

Space use pattern, dispersal and social organisation
of the raccoon dog (*Nyctereutes procyonoides* GRAY,
1834) an invasive, alien canid in Central Europe

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Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema:

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1. Abstract

Between October 1999 and October 2003, 30 adult and 48 young (< 1 year) raccoon dogs (*Nyctereutes procyonoides*) were monitored using radio-telemetry in an area of North-East Germany which has been occupied by this invasive alien species since the early 1990s. Additionally, three pairs of raccoon dogs were observed by continuous radio-tracking during the first six weeks after parturition in 2003. Furthermore 136 raccoon dog pups were ear-tagged between June 1999 and August 2006.

No adult animals dispersed from the area during the study period and home ranges tended to be used for several years, probably for life. The average annual home range size, calculated using 95% fixed kernel, was 382.2 ha \pm 297.4 SD for females (n = 30 seasonal home ranges) and 352.4 ha \pm 313.3 SD for males (n = 32 seasonal home ranges). Paired raccoon dogs had home ranges of similar size, with pair mates sharing the same area all year round.

Raccoon dogs occupied large core areas (85% kernel) covering 81.2% of their home ranges. The home ranges were at their smallest during the mating season. The slightly larger size of home ranges in winter suggests that, due to the temperate climate, raccoon dogs do not hibernate in Germany. Males and females formed a long-term (probably lifelong) pair bond. Same-sex neighbours ignored each other and even adjacent males/females showed neither preference nor avoidance. Thus, it can be assumed that the raccoon dog in Central Europe is monogamous without exclusive territories, based on the results of home range overlap analysis and interaction estimations.

Habitat composition within home ranges and within the whole study area was almost equal. Although, percentage shares of farmland and meadow was 16.35% smaller and 12.06% higher within the home ranges, respectively. All nine habitat types (farmland, forest, settlement, water, meadows, maize fields, small woods, reeds and hedges) were used opportunistically by raccoon dogs. No significant, recognisable difference for habitat preferences between seasons was detected. Male and female

raccoon dog showed equal habitat preference pattern. A comparison of active and inactive locations in different habitats found no remarkable differences. Habitat composition of individual home ranges was used to classify animals. If the percentage of forest within a home range exceeded 50% the individual was classified as a 'forest type' raccoon dog. If the percentage of forest habitats within a home range was less than 5%, the share of pastureland was mean $81.82\% \pm 16.92$ SD. Consequently the individual was classified as a 'agrarian type' raccoon dog. Neither habitat preference nor habitat selection process differed between the two 'types'. Habitat use and preference is discussed with relation to the ability of the raccoon dog to expand its range towards Western Europe.

Males spent noticeably more time (40.5% of the time ± 11.7 SD) alone with the pups than females (16.4% of the time ± 8.5 SD). Females had noticeably larger 95% kernel home ranges (98.24 ha ± 51.71 SD) than males (14.73 ha ± 8.16 SD) and moved much longer daily distances ($7,368$ m $\pm 2,015$ SD) than males ($4,094$ m $\pm 2,886$ SD) in six weeks postpartum. The raccoon dogs being studied left the breeding den in the 6th week after the birth of the pups. *In situ* video observation showed that the male carried prey to the den to provide the female and the litter with food. A clear division of labour took place among parents during the period in which the pups were nursed: males guarded the litter in the den or in close vicinity of it, while the females foraged to satisfy their increased energy requirements.

There were relocations of 59 (43.4%) ear-tagged young raccoon dogs and mean distance from 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 nearer than 5 km from the marking point, whereas only 8.5% relocations were recorded further than 50 km from the marking point. There was no difference in the distances of relocations between sexes. Most (53.7%) relocations of ear-tagged young raccoon dogs were in August and September and, only 34.1% were recorded from October to April. Hunting (55%) and traffic (27%) were the major mortality factors. Radio-collared young raccoon dogs generally dispersed between July and September. The mean natal home range size (MCP 100%) with and without excursions was 502.6 ha ± 66.4 SD ($n = 9$) and 92.1 ha ± 66.4 SD ($n = 17$), respectively. There were no

differences between sexes in the month of dispersal. The direction of travel for dispersing animals appeared to be random, with distances from 0.5 km to 91.2 km. A highly flexible dispersing behaviour is certainly one of the reasons which contribute to the high expansion success of the species.

2. Introduction

Invasive alien species (IAS) are considered to be the second most serious threat to native biodiversity, after habitat loss and fragmentation (i.e. deforestation) (ELTON et al. 1958, WILCOVE et al. 1998, SANDLUND et al. 1999, IUCN 2000, BAILLIE et al. 2004). They are thus a serious impediment to conservation and sustainable use of global, regional and local biodiversity, with significant undesirable impacts on the goods and services provided by ecosystems. In doing so, most IAS share the lack of natural predators in their new location, the ability to reproduce at a high rate and a high ecological flexibility (KINZELBACH 1996, STREIT 1991, SANDLUND et al. 1999, GEITER & KINZELBACH 2002).

In particular allochthone predators are a significant conservation concern, and advances in the management of these populations also require detailed understanding of ethological and ecological aspects to forecast their expansion.

This is – as an example – well documented in Australia. There is abundant anecdotal, circumstantial and experimental evidence that red fox (*Vulpes vulpes* L. 1758) predation is a major threat to the survival of native Australian fauna. Small to medium-sized ground-dwelling mammals and ground-nesting birds, many of which are endangered or vulnerable, are at greatest risk (SAUNDERS et al. 1995). Invasive species have caused more animal extinctions in Australia than any other factor (AUSTRALIAN BIOSECURITY GROUP 2005). Australia has lost 22 mammal species, and implicated in most of these extinctions are foxes, cats (*Felis catus*, L.1758) and sometimes rabbits (*Oryctolagus cuniculus* L. 1758) (JOHNSON 2006, MAXWELL & BURBIDGE 1996).

Extermination of native species is also assumed through the introduction of the dingo (*Canis familiaris dingo* L. 1758) in Australia and the domestic dog (*Canis lupus familiaris* L. 1758) through the first Asian settlers in America (MARTIN & KLEIN 1984). On the other hand HOHMANN & BARTUSSEK (2001) assumed, that the introduction of the raccoon (*Procyon lotor* L. 1758) to Germany approx. 70 years ago, with regard to its widespread present distribution had no negative impact on population trends of native species. Moreover, there is – until today- not a single case known to science,

were IAS caused the extinction of a native species in Central Europe. Bio geographical conditions in Central Europe differ essentially from those on islands (e.g. New Zealand, Hawaii, Guam), where the native fauna is extensively threatened by introduced species (KOWARIK 2003; A. MARTENS, PH Karlsruhe, pers. comm.).

However, recently there are indications that the raccoon is a serious threat (through predation) for the highly endangered pond turtle (*Emys orbicularis* L. 1758) in Brandenburg State (N. SCHNEEWEISS, LUA Brandenburg/Germany, pers. comm.).

Bringing a new carnivore into an area always involves potential danger to native fauna, or even extinction. No introductions should be made without intensive knowledge of ecology and behaviour of the species. Even if the species has been studied in the original range; a species may change its habits, e.g. diet, habitat use and dispersal, in the new geographic range. Thus, the consequences of an introduction are hard to estimate (DE VOS et al. 1956, KAUHALA 1992).

The raccoon dog (*Nyctereutes procyonoides*) is an introduced canid in Europe. It originally occurred in the woodland zone from south-eastern Siberia to northern Vietnam (NOWAK 1999). During 1929-1955 approx. 9,100 animals were released, mainly to 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 km² was colonised (HELLE & KAUHALA 1991, SUTOR 2007). The first recorded sighting in Poland was in 1955 and by 1964 sightings were recorded in Eastern Germany (Mecklenburg-Western Pomerania) (NOWAK & PIELOWSKI 1964). Until the early 1990s only few raccoon dogs were recorded in Germany, but thereafter exponential increase of game kills were evident and in the hunting season 2004/2005 approximately 23,300 animals were gunshot (Deutscher Jagdschutz Verband 2007). To date, the raccoon dog has become a permanent member of the fauna of Germany and the increasing bag numbers indicate that the population has not yet reached the carrying capacity of the environment. Furthermore, beside close-to-nature habitats (reed beds, swamps, mixed forests) intensively used agricultural habitats with low forest cover are being colonised (see also 5.3.2). The rapid increase in size of the raccoon dog population is of conservation and wildlife management interest because it can be locally harmful to

waterfowl colonies and frogs, but their overall significance to the native fauna seems to be slight. So far, little is known about the predation or competition of the raccoon with the native fauna in Europe (KAUHALA 1996a).

Apart from its role as a new predator, long distance dispersal of the raccoon dog can accelerate the spread of rabies, sarcoptic mange and trichinosis. During rabies epizootic in Finland at the end of the 1980s, the species was the main victim of the disease (NYBERG 1992). Furthermore, raccoon dogs are potential vectors of the tapeworm (*Echinococcus multilocularis* Leuckart 1863), since some infections of the dangerous parasite have recently been found in Eastern Germany (THIESS 2004, TACKMANN et al. 2005).

Since empirical field tests are rare, there remains an almost complete absence of empirical data on spatial organization, intra-specific relationship, social system, breeding system, habitat use, population density, dispersal pattern and other relevant behavioural parameters of the raccoon dog in Central Europe.

To fill this gap I started a telemetry study in 1999. The purpose of this work was to determine some major factors behind the success of the raccoon dog to provide baseline information as to the potential of the raccoon dog to expand its range throughout Western Europe. In this connection, an ultimate aim was to understand mechanisms that link space use pattern, social organisation and dispersal to the great expansion success.

In general, records of dispersal can help to define geographical boundaries (e.g. rivers, mountain ranges, vast agricultural areas, large cities) that can limit the colonisation of Central and Western Europe. Furthermore knowledge about dispersal- distances, -times, -routes and analyses of survival and mortality rate can help to assess the expansion process in detail.

Space use patterns (i.e. home range sizes, home range overlap and habitat use) are important measurements to understand social organisation and habitat requirement. Moreover, these are basic biological data to estimate whether a species is ecological flexible and able to build abundant populations in distinct habitats.

Furthermore density estimates and habitat use data are crucial to assess the carrying capacity of the environment and thus to estimate whether the population is still in the phase of rapid growth without density-dependence.

Today, many ecologists investigate how demography and social organisation respond to changing environments (KENWARD 2001). Thus, for an invasive species, data on the space use of juveniles and adults, flexibility of the breeding system and territoriality are suitable to approximate the invasion to new geographical ranges (e.g. The Netherlands, France).

In particular allochthone predators (like the raccoon dog) are a significant conservation concern, and advances in the management of these populations also require detailed understanding of ethological and ecological aspects to forecast their expansion.

This work represents the first quantified and comprehensive data on space use pattern, social organisation and dispersal of the raccoon dog in Central Europe and is therefore of great value to specify and forecast the species population dynamic.

3. Study areas

The main study area (53° 36'N, 13° 14'E; 5-145m a.s.l.) of some 250 km² was located in Mecklenburg-Western Pomerania approximately 50 km west of the German-Polish border. The area is characterized by a temperate climate. The average annual temperature between 1999 and 2003 was 9.7°C and ranged from a mean of 0.8°C in January to a mean of 18.2°C in July. The mean annual relative humidity was 75% (German Weather Service/Neubrandenburg, 2003).

The region, which includes several protected areas, is noted for its great biodiversity. It is characterised by a vast, homogeneous, agricultural landscape with cereal crops (especially maize, *Zea mays* L.). Also typical of the area are close-to-nature habitats like reed beds, swamps, mixed forests, streams, ditches and a large lake (575 ha). Although the human population is sparse in the study area (49 inhabitants/km² Uecker-Randow-District, Residents' Registration Office, 2003), the area is dissected by many dirt roads, facilitating radio tracking. Meadows (32.9 % of the area) for cattle and farmland (28.4 % of the area) were the major land uses in the region.

Forests (27.5 % of the area) are dominated by European beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.), Scots pine (*Pinus silvestris* L.), European larch (*Larix decidua* MILL.) and Norway spruce (*Picea abies* L.). The swamp/marshland areas are dominated by common alder (*Alnus glutinosa* L.) and silver birch (*Betula pendula* L.).

The area is inhabited by a diverse community of predators comprising five medium-sized carnivores, raccoon dog, red fox, raccoon, otter (*Lutra lutra* L. 1758) and badger (*Meles meles* L. 1758).

The other study area (150 km²) was located close to „Penzin“ in North-Western Mecklenburg-Western Pomerania (53° 55'N, 11° 56'E; 4-89m a.s.l.). The average annual temperature between 2004 and 2006 was 9.3°C 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 was 51 inhabitants/km² (Güstrow-District, Residents' Registration Office, 2007) and settlements cover 3.4% of the study area. Vast agricultural landscape with meadows (21.3%) and farmland (48.8%) are the major land uses in the region. There is no forest; only small woods cover 2.7% of the area.

Possible predators to raccoon dogs, especially to juveniles are white-tailed eagle (*Haliaeetus albicilla* L. 1758), domestic dog, badger and red fox. Raccoon dogs were regularly hunted in both study areas (Fig.1).

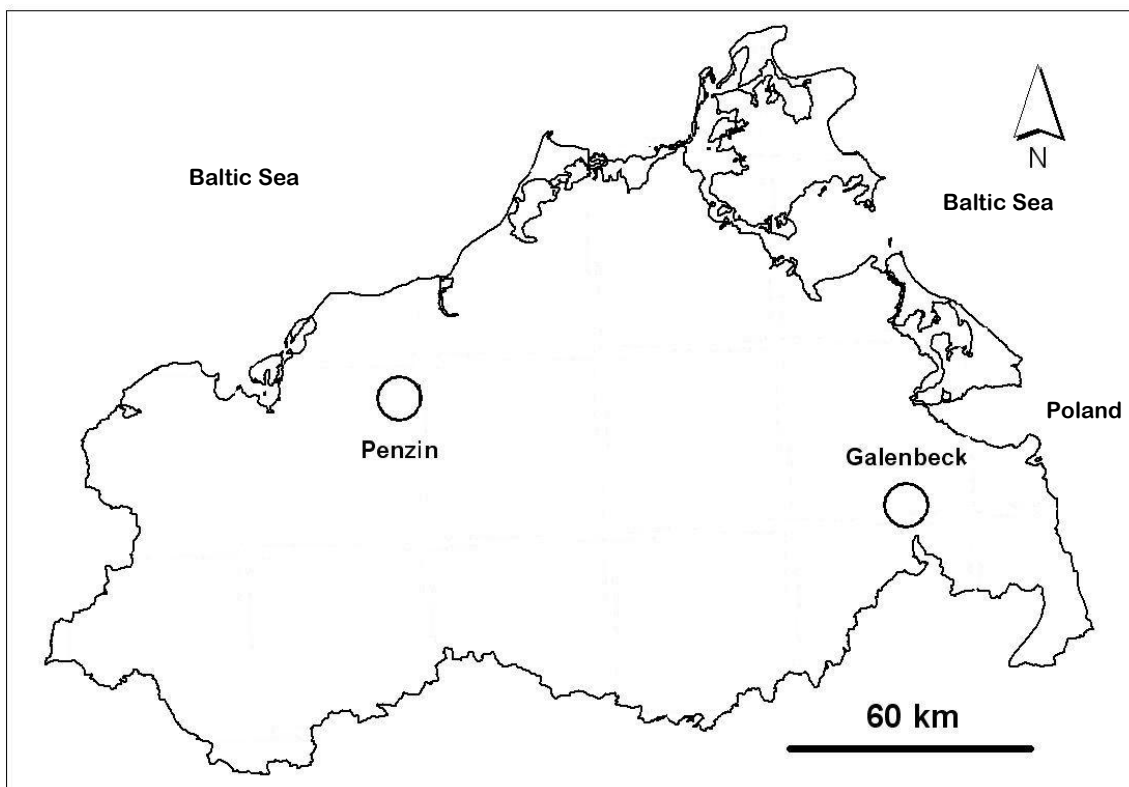


Fig.1 Location of the two study areas in Mecklenburg-Western Pomerania (North-Eastern Germany)

4. Spatial organisation and intra-specific relationship

4.1 Materials and methods

4.1.1 Telemetry and data analyses

104 raccoon dogs were captured alive using wire-box traps and fish bait in the study area "Galenbeck" (raccoon dogs are easy to handle and do not require immobilisation). 74 of these were fitted with radio-collars (WAGENER, COLOGNE) which produced sufficient locations for the home range calculations of twenty-six adults (12 males, 14 females). Resident animals were monitored between October 1999 and October 2003. Each transmitter weighed 180 g and lasted about two years but efforts were made to replace the collars before they ceased functioning. Adults were distinguished from young animals (< one year) by noting body weight, fur and the attrition of teeth, especially incisors. Resident raccoon dogs were identified as those animals that showed no home range shift after being fitted with a radio collar. Locations for dispersing animals were not included in home range calculations. Two raccoon dogs were monitored for at least 3.5 years (one for a 4-year period), two animals for 1.5 to 2 years, eight animals for 1 to 1.5 years, ten animals for 6 to 12 months and four animals for 1 to 6 months.

