, Finland, 19 pp.

Kauhala, K. & Helle, E. 1994: Supikoiran elinpiireistae ja yksiavioisuudesta Etelae-Suomessa. (In Finnish with an English summary: Home ranges and monogamy of the raccoon dog in southern Finland.) - Suomen Riista 40: 32-41.

Kauhala, K., Helle, E. & Pietila, H. 1998: Time allocation of male and female raccoon dogs to pup rearing at the den. - Acta Theriologica 43: 301-310.

Kauhala, K., Helle, E. & Taskinen, K. 1993: Home range of the raccoon dog (*Nyctereutes procyonoides*) in southern Finland. - Journal of Zoology (London) 231: 95-106.

Kauhala, K. & Holmala, K. 2006: Contact rate and risk of rabies spread between medium-sized carnivores in southeast Finland. - Annales zoologici Fennici 43(4): 348-357.

Kauhala, K., Holmala, K., Lammers, W. & Schregel, J. 2006: Home ranges and densities of medium-sized carnivores in south-east Finland, with special references to rabies spread. - Acta Theriologica 51: 1-13.

Kauhala, K. & Saeki, M. 2004: Raccoon dog (*Nyctereutes procyonoides*). - In: Sillero-Zubiri, C., Hoffman, M. & Macdonald, D.W. (Eds.); Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan. IUCN/SSC Canid Specialist Group, pp. 136-142.

Kenward, R.E. 2001: A manual for wildlife radio tagging. - Academic Press, Dorset, UK, 311 pp.

Knowlton, F.F., Gese, E.M. & Jaeger, M.M. 1999: Coyote depredation control: an interface between biology and management. - Journal of Range Management 52: 398-412.

Korhonen, H., Harri, M. & Asikainen, J. 1982: Effect of various diets and energy levels on the growth of farmed raccoon dogs. - Savonia 5: 1-9.

Kowalczyk, R., Zalewski, A., Jędrzejewska, B., Ansorge, H. & Bunevich, A.N. 2009: Reproduction and mortality of invasive raccoon dogs (*Nyctereutes procyonoides*) in the Białowieża Primeval Forest (eastern Poland). - Annales zoologici Fennici 46: 291-301.

Lavrov, N.P. 1971: Itogi introduktsii enotovidnoj sobaki (Npg) vothel'nye oblasti SSSR. - Trudy kafedry biologii MGZPI 29: 101-166. (In Russian).

Linnell, J.D.C., Brøseth, H., Solberg, E.J. & Brainerd, S.M. 2005: The origins of the southern Scandinavian wolf *Canis lupus* population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice. - Wildlife Biology 11(4): 383-391.

Lloyd, H.G. 1980: The red fox. - B.T. Batsford, London, UK, 320 pp.

Macdonald, D.W. & Johnson, D.D.P. 2000: Dispersal in theory and practice: consequences for conservation biology. - In: Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (Eds.); Dispersal. Oxford University Press, Oxford, UK. pp. 358-372.

Mohr, C.O. 1947: Table of equivalent populations of North American small mammals. - American Midland Naturalists 37: 223-249.

Mulder, J.L. 1985: Spatial organisation, movements and dispersal in a Dutch red fox (*Vulpes vulpes*) population: some preliminary results. - Terre et la Vie 40: 133-138.

Nowak, E. 1973: Ansiedlung und Ausbreitung des Marderhundes (*Nyctereutes procyonoides* GRAY) in Europa. (In German with an English summary: Settlement and Propagation of the raccoon dog (*Nyctereutes proconoides* GRAY) in Europe). - Beiträge zur Jagd- und Wildforschung 8: 351-384.

Nowak, E. 1993: *Nyctereutes procyonoides* (Gray, 1834) Marderhund. - In: Stubbe, M. & Krapp, F. (Eds.) Handbuch der Säugetiere Europas. Aula Verlag, Wiesbaden, Germany, 5(1): 215-248. (In German).

Nowak, E. & Pielowski, Z. 1964: Die Verbreitung des Marderhundes in Polen im Zusammenhang mit seiner Einbürgerung und Ausbreitung in Europa. - Acta Theriologica 9(7): 81-109. (In German).

Nyberg, M., Kulonen, K., Neuvonen, E., Ek-Kommonen, C., Nuorgam, M. & Westerling, B. 1992: An epidemic of sylvatic rabies in Finland - descriptive epidemiology and results of oral vaccination. - Acta Veterinaria Scandinavica 33: 43-57.