Raccoon dogs were located with a handheld H antenna (HB9CV) or a 3-element Yagi at different times of night and day (point method) as often as practical (a total of 11,261 locations). TRX-1000s receivers (WILDLIFE MATERIALS, USA) were used to locate the animals. The mean distance between observer and animal was usually less than 1 km. Bearings were taken from at least two points (often via multiple triangulations or more), the angle between the bearings being as close to 90° as possible.

The tracking accuracy was estimated at 91.6 ± 50.0 m (median; $n = 52$) by means of locating hidden transmitters. In addition, visual observations of collared animals on short cut meadows, using binocular and night vision (distance < 300 m), were made

as often as possible to improve the accuracy of the fixes. For tracking with a 2-3 element Yagi antenna, a 1-in-10 rule is acceptable (KENWARD et al. 2003). Thus, the tracking resolution (100 m) and observer-animal distance (< 1000 m) were in a ratio of one to ten. However, location error may be greater if locating moving animals instead of using hidden transmitters.

I grouped animal locations into four different seasons:

- oestrous and gestation (March - April);
- parturition and pup rearing (May - July);
- intensive foraging and fat accumulation (August - October);
- and reduced activity and winter burrow associated activity (November - February).

Estimates of home range size vary depending on the method used to define them (LAUNDRÉ & KELLER 1984, BOULANGER & WHITE 1990, SEAMAN & POWELL 1996). The most widely used home range estimation method is a Minimum Convex Polygon (MCP) (MOHR 1947), which has some advantages including universal comparison, simplicity and robustness when autocorrelated data are used (SWIHARD & SLADE 1985ab, HARRIS et al. 1990, WHITE & GARROTT 1990). However, MCP 100 calculations give no indication of how intensively the animal uses different parts of its range, and the polygons are overly characterised by the peripheral fixes. By contrast, kernel analysis is based on estimating location density as functions of distance and can be used to calculate location distribution (KENWARD 2001). Therefore, I used this method to estimate raccoon dogs' home range size and utilisation distribution to investigate spatial use.

Telemetry data were analysed using RANGES 6 v 1.2 (KENWARD et al. 2003). To avoid autocorrelation I reduced the sample size of the data using AWK (program for data processing) by introducing a two-hour interval between successive locations. Localisations were read in chronological order. A time interval of 2 hours or more between localisations was considered acceptable, shorter intervals were rejected.

Using Schoener's index $S = \frac{t^2}{r^2}$ (SWIHART & SLADE 1985b), I calculated the independence of locations for fixed kernel 95 estimations with default value 1 smoothing factor, where the quotient (t^2/r^2) between the square distance of successive locations (t^2) and the square distance of each bearing towards the centre for all locations (r^2) is calculated. In order to keep valuable data I arbitrarily excluded seasonal home ranges corresponding to a Schoener's -index below 0.92.

Core areas were determined for seasonal home ranges by plotting utilisation distribution graphs with RANGES 6 v 1.2. The slope discontinuity was taken as an indicator of how many fixes constituted the core (KENWARD et al. 2003). I decided to use the kernel 85 % distribution as a core area because in 38.55% of the cases a slope discontinuity appeared at that point. I examined how the core areas changed as successive locations were added and found stable home ranges from the mean of 28.40 ± 20.96 SD locations. Hence, all seasonal home ranges with less than 29 fixes were excluded, resulting in 62 (average SCHOENER'S INDEX 1.52 ± 0.38 SD) independent and stable seasonal home ranges (6,158 total locations) (Fig.2).

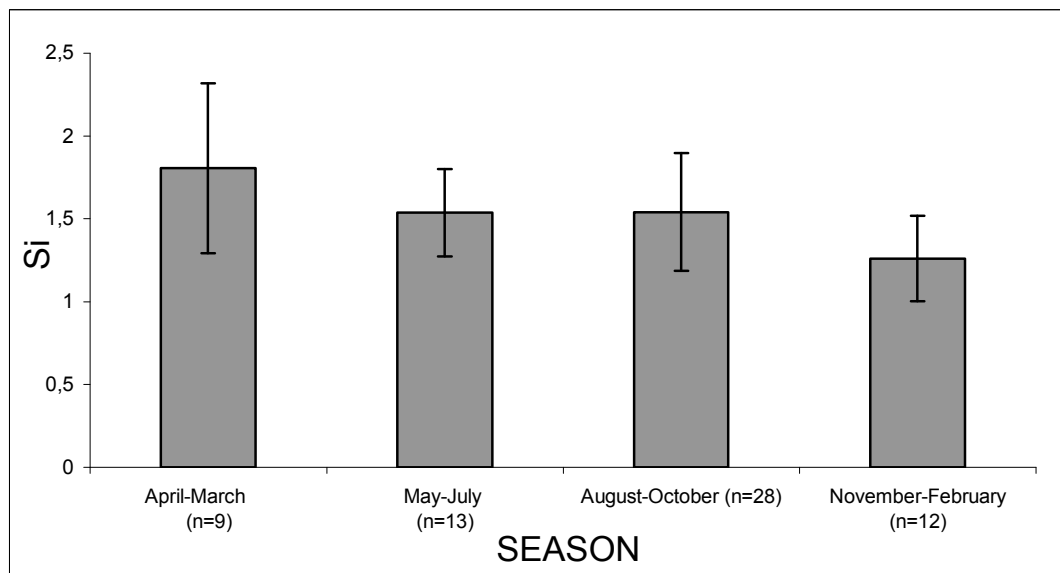


Fig.2 Schoener's Index reflecting the autocorrelation of locations ($S_i \pm SD$) of 62 stable home ranges estimated using fixed Kernel analysis in four different seasons (n = seasonal home ranges, $S_i = 2$ equals independent locations)

Mean stability of MCP 100 home ranges was at 47.88 ± 31.21 SD locations resulting in 61 stable home ranges with a minimum of 48 bearings for further analysis. For map representation I choose MCP 95 because of its superior clarity compared to kernel analysis and because peripheral fixes can be excluded. For overlap calculation (kernel 95 and core area utilisation) the means of percentage home range overlaps of two animals were used. I compared 54 overlapping home ranges of paired mates and 114 overlapping home ranges of adjacent individuals.

Population density was roughly estimated on the basis of kernel 95 home range sizes. I calculated one pair (two adults) for the mean home range size during the breeding season, when home ranges of adjacent raccoon dogs only slightly ($11.7\% \pm 3.0$ SD) overlap. 'Helpers' have not been observed in raccoon dogs (KAUHALA & SAEKI 2004a).

Because the raccoon dog is more of a gatherer than a hunting predator (KAUHALA et al. 1993b, DRYGALA et al. 2000) and roams at a low mean speed of 1.86 to 6.96 m/min (SAEKI 2001), I defined a 15 min input threshold as same-time observations. The observed and possible distances between animals (a random sample of 500 fixes) were compared using Jacobs' index (J_i) with values of between +1 and -1. Values close to +1 indicate attraction, values close to -1 indicate avoidance and values close to zero indicate ignorance (JACOBS 1974). I was able to use all 11,261 fixes regardless of their independence because RANGES 6v1.2 avoids assumptions about autocorrelation and distribution of locations between single pairs of individuals (KENWARD et al. 2003).

I only used single pairs of animals with more than 20 locations (mean 162 ± 224 for pair mates; mean 39.6 ± 22.3 for neighbours). I determined which animals were in pairs by means of intensive radio tracking, as paired mates roam together or close to each other unlike adjacent raccoon dogs (pers. obs.). In Finland the contact rate was high for raccoon dog pairs but low for neighbours (KAUHALA & HOLMALA 2006). Breeding dens were likewise identified through radio tracking of adults and by checking the vicinity of the dens for pup tracks. I compared pair mates and pairs of adjacent individuals of both sexes. Differences in avoidance or attraction within and

between sexes and distributions of observed male-male, female-female and male-female distances were compared.

The risk of pseudo-replication for home range sizes, home range overlap and interaction analysis was low because sufficient seasonal data existed only for six animals radio tracked for more than one year. Thus, I used all 62 calculated seasonal home ranges.

4.1.2 Statistical Analysis

For statistical analysis (SPSS 15.0.1), I removed pseudo-replication by the calculation of means for seasonal home range sizes of those animals radio tracked in consecutive years. The Wilcoxon signed ranks T-test was used to compare home range sizes of males and females and home range overlap between adjacent males and females. Significance of seasonal shifts in home range and variations in home range overlaps towards partner and neighbour were tested with the related samples with missing values test, reflecting the sum of absolute differences between treatments (here seasons = 'D'). Correlation of home range sizes for paired mates was tested with Spearman correlated coefficient test (r_s).

4.2 Results

4.2.1 Home ranges

MCP 100 estimation

The mean annual home range size was 583.0 ha \pm 398.0 for females (n = 28 seasonal home ranges) and 551.6 ha \pm 418.6 for males (n = 33 seasonal home ranges) with no significant difference (Wilcoxon signed ranks T-test, T = 25, n = 9, p = 0.82) between the sexes. I compared home range sizes of both sexes in autumn and also found no significant differences (T = 22, n = 8, p = 0.64).

The maximum average home range size (738.8 ha \pm 441.3) for both sexes was observed between August - October. Even in the winter den-associated season (November - February), raccoon dogs had large home ranges (647.1 ha \pm 427.5). With a mean size of 314.1 ha \pm 112.6 females had the smallest home ranges during the oestrous and gestation period in spring. Whereas there was a distinct difference between the sexes during the pup-rearing season when males (n = 8) had the smallest home ranges (240.0 ha \pm 96.2), and those of the females (n = 8) were much larger (444.1 ha \pm 260.3) (Tab. 1).

Tab. 1 Home ranges sizes (mean, ha \pm SD) of raccoon dogs in different seasons (n = number of seasonal home ranges)

Season (month)	MCP 100				Kernel 85 Distribution (core area)				Kernel 95 Distribution			
	female	n	male	n	female	n	male	n	female	n	male	n
Oestrous and gestation Mar-Apr	314.1 \pm 112.6	3	284.1 \pm 186.8	4	83.4 \pm 44.2	4	101.0 \pm 49.8	5	157.7 \pm 81.1	4	159.2 \pm 69.5	5
Pup rearing May-Jul	444.1 \pm 260.3	8	240.0 \pm 96.2	8	122.2 \pm 79.2	7	93.4 \pm 75.0	6	225.3 \pm 179.5	7	194.1 \pm 181.0	6
Weight gain Aug-Oct	706.6 \pm 401.2	12	766.4 \pm 486.4	14	352.3 \pm 227.8	15	319.1 \pm 229.8	13	554.6 \pm 334.8	15	528.0 \pm 378.7	13
Reduced activity Nov-Feb	669.8 \pm 594.8	5	630.0 \pm 313.8	7	191.8 \pm 98.3	6	191.0 \pm 141.4	6	283.1 \pm 127.0	6	291.4 \pm 190.5	6
Mean for all seasons	583.0 \pm 398.0	28	551.6 \pm 418.6	33	238.3 \pm 198.1	32	212.0 \pm 192.0	30	382.0 \pm 297.4	32	352.4 \pm 313.3	30

Among males there were significant MCP 100 ($n = 33$) differences between seasons ($D = 1598.14$, $p = 0.04$) but these were not evident among females ($n = 28$) ($D = 451.27$, $p = 0.25$).

Kernel 95 Utilisation

The annual kernel 95 % home range allocation pattern of four raccoon dog pairs (pairs 1 to 4) is indicative of the spatial distribution in general. They roamed all over the study area with large overlaps among pair mates. Adult raccoon dogs used the same home range long term (probably lifelong) but some changed their breeding den every year. The breeding den of pair 1 was located in the home range of pair 4 and the breeding den of pair 2 was within the home range of pair 1. Pair mates shared the same area throughout the year. Home ranges of adjacent animals overlapped to varying degrees (Fig. 3).

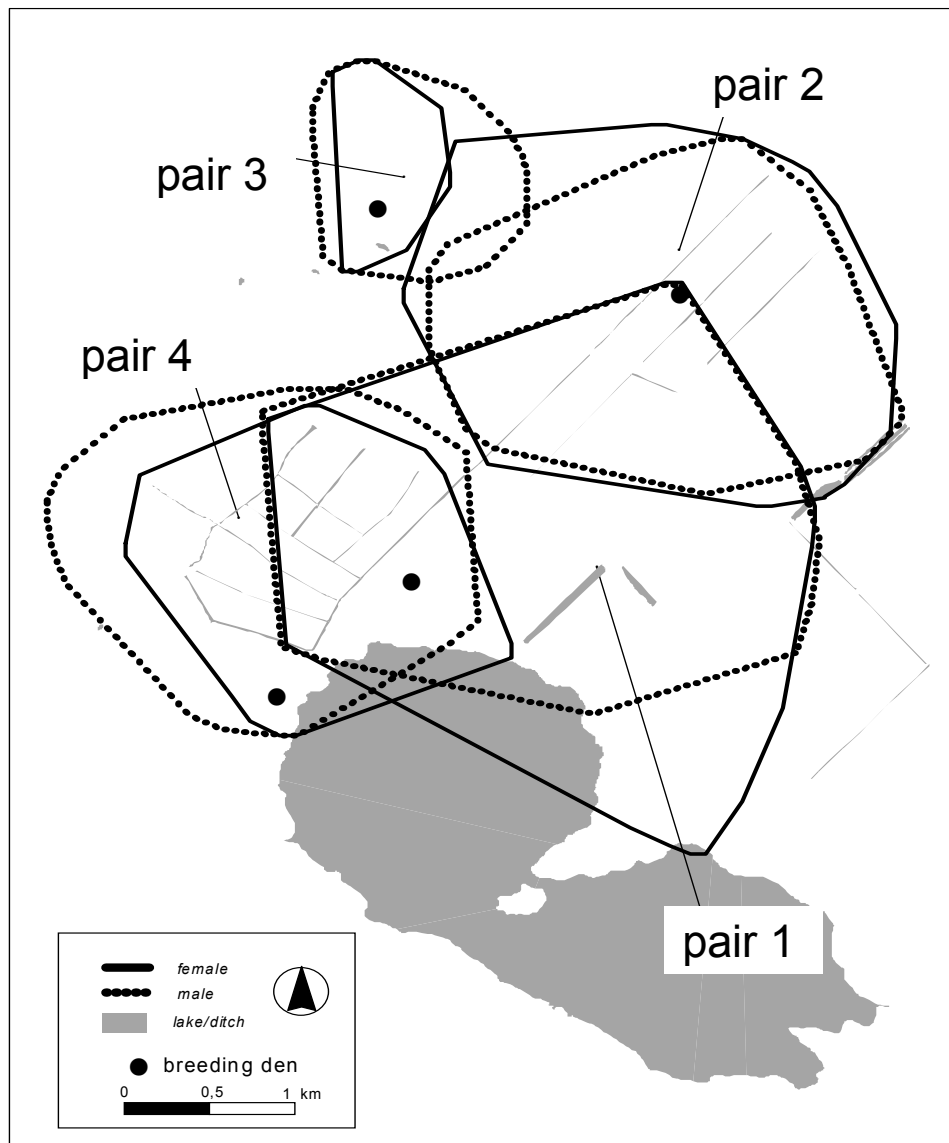


Fig. 3 Mean annual home-ranges distribution pattern (95% MCP) of four pairs of raccoon dogs radio tracked in 2003

The average annual home range size did not differ between sexes, being $382.2 \text{ ha} \pm 297.4 \text{ SD}$ for females and $352.4 \text{ ha} \pm 313.3$ for males ($T = 34$, $n = 9$, $p = 0.203$), neither were there significant seasonal differences in home range sizes among males ($n = 26$); (related samples D-test, $D = 970.75$, $p = 0.1023$) and females ($n = 27$); ($D = 306.61$, $p = 0.08$). Raccoon dogs had their smallest home ranges in the oestrous and gestation period (March - April, $158.5 \text{ ha} \pm 69.9$, $n = 9$). The largest home ranges were recorded during autumn (August - October, $542.2 \text{ ha} \pm 349.4$, $n = 28$) (Tab. 1), with no significant difference between males and females ($T = 18$, $n = 7$, $p = 0.58$), the second largest home range was during winter (November - February, $287.2 \text{ ha} \pm 154.4$, $n = 12$).

After parturition in the pup-rearing period (May - July) female home ranges ($225.3 \text{ ha} \pm 179.5$, $n = 7$) were slightly larger than those of males ($194.1 \text{ ha} \pm 181.0$, $n = 6$) (Tab. 1). I found a significant correlation between the home range size of pair members for fixed kernel 95 home ranges (Spearman correlated coefficient test, $r_s = 0.97$, $n = 9$, $p < 0.001$) (Fig. 3). The calculated population density based on kernel 95 estimation (breeding season) was $0.95 \text{ animals/km}^2$.

Core areas

Raccoon dogs had large core areas covering 81.2% of their home ranges. The mean annual core area estimated with kernel 85 distribution was $238.3 \text{ ha} \pm 198.1$ for females and $212.0 \text{ ha} \pm 192.0$ for males. Annual comparisons showed a clear relation between the sizes of core areas of pair members ($r_s = 0.88$, $n = 9$, $p < 0.01$). Raccoon dogs had comparatively small core areas during periods of oestrous and gestation (March - April; $93.7 \text{ ha} \pm 45.5$) and parturition and pup rearing (May - July; $108.9 \text{ ha} \pm 75.5$). In winter (November - February), the average core area was $191.0 \text{ ha} \pm 116.1$. The largest core areas ($336.9 \text{ ha} \pm 225.1$) were during August - October with no significant difference in size between the sexes ($T = 30$, $n = 9$, $p = 0.43$) (Tab. 1).

There were no significant seasonal differences in core area sizes among males ($D = 682.11$, $n = 26$, $p = 0.13$) but females showed a tendency towards core area size differences between seasons ($D = 208.39$, $n = 27$, $p = 0.06$) and had core areas of between $83.4 \text{ ha} \pm 44.2$ in spring and $352.3 \text{ ha} \pm 227.8$ in autumn.

4.2.2 Overlap analyses

Kernel 95 utilisation

For pair mates, the percentage of overlapping area showed a slight seasonal variation. Home ranges overlapped almost totally ($93.0\% \pm 4.7$ SD) in March - April. From May - June in the pup-rearing season, the paired mates had smaller home range overlaps ($68.9\% \pm 10.0$). Between August - October, there were large overlaps ($90.5\% \pm 5.3$) and during winter (November - February) paired males and females shared $85.4\% \pm 5.5$ of their home ranges.

Adjacent raccoon dogs had moderate home range overlaps for every season. The maximum seasonal overlaps occurred from August - October ($29.2\% \pm 19.8$). During oestrous and gestation (March - April), home ranges of neighbours overlapped to $16.3\% \pm 11.8$. In the pup rearing period (May - June) ranges overlapped to $11.7\% \pm 3.0$ and decreased during winter (November - February) to $2.6\% \pm 9.1$. I investigated whether females behave differently towards their partner and adjacent males and found significant home range overlap with the mate ($D = 37.14$, $n = 9$, $p = 0.02$) but not with the neighbour ($D = 26.86$, $n = 9$, $p = 0.41$). Likewise, males had no significant home range overlaps with adjacent females ($D = 20.02$, $n = 8$, $p = 0.37$).

Core area

I considered seasonal effects by comparing overlap of core areas for adjacent raccoon dogs. The maximum overlap ($20.9\% \pm 18.7$) was observed during the intensive foraging period (August - October). In the pup rearing season (May - July), core areas overlapped by no more than $3.0\% \pm 1.0$. Core areas of pair mates overlapped significantly (mean $83.5\% \pm 9.2$) all year (Fig. 4).

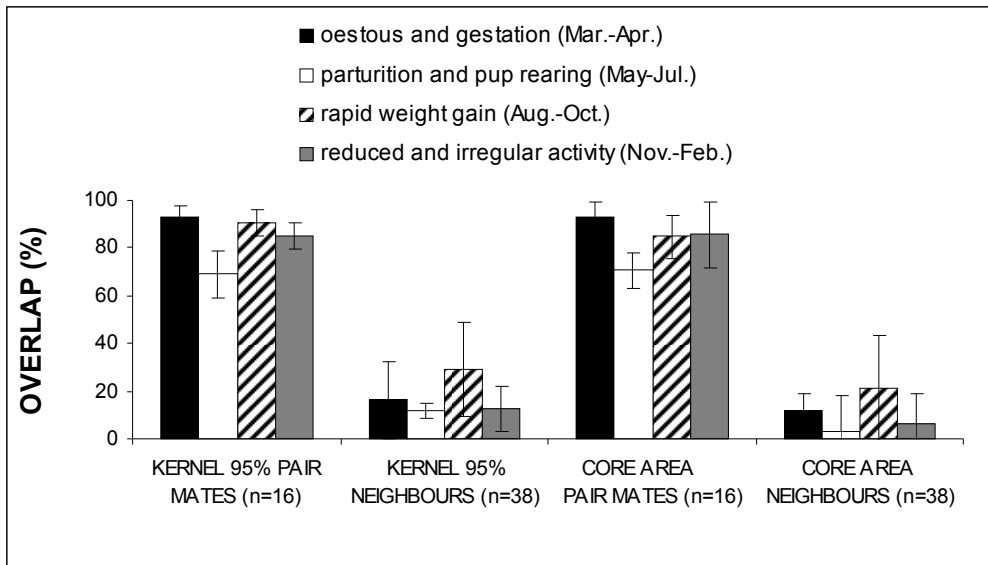


Fig. 4 Home range overlap (\pm SD) of pair mates and adjacent raccoon dogs based on Kernel 95, core area (Kernel 85) utilisation and MCP estimation (n = number of pairs of home ranges examined) in different seasons

4.2.3 Interaction analysis

Pair mates

Data for 10 raccoon dog pairs and 26 seasonal home ranges were used for interaction analyses. Males and females of the same pair showed a clear preference for each other and moved synchronously or very close to each other for most of the year (mean annual $J_i = 0.87 \pm 0.27$ SD). No mate changes were observed. During the periods of winter ($J_i = 0.99 \pm 0.02$) and oestrous and gestation ($J_i = 0.99 \pm 0.004$), the paired mates were exclusively located at the same point. Partners also roamed close together from August to October ($J_i = 0.92 \pm 0.16$). Only after parturition, during the pup-rearing period, did pair members show different spatial allocation ($J_i = 0.59 \pm 0.43$) (Fig. 5).

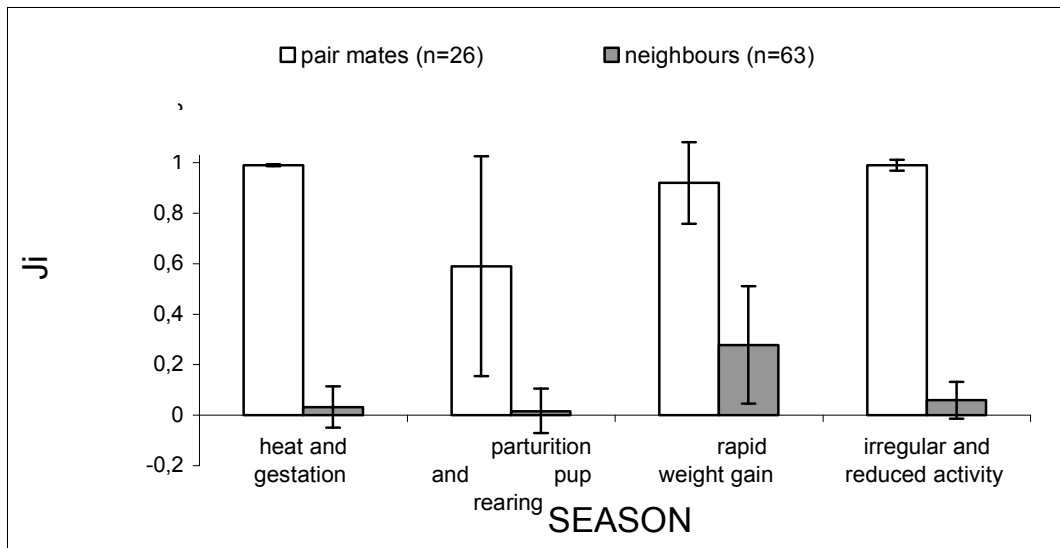


Fig. 5 Jacobs' index ($J_i \pm SD$) among raccoon dogs according to season (n = number of seasonal home ranges)

Neighbours

63 seasonal home ranges ($444.1 \text{ ha} \pm 260.3$) from 23 adjacent raccoon dogs (mean annual $J_i = 0.12 \pm 0.29$) were used for interaction analysis. During periods of oestrous and gestation ($J_i = 0.03 \pm 0.08$), parturition and pup rearing ($J_i = 0.02 \pm 0.09$) and winter ($J_i = 0.06 \pm 0.07$), the observed adjacent animals ignored each other. Only in autumn, a slight preference was shown among neighbours ($J_i = 0.28 \pm 0.23$) compared to the other seasons (Fig. 5). I used means of seasonal data for each pair of raccoon dogs to show differences in behaviour between neighbours. The Jacobs' indices between adjacent males (n = 15); ($J_i = 0.10 \pm 0.18$) and females (n = 13); ($J_i = 0.10 \pm 0.15$) were almost neutral and even neighbouring males and females (n = 34) ignored each other ($J_i = 0.12 \pm 0.19$).

4.3 Discussion

4.3.1 Reliability of the method

Seasonal divisions should reflect real aspects of the animal's ecology (HARRIS et al. 1990), and pooling locations over a long time period to obtain "adequate sample size" can eliminate sensitivity to changes in area use over time (KENWARD 2001). So, in order to counter this, I divided the data into the four biological seasons. Autocorrelation of positional data has particular implications for studies based on radio tracking. If the data are highly correlated, the resulting calculation can be an underestimate of the home range size (SWIHART & SLADE 1985a) whereas data sub-sampled so as to minimise spatial correlation tend to underestimate areas where all the locations are used. Even when fixes are recorded once a day, they still sometimes remain significantly auto-correlated (ROBERTSON et al. 1998, ROONEY et al. 1998, DeSOLLA et al. 1999).

However, ignoring autocorrelation may result in underestimated range sizes (CRESSWELL & SMITH 1992, SWIHART & SLADE 1985a). Sampling so Schoener's Index is approximately 1 can therefore provide a more practical interval than requiring an interval that confers 'independence' (KENWARD 2001). Thus, to meet both requirements I excluded all seasonal home ranges with Schoener's Index below 0.92 for kernel distribution analysis. MCP 100 home range analysis is not affected by autocorrelation of successive fixes (HARRIS et al. 1990), so I used all locations. SEAMAN et al. (1999) recommended that home range studies using kernel estimates should obtain sample sizes of at least 30 fixes to reduce average size bias. Using the point method, KAUFALA et al. (1993a) identified a minimum of 35 relocations as stable home ranges for raccoon dogs in southern Finland. I found stable home ranges with a mean of 29 locations for fixed kernel estimates and a mean of 48 fixes for 100% MCP analyses.

4.3.2 Home ranges

Reported home range sizes based on telemetry data for raccoon dogs varies from 177.2 ha in Japan (Saeki 2001) to 700.0 ha (no winter home ranges included) in southern Finland (Kauhala et al. 1993a) for MCP 100 estimations. The mean MCP 100 home range size (567.3 ha) in Germany was between these estimates and agreed with MCP 100 home range sizes (570.0 ha) from south-east Finland (Kauhala et al. 2006). However, environmental conditions in Finland and Japan differ essentially from those in Germany, so results produced in these two countries may not be comparable with our data. The Japanese raccoon dog belongs to another subspecies, *N. p. viverrinus* (Temminck 1838), which has adapted to a variety of different (inter alia subtropical) habitat types. Moreover, it can be assumed that food availability was greater in our study area than in Finland due to the longer growing season and ensuing abundance of food (especially vegetable matter and carrion) and that raccoon dogs do not need to hibernate in Germany. However, the calculated population density (0.95 adults/km²) in Germany was comparable to that recently estimated in south-east Finland (min 0.38 adults/km² and max 0.77 adults/km²) (Kauhala et al. 2006).

Raccoon dogs expanded their home ranges during August-October to feed especially in maize (*Zea mays*) fields to accumulate fat reserves. They had the smallest home ranges during the mating season. Due to early pair formation in autumn, lasting pair bonding and synchronised movement of pair mates, they can reduce their radius during oestrous and pregnancy and live on their fat reserves. Slightly larger home ranges in winter were probably due to the large distances between winter dens on agricultural land. One pair had its core area in a damp birch forest and reed bed area during the harsh winter of 2002/2003 when temperatures fell to below -20° C. The animals were located 6.25 km away in an old fox burrow, having probably moved in search of better shelter as they returned when the frost period was over. Even in their more northern distribution area, raccoon dogs are occasionally active in mild winters (Heptner & Naumov 1974, Kauhala et al. 1993a).

4.3.3 Social organisation

Canids have developed omnivorous food habits and large litter sizes, which permit and promote the development of tolerance between the sexes; hence a permanent or seasonal pair bond seems to be the basic social unit in this family (KLEIMAN & EISENBERG 1973). All these characteristics concur with the observed social behaviour of raccoon dogs in the present study. However, exceptional among canids is the low developed territoriality and bi-paternal breeding system, I found.

In Finland raccoon dogs are monogamous and the territories of adjacent pairs can widely overlap. The paired mates share their home ranges and move together throughout the year, reflected in a high Jacobs' index ($J_i = 0.89$) (KAUHALA et al. 1993a, KAUHALA & SAEKI 2004a, KAUHALA & HOLMALA 2006). I found that males and females build a stable pair bond. Mated pairs roam together in close vicinity with almost totally overlapping home ranges throughout the year.

In the breeding season (approximately May-July) when females had larger home ranges, the core areas in particular overlapped to a lesser degree and individuals showed smaller Jacobs' indices (J_i) towards their partners. The division of labour between paired mates explains these differences. The males guard the litter at the dens when females are out foraging to satisfy their increasing energy requirement during lactation (IKEDA 1983, YAMAMOTO 1987, KAUHALA et al. 1993b, KAUHALA et al. 1998a).