Pils, C.M. & Martin, M.A. 1978: Population dynamics, predator-prey relationships and management of the red fox in Wisconsin. - Wisconsin Department of Natural Resources, Wisconsin, USA, Technical Bulletin 105, 56 pp.

Pulliainen, E. 1985: The expansion mechanism of the wolf (*Canis lupus*) in northern Europe. - Revue Ecologie (Terre et la Vie) 40: 157-162.

Residents' Registration Office 2003: Mecklenburg-Vorpommern, Statistisches Amt. - Available at: http://www.statistik-mv.de/cms2/STAM_prod/STAM/de/bhf/index.jsp (Last accessed on 17 February 2010).

Residents' Registration Office 2007: Mecklenburg-Vorpommern, Statistisches Amt. - Available at: http://www.statistik-mv.de/cms2/STAM_prod/STAM/de/bhf/index.jsp (Last accessed on 17 February 2010).

Saeki, M. 2001: Ecology and conservation of the raccoon dog (*Nyctereutes procyonoides*) in Japan. - PhD dissertation, Oxford, UK, 272 pp.

Sidorovich, V.E., Polozov, A.G., Lauzhel, G.O. & Krasko, D.A. 2000: Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog *Nyctereutes procyonoides* on native predators in northern Belarus. - Zeitschrift für Säugetierkunde 65: 271-285.

Sidorovich, V.E., Soloveij, I.A., Sidorovich, A.A. & Dyman, A.A. 2008: Seasonal and annual variation in the diet of the raccoon dog *Nyctereutes procyonoides* in northern Belarus: the role of habitat type and family group. - Acta Theriologica 53: 27-38.

Sutor, A. 2008: Dispersal of the alien raccoon dog *Nyctereutes procyonoides* in Southern Brandenburg, Germany. - European Journal of Wildlife Research 54(2): 321-326.

Tackmann, K., Goretzki, J., Sutor, A., Schwarz, S. & Conraths, F.J. 2005: Der Marderhund (*Nyctereutes procyonoides*) als neuer Endwirt für *Echinococcus multilocularis* in Ostdeutschland - erste Ergebnisse einer Studie in Brandenburg (In German with an English summary: The neozoon raccoon dog as a new definitive host population for *Echinococcus multilocularis* in East Germany). - Beiträge zur Jagd- und Wildforschung 30: 323-330.

Thiess, A. 2004: Untersuchungen zur Helminthenfauna und zum Vorkommen von *Trichinella* sp. Beim Marderhund (*Nyctereutes procyonoides*) in Brandenburg (In German with an English summary: Studies on the Helminth Fauna and the Affection with *Trichinella* Species of the raccoon dog (*Nyctereutes procyonoides*) in the Federal State Brandenburg). - PhD dissertation, Freie Universität, Berlin, Germany, 71 pp.

Trewhella, W.J., Harris, S. & McAllister, F.E. 1988: Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): a quantitative analysis. - Journal of Applied Ecology 25: 423-434.

Wabakken, P., Sand, H., Liberg, O. & Bjärvall, A. 2001: The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. - Canadian Journal of Zoology 79: 710-725.

Westerling, B. 1991: Raivotauti Suomessa ja sen torjunta Suomessa vuosina 1988-90. (In Finnish with an English summary: Rabies in Finland and its control 1988-90). - Suomen Riista 37: 93-100.

White, P.C.l. & Harris, S. 1994: Encounters between red foxes (*Vulpes vulpes*): implications for territory maintenance, social cohesion and dispersal. - Journal of Animal Ecology 63: 315-327.

WHO 2004: Distribution of rabies in Europe. - Rabies Bulletin Europe 28(4): 11-24.

WHO-Rabies-Bulletin-Europe 2010: Available at: http://www.who-rabies-bulletin.org/Queries/Distribution.aspx? Issue = 2007_4 (Last accessed on 17 February 2010).

Yamamoto, Y., Terao, K., Horiguchi, T., Morita, M. & Yachimori, S. 1994: Home range and dispersal of the raccoon dog (*Nyctereutes procyonoides viverrinus*) in the Mt. Nyugasa, Nagano Prefecture, Japan. - Natural Environmental Scientific Research 7: 53-61. (In Japanese).

Yashiki, H. 1987: Ecological study on the raccoon dog, *Nyctereutes procyonoides viverrinus*, in Shiga Heights. - Bulletin of Institution of Nature Education, Shiga Heights, Shinshu University 24: 43-53. (In Japanese).