Core areas covered 81.2 % of raccoon dogs' home ranges, indicating that they use their home ranges evenly. The almost neutral Jacobs' index (J_i) throughout the year between adjacent individuals is also confirmed by high intra-specific tolerance: adjacent animals were seemingly ignored. Neighbours of the same sex and even adjacent males/females showed neither preference nor avoidance. This confirms results from a Finnish study where neighbouring racoon dogs had a neutral Jacobs' index ($J_i = 0.04$) (KAUHALA & HOLMALA 2006). However, core areas of most adjacent individuals or pairs did not overlap in the pup-rearing season which suggests a degree of avoidance, if not territoriality and defence, of the breeding den vicinity when the pups are small. These results also agree with the studies of KAUHALA et al. (1993a, 2006) in Finland.

In all other seasons I found a combination of weak, intra-specific population pressure due to under-developed territoriality and probable lifelong pair bonds. In addition, because of their high tolerance towards conspecifics, adjacent raccoon dogs can have individual home ranges that have large overlaps.

Thus, with respect to home range overlap analysis and dynamic interaction estimations, I conclude that the raccoon dog in Germany is monogamous without defending an exclusive territory.

5. Habitat use

5.1 Materials and methods

5.1.1 Telemetry and data analyses

For capturing and aging animals, telemetry techniques, tracking accuracy, autocorrelation of data and home range stability see 4.1.1. Radio locations were classified as active or inactive based on amplitude fluctuation and bearing shift (ANDELT 1985).

I derived habitat information from GIS databases by the office of surveying of Mecklenburg-Western Pomerania (2001). To improve the background map I additionally digitized ditches, reed, maize fields and small woods using Arc View GIS 3.2a. I did not divide forests into different habitat categories and forest patches smaller than 3 ha were categorised as small woods. Public roads and dirt roads were not taken into consideration.

Because distinct seasons and agricultural activities were prominent in the study area, habitat quality was considered to be influenced by seasons. Thus, to show seasonal differences in habitat use, I grouped animal locations into four different seasons: oestrous and gestation (March – April); parturition and pup rearing (May – July); intensive foraging and fat accumulation (August – October); and reduced and winter-burrow associated activity (November – February).

Habitat structure is usually measured by profiles of vegetation which have functional relationships with the species in focus (McCOY & BELL 1991). Thus, habitats were grouped into nine broad classes: forest (including both coniferous and deciduous forest), settlement (villages and farms), water (lakes, streams, ditches, pounds and shore areas), meadows (pastureland and lie fallow fields), farmland, maize fields, small woods, reeds and hedges.

Although habitat use among animals differed, I combined data from all individuals to obtain an overall picture of habitat use in different seasons (WHITE & GARROTT 1990). For annual comparisons, seasonal data were pooled and averages used.

To specify analyses, burrow-associated locations were excluded during the pup rearing and winter periods.

By analysing a circular sub-section of the GIS background map, I obtained habitat composition for the total study area. Home ranges of most raccoon dogs were located around a large lake. Thus, in order to consider all animals, I choose a sector (9 km radius) with the geographical centre of that lake. Habitat composition was obtained for home ranges estimated with 95% fixed Kernel distribution. As raccoon dogs have large core areas (> 80% home range size) (KAUHALA et al. 1993b), I did not calculate habitat use and preference separately for core areas. Relative habitat use was obtained for locations within home ranges. To estimate which habitats are used for shelter and foraging I compared the percentage distribution of active and inactive locations in habitats. To assess habitat preferences within the home ranges I used the symmetrical index; $P_i = \frac{U - V}{(U + V - 2UV)}$, where U = the proportion for habitat used and V = the proportion of habitat available, suggested by JACOBS (1974), which varies from $P_i = -1$ to $P_i = +1$. Values close to +1 indicate preference, values close to -1 indicate avoidance and values close to zero indicate habitat use equivalent to habitat availability. To compare males with females I combined Jacob's indices (P_i) from seasonal home range data.

Habitat composition of individual home ranges was used to classify animals. If the share of forest within a home range (n = 18) exceeded 50% (mean 68.2% \pm 14.98 SD) the individual was classified as a 'forest type' raccoon dog. If the share of forest habitats within a home range (n = 22) was less than 5%, the share of pastureland was mean 81.82% \pm 16.92 SD. Consequently the individual was classified as a 'agrarian type' raccoon dog.

5.1.2 Statistical Analysis

To avoid pseudo-replication in statistical analysis (SPSS 15.0.1) I pooled data from the same animal and season in consecutive years using means. To test for habitat preferences, I compared the values of Jacobs' index (P_i) for habitats using Kruskal-Wallis H-tests. Differences between habitat preferences in different seasons were tested separately for sex and habitat. The relative distribution of bearings in habitats using active and inactive fixes was tested with Wilcoxon signed-ranks T-test.

Significance of habitat preference between 'forest type' and 'agrarian type' raccoon dogs was tested using Mann-Whitney U-test. Inequality of data required a final Fischer's Omnibus Test for all analyses.

5.2 Results

5.2.1 Study area, home range location and percentages of locations in habitats

The defined study area (254.34 km²) is only sparsely populated (0.63% settlement). Deciduous forest (27.54%), farmland (28.38%) and meadows/pasture land (32.92%) are the prominent habitat types in the region.

Habitat composition within home ranges and within the whole study area was almost equal. Although percentages share of farmland and meadow was 16.35% smaller and 12.06% higher within the home ranges, respectively. Locations (n = 6,157) were distributed to 43.20% in deciduous forest and to 30.42% on meadows/pasture land. Whereas only 6.94% of the locations were realised on farmland and 3.28% on maize fields (Tab. 2).

Tab. 2 Habitat composition in the total study area (254.34 km²) and in raccoon dog home ranges (n = 62) and distribution of locations (n = 6,157) in habitats

habitat type	% entire study area ¹	% home ranges (n = 62) ± SD	% locations in habitats ¹
hedge	1.15	1.66 ± 1.54	1.53
small wood	4.23	2.34 ± 2.91	5.05
reed	1.11	2.49 ± 3.14	4.59
settlement	0.63	0.64 ± 1.04	0.32
forest	27.54	28.91 ± 28.36	43.2
meadow	32.92	44.96 ± 31.28	30.42
water	4.19	6.95 ± 9.00	1.43
farmland ²	28.38	12.05 ± 14.75	10.22

(¹ 'rows' percentages do not add to 100 due to rounding; ² maize-fields included)

5.2.2 Relative use of habitats within home-ranges

All habitat types were used opportunistically by raccoon dogs. Males showed significant differences in where they spend their time (Fisher's Omnibus Test [one exact Wilcoxon Test per sex and habitat]: $\chi^2 = 27.19$, $df = 16$, $p = 0.04$), whereas females did not ($\chi^2 = 23.32$, $df = 16$, $p = 0.10$). A comparison of active and inactive locations in different habitats found no remarkable differences.

Animals used habitats in one of two ways in the study area. One type of raccoon dog, the 'agrarian type', occupied a more managed agricultural environment, such as meadows and grasslands (mean = 81.8% home range share; $n = 22$ home ranges) and included < 5% forest cover in home ranges. The second type of raccoon dog, 'forest type', inhabited home ranges with > 50% forest cover (mean = 68.2% home range share; $n = 18$ home ranges). Mean seasonal home range size differed between 'raccoon dog types' and were $2.39 \text{ km}^2 \pm 2.14 \text{ SD}$ for the 'agrarian type' and $3.13 \text{ km}^2 \pm 4.40 \text{ SD}$ for the 'forest type'. Both types had a comparatively low (< 14.1%) share of all other habitat types in their home ranges.

5.2.3 Preference within home ranges

No dispersal was detected and each resident adult stayed within its home range throughout the time it was monitored. Raccoon dogs showed almost neutral preference indices (P_i) for most habitat types. I.e. forests, reeds, small woods and hedges were used to an extent more or less equivalent to availability (Fig. 6).

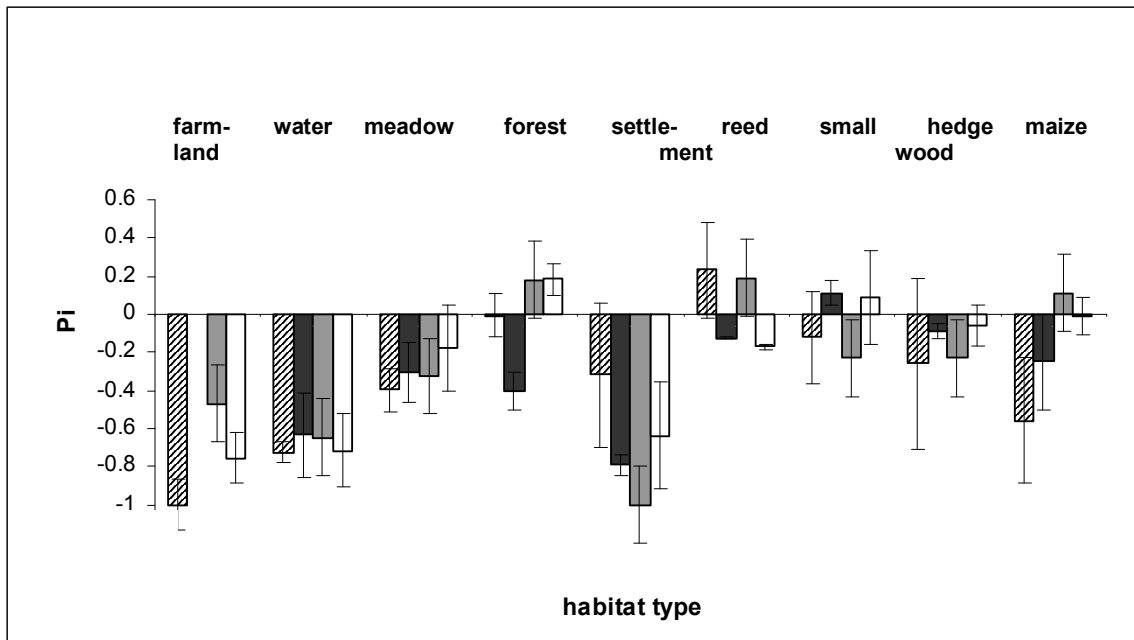
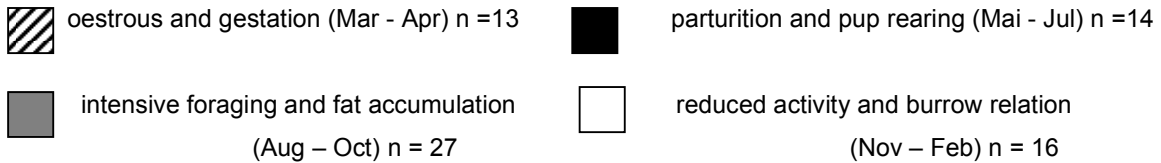


Fig. 6 Habitat preference by raccoon dogs in different seasons (n = number of home ranges)



However, animals avoided open farmland except during the pup-rearing period when a neutral preference index (Pi) was estimated. Water surface (lakes, ponds and ditches) and settlements were clearly avoided all year and open meadows were less visited than expected based on availability throughout the year. Forests were used in proportion to their availability during the oestrous and gestation period and preferred in the period of intensive foraging and fat accumulation (autumn) and during winter. Forest covered habitat was less frequently visited than expected during the parturition and pup rearing period.

Raccoon dogs used maize fields equivalent to availability during autumn and winter. In spring and early summer the animals avoided fallow fields. Reed beds, small woods and hedges were of some importance, but had a more or less neutral

preference index (Pi) throughout the year. However, no significant recognisable difference for habitat preferences between seasons was obvious (Fisher's Omnibus Test [one Kruskal-Wallis H-Test per sex and habitat]: $\chi^2 = 28.94$, $df = 30$, $p = 0.52$). An effect of sex on habitat preference (Pi) could not be verified. Slight differences were detected only for hedges, which were less avoided by females, and cereal fields (maize) which were preferred by females but avoided by males (Fig. 7).

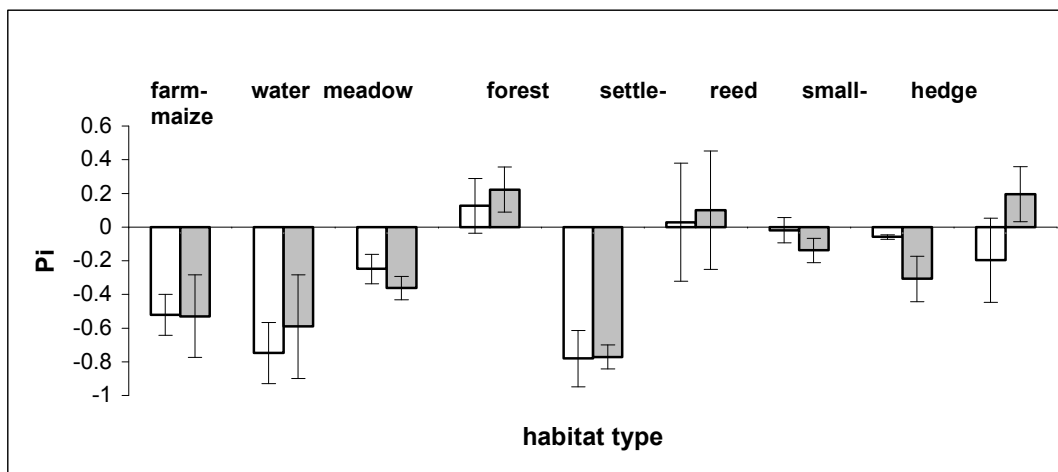


Fig 7 Habitat preference by female and male raccoon dogs (n = number of seasonal home ranges)

□ male (n = 37) ■ female (n = 33)

Regarding habitat preference for 'agrarian type' and 'forest type' raccoon dogs both types of animals showed comparable indices (P_i) for most habitats (Fig. 8).

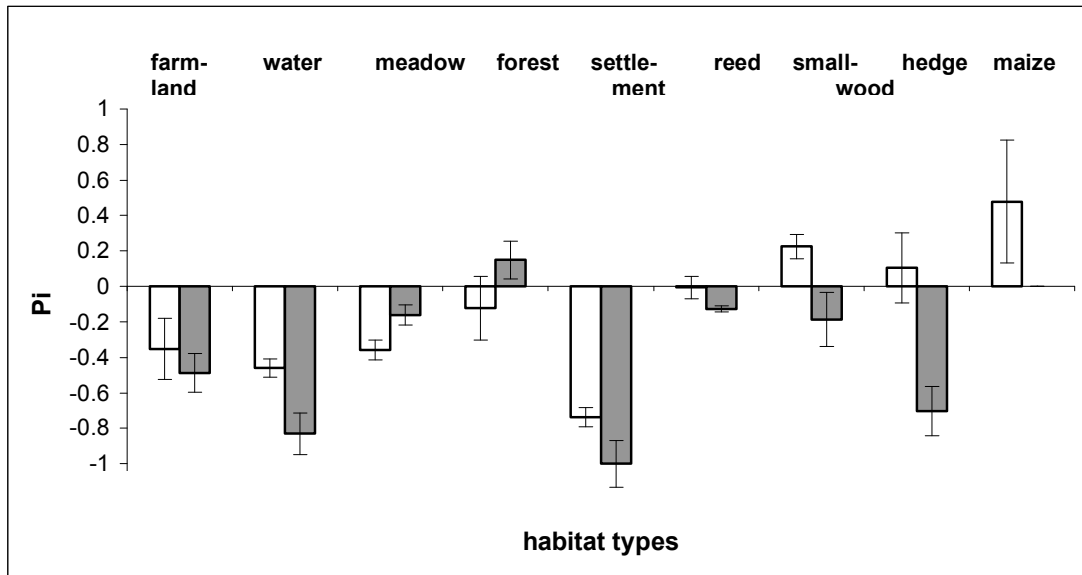


Fig. 8 Habitat preference of raccoon dogs with high and low forest cover within their home ranges (n = number of seasonal home ranges)

■ 'forest type' > 50% forest cover (n = 18) □ 'agrarian type' < 5% forest cover (n = 22)

However, some differences were notable. Hedges and small woods were preferred by the 'agrarian type', but not by the 'forest type'. Alternatively, there was a preference for forest covered habitats by the 'forest type', but not by the 'agrarian type'. Maize was preferred by the 'agrarian type'. There was no difference in habitat preference (P_i) for males (Fisher's Omnibus Test [one exact Mann-Whitney U-test per sex and habitat] : $\chi^2 = 14.45$, df = 18, p = 0.70) and females ($\chi^2 = 14.56$, df = 18, p = 0.69) concerning both habitat types.

Likewise, no difference in habitat preference ($\chi^2 = 11.62$, df = 18, p = 0.87) was detected in the intensive foraging and fat accumulation season (August – October) for 'agrarian type' and 'forest type' raccoon dogs. Insufficient data preclude significant tests for the other seasons.

5.3 Discussion

5.3.1 Reliability of the Method

In raccoon dogs there is a weak, intra-specific population pressure due to low-developed territoriality and probable lifelong pair bonds (KAUHALA et al. 1998a, DRYGALA et al. 2000, KAUHALA & SAEKI 2004b, KAUHALA et al. 2006). Thus, in contrast to pack living canids each animal provides an independent measure of habitat use within the population.

I grouped animal locations into four different seasons which best represented the behavioural changes in raccoon dogs that could affect habitat use and preference (SCHOOLEY 1994). Furthermore to consider autocorrelation of positional data I excluded all seasonal home ranges with Schoener's Index below 0.92 for kernel distribution analysis used for habitat use calculation (see also 4.3.1).

5.3.2 Habitat selection and preferences

This is the first study on habitat use of the raccoon dog in Central Europe. Therefore, information about the habitats, feeding sites, and refuges that are important to raccoon dogs is crucial to predict the ability of this introduced species to expand further.

Previous studies of the introduced raccoon dogs were conducted only in industrial forest areas of southern Finland, where, in contrast to North-Eastern Germany, seasonal difference in habitat use was reported. Raccoon dogs do hibernate in winter-dens, favoured shore areas in summer and in autumn used old moist heaths more often where food was abundant (KAUHALA 1996b).

However, because environmental conditions in Finland differ from those in North-Eastern Germany, these results may not be self-evidently applied to German raccoon dogs. The present study indicates that, both forest areas and agricultural habitats offer adequate cover and feeding opportunities for raccoon dogs.

Compositional analysis ranks the relative use of habitat and infrastructure compared to the availability in the entire study area or within the home ranges (AITCHISON 1986, AEBISCHER et al. 1993a, b).

Percentage availability of habitat types was comparable within raccoon dogs' home ranges and the whole study area in North-Eastern Germany. However, animals choose home ranges with higher meadow/pasture land and lower farmland share. Raccoon dogs under study were frequently observed on meadows, where mice, shrews, amphibians and insects are abundant. Because of the opportunistic and omnivorous feeding behaviour, usable resources are probably densely and homogeneously distributed in the habitat. Nevertheless, because of high share (44.96% of home ranges) raccoon dogs showed a tendency to avoid meadows. Farmland was less attractive to raccoon dogs because fields were left fallow for most of the year (approximately 9 months).

The most precise estimates of habitat use come from analysing telemetry locations using locations and the geographic range of habitats to estimate preference (KENWARD et al. 2003). Therefore, I used the habitat preference index (PI) recommended by Jacobs (1974) for all analysis except comparisons of active and inactive fixes, where home range calculations are of no use.

Errors in radio locations decrease the accuracy of the habitat use analyses and may create bias (NAMS 1989). The tracking resolution in this study was 100 m, which is moderate given the comparatively large patches of habitat types. I also made visual observations of collared animals as often as practical to improve the accuracy of fixes.

Analysis for different seasons could not find any significant differences in habitat preference by season, suggesting that habitat quality is not spatially or temporally heterogeneous for raccoon dogs. This might be due to the diet and foraging behaviour of the species, which is a true omnivore and more a gatherer rather than a predator (KAUHALA et al. 1993a), feeding on constantly distributed, small food items throughout the year (DRYGALA et al. 2000, 2002). Furthermore, habitat quality did not differ substantially between seasons because of a temperate climate and because small rodents were abundant all year in different habitat types (meadows, forest, reeds).

Regarding the selection of home ranges and the percentage of habitat types in home ranges, two categories 'agrarian type' and 'forest type' were distinguished. The larger percentage parts of locations were in deciduous forest and on meadows/pasture land, reflecting this classification.

At the scale of habitat selection within home ranges (P_i), results showed no significant difference of preference or avoidance for the two habitat type users. I concluded that raccoon dogs under apparently sub-optimal conditions, in agrarian habitats do not depend on forest covered areas.

Furthermore, smaller home range sizes of the 'agrarian type' raccoon dog indicate higher food abundance in meadows and pasture land than in forest habitats. E.g. population density of small rodents is essentially higher in agrarian than in forest habitats in Germany (NIETHAMMER & KRAPP 1978, 1982).

I found that raccoon dog populations can persist in agricultural habitats with a large amount of open landscape. In such areas, raccoon dogs prefer small woods, hedges, and crop fields to a slightly higher degree than do animals that primarily use forest covered areas. Thus, habitat composition seems to have no significant effect on raccoon dog abundance. Also in its more northern distribution area climate is the major factor behind regional variation in productivity, mortality and population growth, rather than habitat composition (KAUHALA 1992).

In species with flexible habitat use, above average association with a habitat does not necessarily mean that it is critical for an animal (WHITE & GARROTT 1990). For instance, in 2003 one radio collared raccoon dog pair successfully raised a litter in a solely agricultural, intensively-used habitat (pers. obs.). Apparently, the more fragmented habitat in agricultural areas offers the raccoon dog adequate cover and feeding opportunities. The opportunistic ability of the raccoon dog to establish viable populations both in environments with high forest cover and in open landscape with high agricultural use is essential for its further success colonising densely populated Western Europe.

Equivalent trends in habitat preference between active and inactive fixes indicated an opportunistic and flexible habitat use. Raccoon dogs often used meadows as foraging and day resting sites in undisturbed environment and were only located in

dens during the breeding period and under severe winter conditions. They apparently do not need dense vegetation for shelter.

In contrast to studies in Japan, where raccoon dogs recently appeared in urban areas (SAEKI 2001), presently results indicate that resident raccoon dogs till now avoid settlements and I never observed them crossing villages, even when these were located in the middle of their home ranges.

The success of the raccoon dog in eastern Germany despite human eradication efforts and road kills can be attributed in large measure to its omnivorous feeding behaviour (KAUHALA et al. 1993a) and opportunistic use of habitat. Previous studies have shown that raccoon dogs successfully exploit forested habitats (KAUHALA et al. 1993b, KAUHALA 1996b, SAEKI 2001) and this work indicates that they are also well-adapted to agricultural and forested areas. Food, water, daytime shelter, den sites for nursing, and habitat corridors connecting these were the important habitat components for raccoon dogs.

6. Ranging and parental care during pup rearing

6.1 Materials and methods

6.1.1 Radio tracking

From April to June 2003, three pairs of raccoon dogs were radio-tracked during the whelping season (esp. the first six weeks after parturition). For capturing and aging animals, telemetry techniques and tracking accuracy see 4.1.1. Each raccoon dog pair ($n = 3$) was radio-tracked once a week for a 24-h session of continuous radio-tracking during the first six weeks after the pups were born. Contact with the observed pair was consistently maintained and I managed to locate both, male and female every 15 min (in a total of 3.456 locations). Thus, the number of locations for every 24-h radio-tracking session ($n = 36$) was always exactly 96. Radio locations were classified as active or inactive based on amplitude fluctuation and bearing shift (ANDELT 1985).

I estimated “daily range” sizes and overlap, daily movement distance (DMD) for 24-h periods, average distances to the breeding den, and time allocation to pup rearing at the den using RANGES 6 V1.2. Home ranges were calculated using 95% fixed kernel distribution (K 95). Daily range sizes were estimated separately for males and females for each 24-h tracking session. Differences among mate pairs – in home range size, DMD, distance of the animals to the breeding den and time allocation to pup rearing at the den – were interpreted here as showing variations in terms of parental care.

I analysed autocorrelation of data using RANGES 6 V1.2. Statistical independence of fixes varied greatly among subsets of data. REYNOLDS & LAUNDRE (1990) and DESOLLA et al. (1999) showed that data with independent sampling intervals underestimated both home range size and DMD. Furthermore, DESOLLA et al. (1999) found that the fixed kernel estimates were more accurate with maximum numbers of auto-correlated fixes than independent subsets of data. Therefore, I used all the continuous tracking fixes for daily home range estimates.

Parturition was determined through monitoring the radio-collared animals during April and May. Paired mates roam together or close to each other before parturition, but

postpartum one adult always guards the litter while the other is searching for food. Thus, when paired mates were located far away from each other and one adult permanently stood at the breeding den, I could be sure that delivery had taken place and I started radio-tracking (24-h/week) until the animals left the breeding den. To improve determination of parturition, I caught, measured and weighed the pups near the breeding den during July and August.

When the parents are guarding the litter at the den, they tend to move somewhat around the den. Thus, I categorised animals as being “at the den”, if the bearing indicated the direction as being within approximately 50 m of the den. The time spent by males and females at the den was calculated by including all locations inside a diameter of 100 m around the breeding den.

The distance covered during the 24-h blocks was calculated as the sum of straight line distances between consecutive locations. I also calculated the average distance between the breeding den and each location.

6.1.2 Video observation

Filming was performed at an unused badger den, which was occupied by a raccoon dog pair for pup rearing between April 25th and June 25th, 2003 (for a total 1009.7 h; from two weeks before until seven weeks after parturition). The raccoon dogs used only one entrance. Thus, I interpreted all observations made in a 6 m radius around the entrance as having taken place “at the den”. Paired mates were identified by body shape and fur shade and a white, reflective tape that was fixed on the males’ radio collar. To estimate the allocation of time with regard to pup rearing, the percentage of time spent away from the breeding den was calculated. In addition, the food items carried back to the den were recorded and, if possible, identified.

6.1.3 Statistical analyses

I used the independent-samples T-test procedure (SPSS 15.0.1) to tests the significance of the differences between male and female raccoon dog for daily range size, DMD, activity pattern, and time allocation at breeding den in six weeks postpartum. Because of small sample size (six animals) and high individual differences within sexes, the results should be considered with caution. Descriptive statistic values are given in bar charts and averages are given with standard deviations (SD).

6.2 Results

6.2.1 Radio tracking

Daily range size between sexes were not equal (T-test: $t = -2.73$; $df = 4$; $p = 0.13$) and mean (\pm SD) daily range (kernel 95%) in males was smaller than that of females (14.73 ± 8.16 ha and 98.24 ± 51.71 ha, respectively). In contrast to males, females increased their daily ranges continuously in the first six weeks postpartum (Fig. 9).

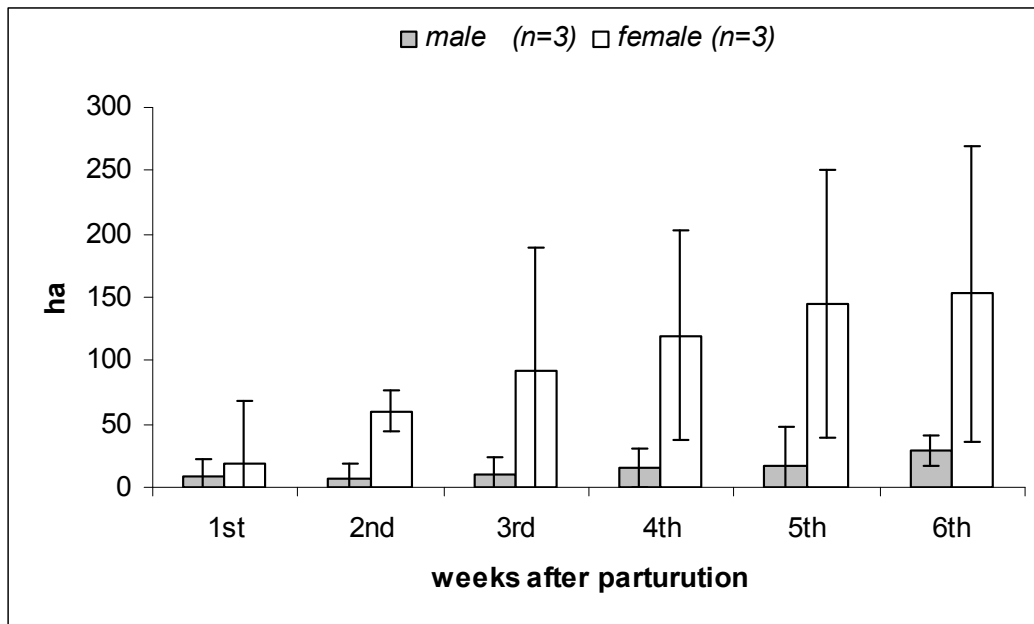


Fig. 9 Daily range sizes (kernel 95%) of adult female and male raccoon dogs in the first six weeks postpartum calculated for the 24-h continuous radio-tracking sessions

In the sixth week after parturition, all three raccoon dog pairs had left the breeding den. Males had smaller home ranges, as they most probably spent more time guarding and roaming with the pups, whereas females extended their daily range sizes, most probably for the purpose of solitary foraging.

Before birth of the litter DMD and daily range sizes of a selected pair was similar. In the first week and fifth week postpartum the male had very small daily range sizes while guarding the litter. In the sixth week postpartum, when the breeding den was

abandoned the male roamed, most likely together with the pups in the surrounding. The female had much larger daily range sizes, longer DMD and used different areas than the male, away from the breeding den to forage and to rest undisturbed from the pups (Fig. 10).

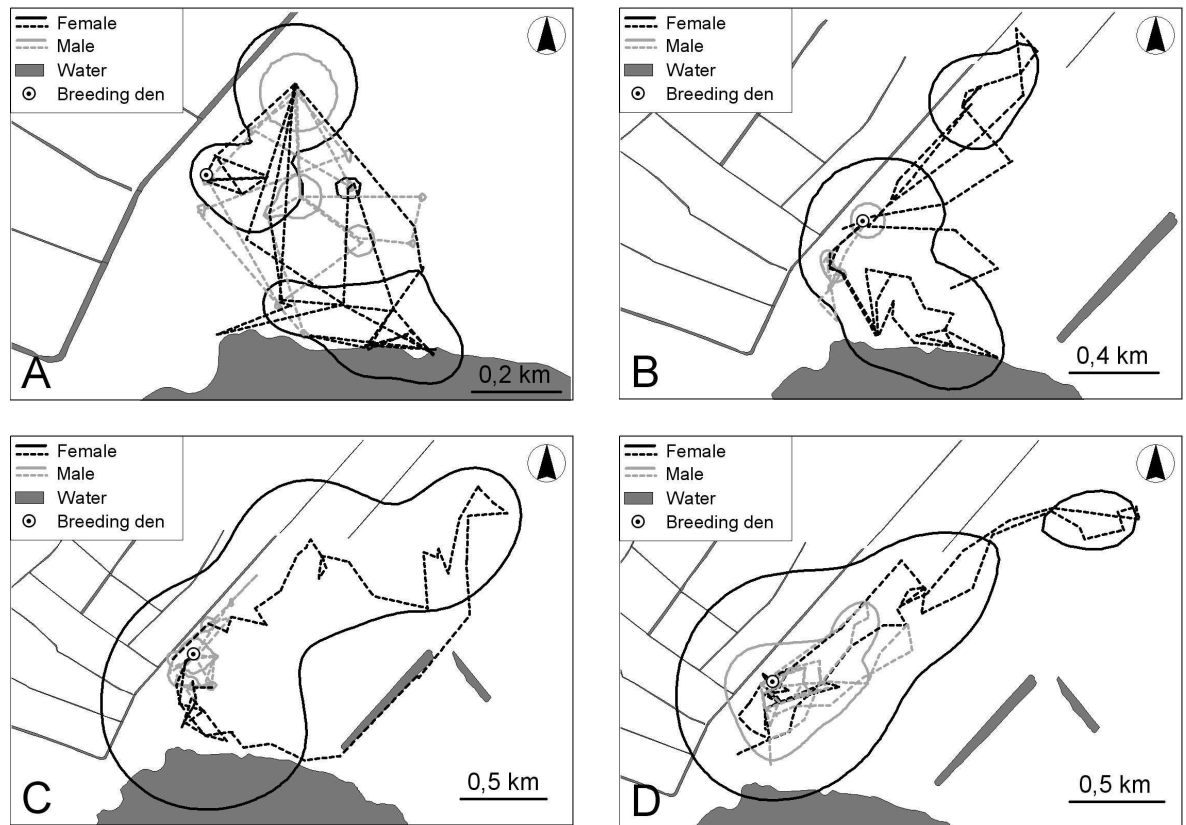


Fig. 10 Examples of daily movement distance (DMD, dashed lines) of simultaneously-located paired mates in their daily range (kernel 95%, solid lines), A before parturition (2-3 May), B first week postpartum (14-15 May), C fifth week postpartum (12-13 June), D sixth week postpartum (18-19 June)

Within pairs, male home ranges overlapped with those of their mate in 99.2 ± 1.4 (mean \pm SD), whereas female home ranges overlapped with their mate's only $28.0\% \pm 15.6$. The average overlap between two adjacent raccoon dog pairs during six

weeks postpartum was 33.4%. However, the adjacent radio-collared adults never approached the breeding dens of another pair during the entire study. On average, females moved much longer distances (DMD: 7,368 m \pm 2,015) than males (DMD: 4,094 m \pm 2,886) during the 24-h sessions in the first six weeks after delivery ($t = -1.46$; $df = 4$; $p = 0.31$). In the first week, males and females travelled almost identical distances (DMD: 4,532 \pm 3,620 m and 4,842 \pm 1,243 m, respectively), whereas in the fifth week females roamed noticeably (but statistically insignificant) further than males (9,845 \pm 1,005 m and 4,634 \pm 3,603 m, respectively). In the sixth week, the DMD roamed by males and females were again similar (8,379 \pm 430 m and 7,115 \pm 2,726 m, respectively) (Fig. 11).

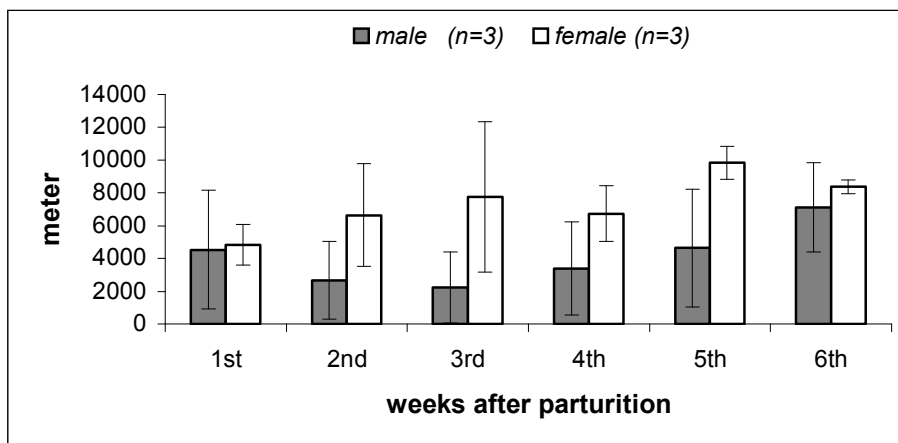


Fig. 11 Daily movement distance (DMD) covered by adult female and male raccoon dogs during 24-h radio-tracking sessions in the first six weeks postpartum

Male and female raccoon dogs were active for a similar percentage of the day ($63.2 \pm 3.2\%$ and $61.0 \pm 4.6\%$, respectively; $t = 0.59$, $df = 3.17$, $p = 0.59$) during the first six weeks postpartum. Males were located considerably closer (175 ± 16 m) to the dens than females (407 ± 40 m). Among females, the distance to the dens increased continually from the first (178 ± 18 m) to the sixth week (710 ± 46 m). From the fifth week onwards, females clearly ventured further from the dens, whereas males

stayed at short distance until the fifth week (94 ± 17 m). In the sixth week, they left the dens as well, which is shown by the greater distances (580 ± 15 m). However, even then, the females moved yet farther (710 ± 45 m) from the breeding den than males (Fig. 12).

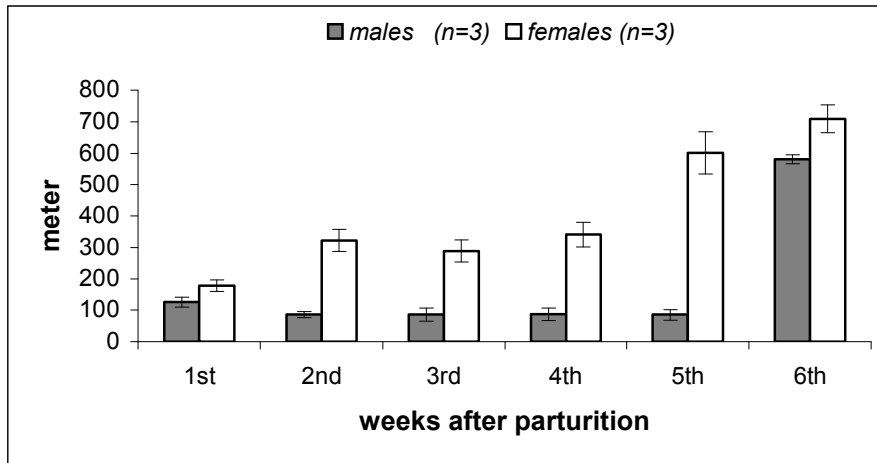


Fig. 12. Average distance to the breeding den of adult female and male raccoon dogs during the first six weeks after parturition

No differences ($t = 1.37$; $df = 3.43$; $p = 0.40$) in the percentage of the time present at the breeding dens were detected between sexes. Males spent noticeably more time ($40.5 \pm 11.7\%$) alone with the pups than females ($16.4 \pm 8.5\%$) and both parents were present at the dens a mean of $27.3 (\pm 14.6\%)$ of the time for 24-h continuous radio-tracking periods ($n = 36$) during the whole study (Fig. 13).

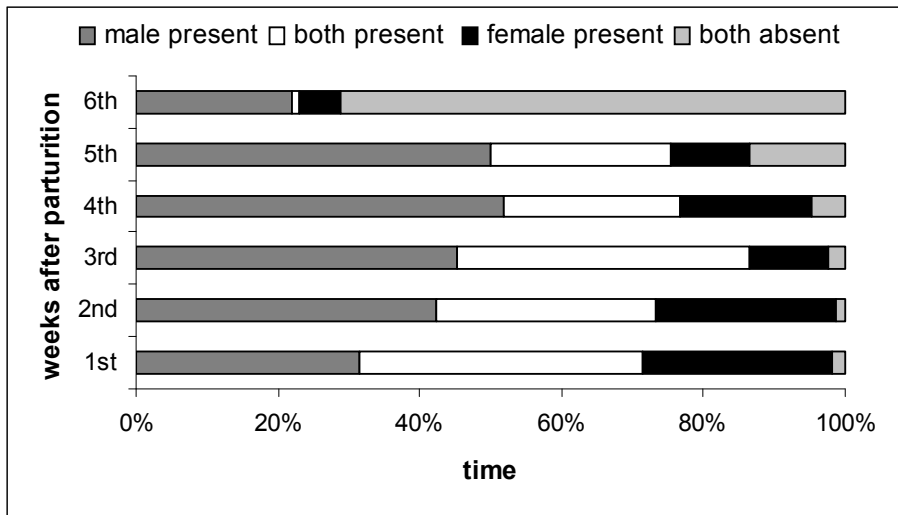


Fig. 13 Time allocation (%) of adult raccoon dog pairs ($n = 3$) at the breeding den during continuous observation (24-h/week) for the first six weeks after parturition investigated by radio telemetry

During their first month, the pups were hardly ever left alone ($2.6 \pm 1.6 \%$). When taking care of the pups alone, one parent invariably remained at the den until its mate returned. The absence of both parents at the den increased to $13.5 \pm 12.0\%$ in the fifth week. In the sixth week, both parents were absent most of the time ($71.2 \pm 39.6\%$). Both males and females decreased the time at dens (to $5.9 \pm 2.7\%$ and $21.9 \pm 37.9\%$, respectively) and mate pairs were almost never recorded together (1.0% of the time ± 3.1 SD) at the breeding dens in this time.

6.2.2 Video observation

During the two weeks before giving birth, the female and the male spent almost identical periods away from the breeding den (34.3 and 31.1% of the time, respectively). The mate pairs simultaneously left and reappeared at the den. Parturition took place on May 7th, and that day the female and male left the den for 3.18 h and 0.33 h, respectively, during 24-h. The amount of time recorded for each partner as being absent from the den increased successively for both during the subsequent seven weeks, during which the female spent noticeably more time (51%) foraging or resting and, therefore was absent from the den for longer than the male (40.7%).

In the first two weeks after parturition, both male and female spent a small amount of time away from the pups (14.0% and 23.5% of the time, respectively) (Fig. 14).

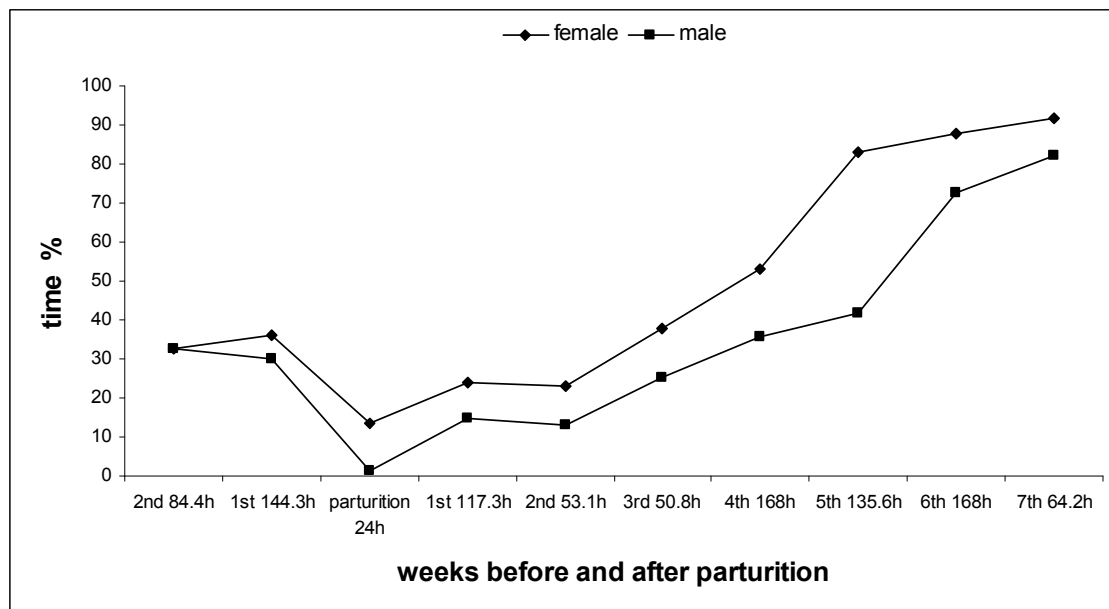


Fig. 14 Time (%) spent absent from the breeding den in weeks before and after parturition investigated by video observation (h = hours recorded, 1009.7 in total)

Pups (n = 9) were recorded at the age of 19 days in the entrance of the burrow for the first time and were seen to chew on solid food. Usually the male guarded the litter inside or in front of the den as the female slept, preferably alone, beside the entrance of the den. Both parents carried the pups back to the breeding den until the age of approximately four weeks. Behaviour among mate pairs differed noticeably in the fifth week when the male left the den only for 41.7% of the time, whereas the female was absent 82.9% of the time and the pups were even left alone for a few hours. From the fifth week onwards, the female only approached to nurse the pups for a couple of minutes until 45 days (seventh week) after parturition when all the raccoon dogs left the den. No other raccoon dogs (i.e. helpers) were recorded in the vicinity of the burrow entrance.

The male carried prey to the den to provide the female and the litter with food (Tab. 3).

Tab. 3 Food items (n = 44) carried to the breeding den by male raccoon dog – according to video observations of a raccoon dog pair during pup rearing season

Food item	No.
bird (Passeriformes)	1
egg (chicken egg size)	1
roe deer leg (<i>Capreolus capreolus</i>)	2
roe deer fawn (<i>Capreolus capreolus</i>)	2
mole (<i>Talpa europea</i>)	1
frog/toad (Amphibia spec.)	4
grass snake (<i>Natrix natrix</i>)	14
small mammal < 100g (indet.)	7
fur (indet.)	1
unidentified item < 100g (indet.)	11

The diet of raccoon dogs recorded on video during the whelping season consisted of small food items including amphibians and small mammals, but also of larger grass snakes (*Natrix natrix* L. 1758) and roe deer fawns (*Capreolus capreolus* L. 1758) and parts of carcasses carried to the den by the male. After leaving, the male returned to the den with food items (n = 44) in 88.2 ± 69.3 minutes.

6.3 Discussion

It is assumed that the social system in canids is correlated with body size (MACDONALD & MOEHLMAN 1983, MOEHLMAN 1986). Medium-sized canids (6.0 - 13.0 kg) appear to be strictly monogamous and the adult sex ratios in the populations are equal. Both sexes invest equal amount of time in parental care and the males participate actively in the rearing of the young (KLEIMAN 1977, MOEHLMAN 1989, GEFFEN et al. 1996). Previous studies from Japan and Finland indicate that the raccoon dog is monogamous and both parents participate in pup rearing (IKEDA 1983, YAMAMOTO 1987, KAUHALA et al. 1993a, 1998a). Furthermore, it is a common behaviour in the raccoon dog, in which males spend more time at the den with pups than females (KAUHALA et al. 1998a).

Analyses in the present study confirm the results of these earlier studies and point to a highly developed division of labour between mate pairs during the pup-nursing period. Due to the large size of the litter, the female raccoon dog probably can not competently rear her young alone and requires substantial male investment. In Finland, raccoon dog pups are very vulnerable in the first weeks postpartum and pups were carried back to the den by the male when they were 21 days old, which led to the conclusion that it is the male's task to guard the pups (KAUHALA et al. 1998a). In North-Eastern Germany, predation by the red fox and badger is likely, and the litter must be guarded against predators. Pups were seldom, if ever, left alone during their first four weeks, which may also serve to prevent hypothermia, since temperature in North-Eastern Germany can be below 0 °C in May. On the other hand, the lactating female, with her high energy requirements, had to wander around in search for food, while the male stayed with the litter. From the third week after birth both parents carried the pups back to the den.

These results coincide with studies from Finland where pups were very rarely left alone during the first month after birth (KAUHALA et al. 1998a), and being to emerge from the den at three to four weeks of age and weaned at approximately four to five weeks (KAUHALA & SAEKI 2004a). Radio-collared cubs left the den at the age of 5 to 6 weeks (KAUHALA & HELLE 1994). In North-Eastern Germany, the breeding dens were

abandoned in the sixth week postpartum, and pair mates had similar DMD; however, females showed much larger daily range sizes demonstrating a higher energy requirement caused by the fast-growing litter. Thus, I assume that the process of weaning was still not finished when the pups were in their sixth week.

Additionally, there was a clear difference in time allocation at a nursing den for a pair video recorded in the wild. After parturition, the male attended to the den more often than the female and started carrying food to the den. When one of the parents returned, the other often left the den. In doing so, activity level did not differ between sexes, which is also reported for breeding raccoon dogs in southern Finland (KAUHALA et al. 2007). I never recorded, through video and telemetry, adjacent radio-collared raccoon dogs near the breeding den of another pair. According to Kauhala and Saeki (2004) core areas of different pairs are totally exclusive, especially during the breeding season. However, comparable to the present results pair mates' home range overlap in spring to $78.0 \pm 24.7\%$ and those of adjacent raccoon dogs to 28% in southern Finland (KAUHALA et al. 2006).

Among social canids, exhibiting parental care indirectly by bringing food to the lactating female and directly by bringing food to the young is the rule (KLEIMAN & EISENBERG 1973, YAMAMOTO 1987). Raccoon dogs were also observed to provide food for the young by both parents (SAEKI 2001) in Japan. According to a study carried out on raccoon dogs in captivity, the male brings food to the female, especially during the first days after parturition (IKEDA 1983). This behaviour was also confirmed in the present study, but extended to the entire denning period, some seven weeks after parturition.

I made the assumption that within my research area, food was relatively abundant and food patches were densely distributed. The male was able to carry small and medium size food items (< 3 kg) to the den within less than a mean of 1.5 h. Thus, providing food to support the lactating female and a fast-developing litter is energetically profitable. As food items are usually small, I found no food remains, except roe deer fawn hoofs and legs near the dens.

In contrast, YAMAMOTO (1987) and KAUHALA et al. (1993b, 1998a) suggested that carrying food to the den may be energetically inefficient when food items are

presumed to be small, scarce, and widely distributed. These studies, however, were carried out in captivity or based on radio-tagging analysis. Caged animals may act differently than those in the wild and telemetry data do not cover specific behaviour patterns. Hence, I cannot rule out the possibility that male raccoon dogs provide food to the female and litter in other areas of their range.

Raccoon dogs have not been seen to regurgitate food to pups either in the wild or in captivity (YAMAMOTO 1987). Indeed, in the present study, regurgitation of food for the pups or the female was also never recorded. It could be postulated that raccoon dogs are morphologically unequipped to transport food in their stomachs to supply their mate pair and offspring.

As raccoon dogs tended to share its home range with its mate and 4-6 neighbours (KAUHALA & HOLMALA 2006), it is probable that long-term monogamy without defence of an exclusive territory is obligatory (KAUHALA et al. 1993a, 1998a). Monogamy may be favoured when more than a single individual (the female) is needed to rear the young (KLEIMAN 1977). Raccoon dogs give birth to large litters (nine pups in average) (HELLE & KAUHALA 1995, BOGE 2006) and appear to be relatively *r*-selected when food is abundant and climate is mild. Hence, females have a greater reproductive burden than a solitary female can bear, as the provisioning of fast-developing pups and defending them against predators at the same time supposed to be difficult without males' parental investigation.

This study confirmed that male raccoon dogs play an active role in pup-rearing, which is an important factor in terms of pup survival and, hence, is a key to both male and female reproductive success. In conclusion, bi-parental care and flexible food acquisition is likely contributing to reproductive success of the raccoon dog throughout Central and Western Europe.

7. Dispersal of the raccoon dog

7.1 Materials and methods

7.1.1 Ear-Tagging

From June 1999 until October 2003 I captured and released at the point of capture 82 young (< 1 year) raccoon dogs (39 males; 43 females) in “Galenbeck” and from August 2004 until August 2006, 54 young raccoon dogs (33 males; 21 females) in “Penzin”. Because the whole State of Mecklenburg-Western Pomerania (as is supposed for entire Central Europe) is suitable raccoon dog habitat (see also 5.3.2) and the straight line distance between the two study areas is only 123 km, I pooled data from animals for both study areas for further analysis.

The 136 raccoon dogs were captured alive using wire-box traps and fish bait. Raccoon dogs are easy to handle and need not to be immobilised. Adults were distinguished from young by means of body weight, fur, and attrition of teeth, especially that of incisors. Individuals until one year of age (April) were classified as juveniles. All animals were sexed, weight and fitted with numbered plastic ear-tags (Rototags®).

Dispersal is defined as the movement an animal makes from its birthplace to where it might reproduce (HOWARD 1960). In this study the distance between the marking place and the place where the animal was recovered by chance (e.g. hunting, road kills) was measured 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 the data I recorded the date (month) of relocation and classified raccoon dogs in young (< one year) animals killed in their first year (relocation distance) and relocations for adult (> one year), resident animals (real dispersal distance). To specify the age of dispersing juveniles, I assumed the 1st of May as date of parturition (NOWAK 1993, KAUHALA et al. 1998a, BOGE 2006).

Mean home range size for adults for the study area “Galenbeck” (see 4.1.1. and Tab. 1) was used to estimate the dispersal distance for raccoon dogs by using the formulas of TREWHELLA et al. (1988):

- Mean dispersal distance for males = $2.778 + 4.038 \times \text{home range size}$;
- mean dispersal distance for females = $3.853 + 2.659 \times \text{home range size}$.

To compare the present data with a study from Finland I used the formulas, originally calculated for red-foxes also for raccoon dogs, because both species live in pairs (see esp. KAUKHALA et al. 2006). I 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, I displayed the dispersal direction (direction of relocation from release site) and distance. Furthermore, the fate of ear-tagged raccoon dogs was recorded and percentage allocation of mortality factors was analysed.

7.1.2 Radio tracking

In the main study area “Galenbeck” 48 young (< one year) animals (25 females; 23 males) were fitted with expandable radio-collars (Wagener, Cologne). Each transmitter weighed 56 g and lasted about one year. (For telemetry techniques and tracking accuracy see 4.1.1). Raccoon dogs were monitored between June 1999 and October 2003. I located the animals with a handheld H antenna (HB9CV) or a three-element Yagi-antenna and TRX-1000s receivers (Wildlife Materials, USA) at different times of night and day (point method) as often as practical (a total of 2,877 locations). The mean distance between observer and animal was usually less than 1 km. As recommended by GARROTT et al. (1986), I used multiple triangulations with at least three bearings per localisation to eliminate reflected signal errors.

Telemetry data were analysed using ArcView GIS 3.2a. Because all animals showed home range shift after being fitted with a radio collar, I did neither analyse stability of short-term home ranges nor autocorrelation of locations.

I managed to track the dispersal movements of two juveniles, starting usually before dawn. In doing so I tried to locate the animals every 15 min until they stopped roaming and rested over the day. All 48 radio-collared raccoon dogs left their natal

home range. Thus, I was able to identify at least the month when young raccoon dogs start to disperse.

I managed to capture 17 juvenile weights less than 2 kg, prior to dispersal in natal home range. Natal home range sizes were estimated according minimum convex polygon methods 100% (MOHR 1947). To estimate the area covered by excursions for young raccoon dogs, I calculated the natal home range sizes (ha) with and without excursions.

7.1.3 Statistical analysis

For statistical analysis (SPSS 15.0.1), Mann-Whitney U-test was used to compare difference in the distances of relocation between sexes. Significance of differences between month in distances of relocation, month of dispersal and fate of ear-tagged raccoon dogs was tested with the non-parametric Chi²-test. I tested differences between sexes in the month of dispersal with Pearson's Chi²-statistic. All values are presented as mean \pm SD. All tests were two-tailed with level of significance of $p \leq 0.05$.

7.2 Results

7.2.1 Ear-tagging

From the 136 ear tagged young raccoon dogs only 18 cups had survived beyond the first year. Thus, dispersal mortality rate for young raccoon dogs was 69.5% in this study. The mean distance of relocations from marking point for all raccoon dogs ($n = 59$; i.e. 43.4% of all marked) was 13.5 ± 20.1 km. The mean distance for relocations of young raccoon dogs ($n = 41$) was 11.6 ± 18.4 km. Whereas the mean dispersal distance for adults ($n = 18$) was 17.8 ± 23.4 km.

55.9% (of both males and females) were relocated nearer than 5 km from the marking place, whereas 8.5% relocations were recorded further than 50 km from the marking point. No animals were recaptured in their natal home range. There was no difference in the distances of relocations between sexes (Mann-Whitney U-test, $Z = -0.44$, $p = 0.66$, $n = 59$) (Fig. 15).

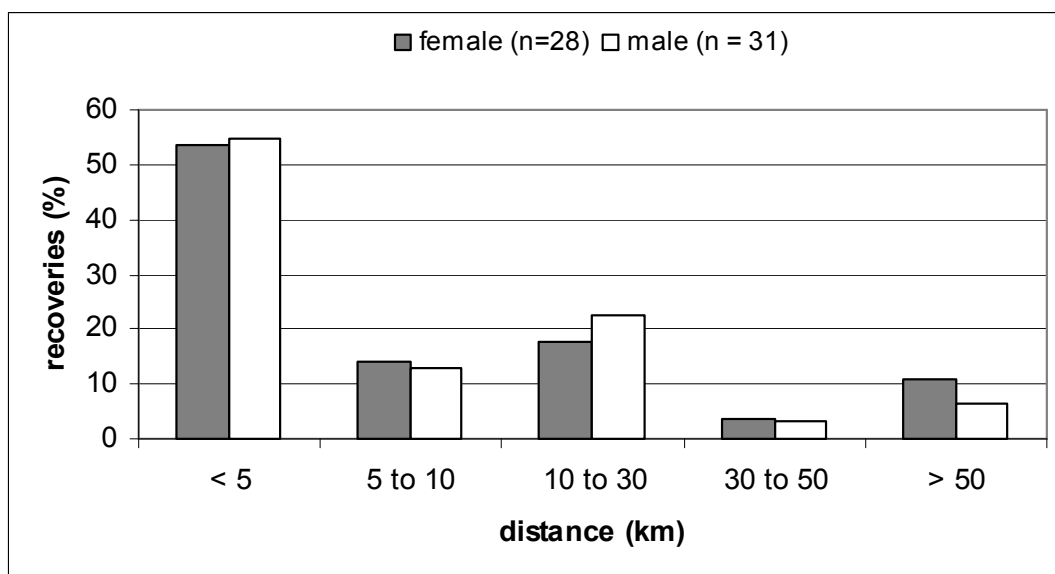


Fig. 15 Distance of relocations for young raccoon dogs ($n= 59$) from point of capture

By using the formulas of TREWHELLA et al. (1988) for the relationship between dispersal distance and home range size, females and males dispersed 14.0 km and

17.0 km, respectively. Most (53.65 %) relocations for ear-tagged young raccoon dogs ($n = 41$) were in August and September (Chi²-test; $\chi^2 = 33.87$; $df = 9$, $p < 0.0001$); only 34.1 % were recorded from October to April. There were no relocations in May and June (Fig. 16).

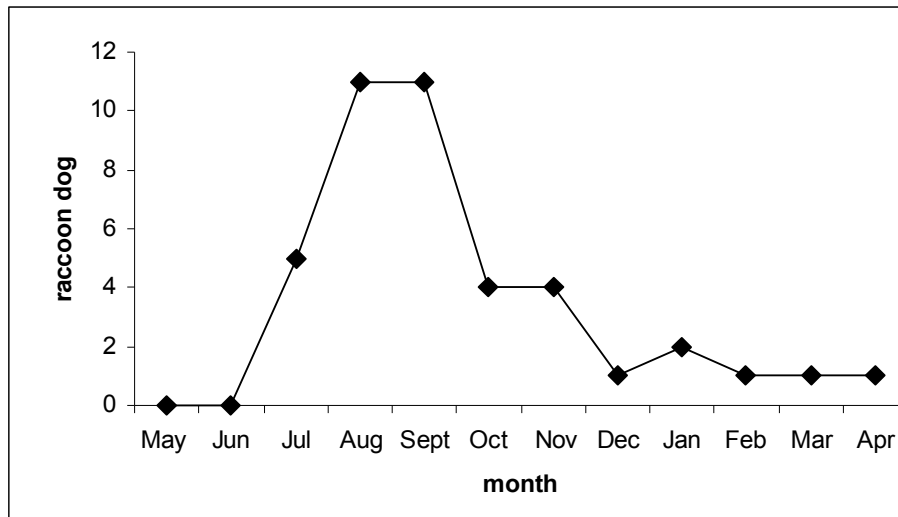


Fig. 16 Month of relocations for young (< one year) raccoon dogs ($n = 41$)

For relocations hunting (55%) and traffic (27%) were the major mortality factors ($\chi^2 = 31.0$; $df = 5$, $p < 0.0001$). 38% raccoon dogs were shot as juveniles and 17% as adults. Whereas, 8% were killed by domestic dog, 2% were recorded with unknown cause of death and from 8% the radio-collar expired after approximately one year.

The direction of straight-line travel for dispersing animals appeared to be random, with distances between 0.5 km to 91.2 km. Littermates may occasionally disperse together or follow similar routes. The parallel progress of filling up the distribution area and expanding into new areas was well founded by flexible dispersal distances and direction (Fig. 17).

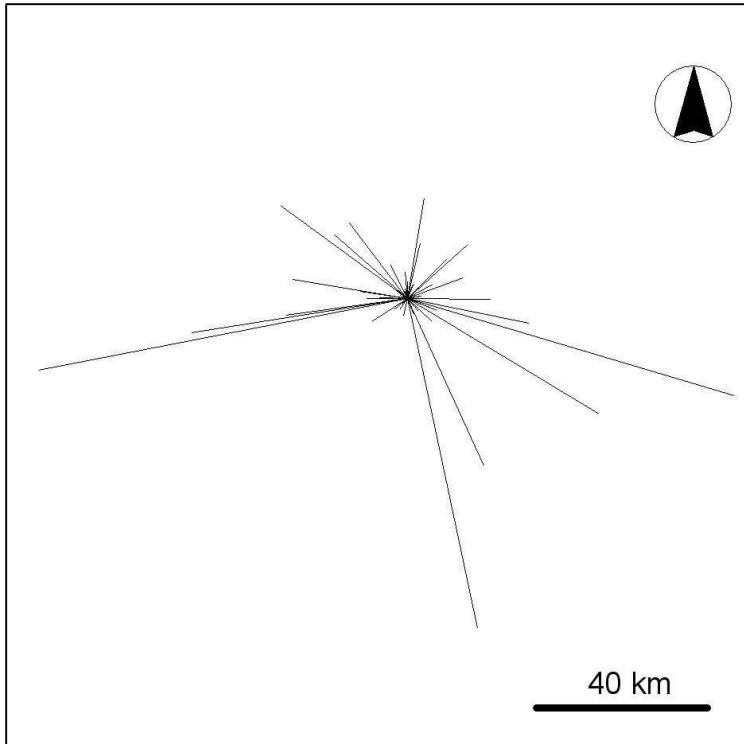


Fig. 17 Dispersal distance and direction of young raccoon dogs ($n = 59$). For simplification, all marking points were standardized to one location

7.2.2 Radio tracking

I gained data for 48 young, radio-collared raccoon dogs. All radio tracked animals displayed exploratory behaviour. Most dispersed between July and September ($\chi^2 = 24.9$; $df = 6$; $p < 0.001$). During winter almost no dispersal was recorded, but in April during the mating season two male 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 of the month dispersal starts (Chi²-test; $\chi^2 = 4.30$; $df = 6$, $p = 0.64$) (Fig 18.)

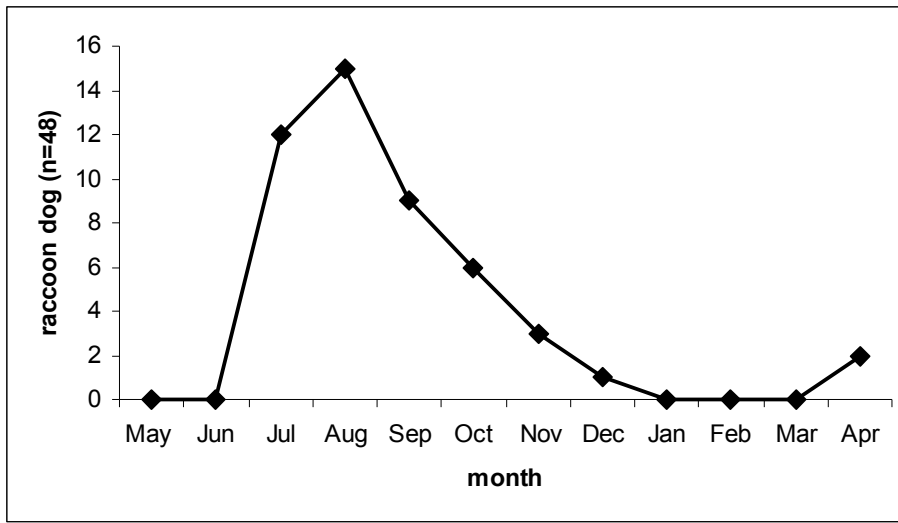


Fig. 18 Month of dispersal for radio-collared young (< one year) raccoon dogs (n = 48)

Juveniles (n = 17) caught in parental home range weighed $1.46 \text{ kg} \pm 0.33$. The mean natal home range size with and without excursions was $502.6 \text{ ha} \pm 66.4$ (n = 9) and $92.1 \text{ ha} \pm 66.4$ (n = 17), respectively.

The radio-collared young raccoon dogs showed a variety of dispersal patterns and the impression of flexible behaviour was confirmed. Some animals literally 'got up and went' one night, others did excursions before dispersing, further ones changed between two areas before they eventually settled down permanently. Some roamed the landscape while others walked in straight line before stopping (Fig 19).

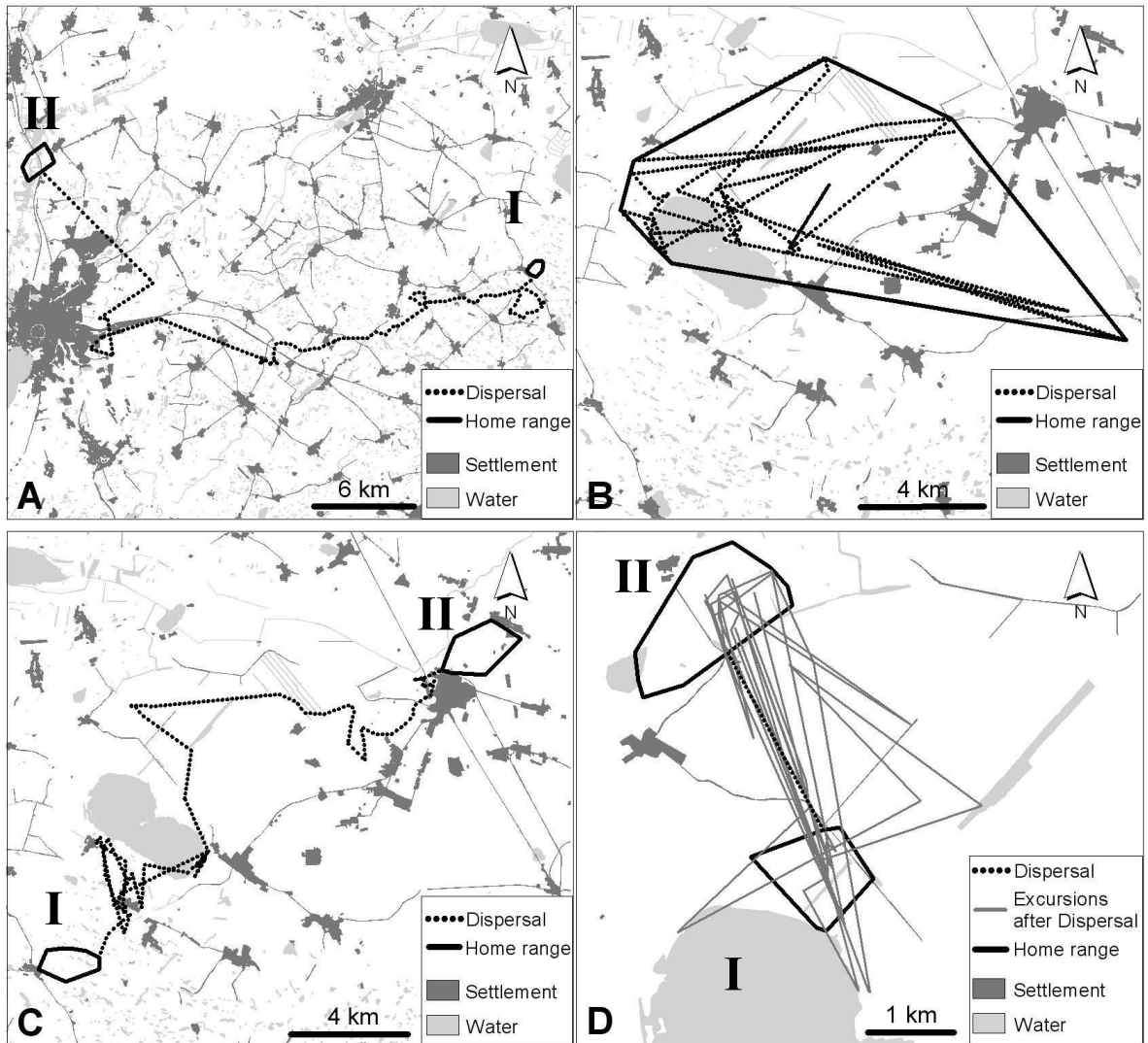


Fig. 19 Examples of home ranges (I natal home range, II temporary range after dispersal; Kernel 100%) and dispersal pattern (line of consecutive locations) for young raccoon dogs. **A** – male left natal area and dispersed 28.5 km as a straight line (58.1 km total distance), in 5 days in August, when it established its home range in a suitable habitat, but might disperse again. The young raccoon dog almost travelled eastwards in a straight line, until the periphery of a larger city where it turned north. **B** – male showed extremely large home-range size (> 15,000 ha) while roaming solitary in search of suitable habitat and paired in its 1st year. The animal lost radio-collar at one year of age and was road killed 1 km out of the displayed range in its 2nd Sept. **C** – female dispersed 16.3 km (47.9 km total distance) in 10 days (Oct./Sept.) from natal home range. The animal was shot in its 1st Jan in the new range. **D** – female showed oscillating motions by gradually extending activities into a neighbouring area, but kept returning to natal home range until August. The animal became resident in close vicinity (3.05 km) with peripheral overlap to parental home ranges. Pair mate and reproduction was recorded in its 2nd year.

7.3 Discussion

7.3.1 Reliability of the method

Capture-mark-relocation data do not show whether any individual raccoon dog has completed its dispersal movement when it is recovered. Furthermore it is a minimum estimate of distance travelled, as movements are often complex.

For the present study analysis the term relocation distance is used to include all relocations, but dispersal only includes those animals known to have settled as an adult resident animal. Thus, herein dispersal distances from young raccoon dogs, killed during dispersal are excluded. Therefore, the mean distance roamed and recorded for resident adult raccoon dog are regard as the most reliable distance of dispersal.

Raccoon dog pups left the breeding den in the 6th week post partum and thereafter roam another few weeks guarded by their parents (KAUHALA et al. 1998a, see also 6.2.1). To improve the data on natal home range size I considered only juveniles (n = 17) weighing less than 2 kg. If we assume the 1st of May as date of parturition for raccoon dogs in Central Europe (NOWAK 1993) these juveniles were at the age of 7.9 ± 1.1 weeks when trapped. Thus, estimated home range sizes are definitely for juveniles prior to dispersal.

Using telemetry, I was at least able to record the month when juveniles (n = 48) started to disperse from the point of capture. For animals showing temporary or stable home-ranges after dispersal, always the last relocation during dispersal was used to determine the month of dispersal. Because raccoon dogs can disperse as late as April in the year after parturition, I can not rule out a bias towards early dispersers.

7.3.2 Dispersal

This work represents the first quantified and comprehensive data on dispersal of the raccoon dog in Central Europe and is therefore of great value to specify and forecast the species population dynamic. Previously, there has been only a single study in Germany that has examined dispersal in raccoon dogs and the number of dispersal

events recorded was rather small ($n = 11$) (SUTOR 2007). Therefore, information about dispersal distances and direction, relocation distances, date of dispersal, both for male and female raccoon dogs are crucial to predict the ability of this invasive species to expand further.

All marked young raccoon dogs dispersed from their natal areas and some (8.5%) travel considerable distances (> 50 km) before settling. In a study from Southern Finland 17% of juveniles dispersed more than 40 km (KAUHALA & HELLE 1994). In Europe “long distance runners” in western direction are responsible for first records in the new distribution area. 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 continues to disperse. These data illustrate the ability of this medium-sized canid to reach areas far away in a relatively short time, which contributes to the raccoon dog’s fast expansion.

However, for most young raccoon dogs (55.9%) relocations were reported close (< 5 km) to their natal home range. This is comparable to the study from KAUHALA et al. (1993a), where 50% of relocations for juveniles were made within a radius of 5 km. Also in Southern-Brandenburg (Eastern Germany) three raccoon dogs, ear tagged as juveniles were discovered again quite near at their marking place after one year (SUTOR 2007).

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 belongs to the distribution area of the raccoon dog. The most western edge of distribution is currently Lower-Saxony and Saxony-Anhalt with 464 and 287 records in the hunting season 2005/2006, respectively. Nevertheless, there are single reports from Bavaria (21), Thuringia (56), Hessen (13) and North Rhine-Westphalia (11) (Deutscher Jagdschutz Verband 2007). Additionally first records from Denmark, the Netherlands, France, Switzerland, Austria and the Republic of Macedonia are reported (KAUHALA & SAEKI 2004a, CIROVIC’ 2006).

According to (KNOWLTON et al. 1999) increased mortality is often associated with dispersal as animals move into unfamiliar areas and low-security habitats. I assume

that survival and reproductive success is highest for raccoon dogs with short dispersal distances because a higher dispersal-mortality is likely during long migrations.

Because of a high mortality rate (69.5%) among juveniles and a high reproduction potential (nine pups in average, BOGE 2006) raccoon dogs appear to be relatively *r*-selected in Central Europe which clearly is supporting the further expansion. These results coincide with a study from Finland were: 1) the species spread through the southern and central parts in about two decades since the mid-1950s, 2) 88% of juveniles died in their first year, 3) mean litter size was nine, 4) the population reached its carrying capacity circa 30 years after the first regular records (HELLE & KAUFHALA 1991, 1993, 1995; KAUFHALA 1992).

There are continuous observations since the beginning of the 1990s in Eastern Germany. Thus, considering the results from Finland, I believe that the carrying capacity of the environment will be reached approx. in the 2020s. However, because environmental conditions in Scandinavia differ from those in North-Eastern Germany, the Finnish results may not be self-evidently applied to German raccoon dogs and the peak of population density may even be reached later.

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, prevent 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 (see 4.3.3) juveniles are most probably not pushed out of the 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 (SIDOROVICH et al. 2008). For this reason there is no need for long dispersal distances. Hence, the search for a partner is probable the main reason for long dispersal distances in the raccoon dog in general.

There seems to be no consistent pattern in dispersal distance or direction and young raccoon dogs of both sexes disperse equal distances. A common behaviour was dispersal via one or more temporary home ranges until a definite home range was

established. Others, over a long period gradually extended activities into neighbouring areas before settling in the vicinity of their natal home range. This is reflected in a small natal home range sizes but large temporal home range sizes including excursions into neighbouring areas. On the other hand some juveniles suddenly left their natal home range and never returned. Another dispersal-pattern showed by juveniles, was roaming as a pair or alone in comparable large areas before settling.

Also in the red foxes a common pattern was dispersal through one or more temporary home ranges. From these temporary ranges the fox kept making exploratory trips, often progressively further and partly along routes taken earlier, until a definite territory was established (MULDER 1985). In doing so 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 (KAUHALA & SAEKI 2004a). In the present study most relocations and month of dispersal for young raccoon dogs were recorded between July and September. Thus, raccoon dogs usually disperse before they reach sexual maturity in the age of 3 to 5 months in Central Europe.

Current population densities of 0.95 animals/km² (see 4.2.1 / Kernel 95 utilisation) is 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 possibly recorded, because roaming animals tried to find a partner in raccoon dog free areas, and thus did not settle.

The mean dispersal distances were estimated to 19 km for males and 14 km for females in Finland (KAUHALA et al. 2006). According to the same method (TREWHELLA et al. 1988) males (17.0 km) and females (14.0 km) dispersed almost identical distances in North-Eastern Germany. All these data concur with the most reliable; mean dispersal distance (17.8 km) for raccoon dogs, recovered as resident adults in the present study.

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).

In the red foxes, because of high 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 (ALLEN & SARGEANT 1993, MACDONALD & JOHNSON 2000). Furthermore, in foxes males typically disperse further than females (e.g., males 13.7km, females 2.3km in Welsh hills; LLOYD 1980), whereas in the present racoon dog study juveniles of both sexes disperse and no bias towards males was recorded.

Raccoon dogs have a monogamous social system with bi-parental care, large home-range overlap without defending an exclusive territory (KAUHALA et al. 1998a, see also 4.2.1). Moreover, in contrast to the red fox 'helpers' have not been observed (KAUHALA & SAEKI 2004a). Young racoon dogs most likely do not remain in parental home range because they would only use resources without supporting the reproduction success of the breeding pair. Consequently I assume that in racoon dogs, dispersal distance is strongly influenced by innate species traits that prompted the animals to travel a set distance before stopping, or by habitat features, or both.

It can be concluded that racoon dogs as flexible disperser, in anthropogenic landscape such as Central Europe should do well in the next decades.

8. Discussion - Assessment and Conclusions

8.1 Prognosis of further expansion

The raccoon dog spread fast from the places of introductions to the neighbouring countries. Today it is common in North-Western parts of Russia, Finland, the Baltic states, Belarus, Ukraine, Moldova, Poland, Hungary, Slovakia, Czech Republic, Romania, Bulgaria, Serbia and Germany, and it is occasionally seen in Norway, Sweden, Denmark, the Netherlands, France, Switzerland, Austria, Slovenia, Bosnia, Macedonia and Italy (CIROVIC´ 2006, KAUHALA & SAEKI 2004b, KAUHALA 2008).

According to the general trend of range extension of the raccoon dog across the European continent during the 20th century, an expansion of the species' range into Western and Southern Europe is expected. In Poland only the highest mountains in the South (Carpathians) are not occupied (KOWALCZYK 2008). According to (Nowak 1984) the raccoon dog inhabits highlands up to 800 m a.s.l. However tracks were frequently found at approx. 2000 m a.s.l. in the Caucasian Mountains (Kaukasky Zapovednik, Russia) (pers. obs.).

In Germany the population is growing very fast and still expanding its range westwards and southwards. Genetic analysis showed a close relationship between German, Finnish and Estonian individuals and confirmed that Germany was colonized from Finland along the Baltic Sea coastline (SCHWARZ et al. 2004). Recently, the species has even managed to cross the Alps and the first individuals have been observed in Northern Italy (KAUHALA 2008). Previous data from Poland showed that the expansion process is not always through a broad line. First isolated "population-islands" can even be a few hundred km apart from the real distribution area. This "island" will then be connect to the main population through dispersal of juveniles in all direction (NOWAK & PIELOWSKI 1964). Dispersal in a sun-ray pattern is also confirmed for the present study.

In southern Finland the mean dispersal distances are 14-19 km (KAUHALA et al. 2006), which is almost identical to the mean dispersal distances of 17.8 ± 23.4 km in the present study. However, regular observations of raccoon dogs for Finland and North-Eastern Germany were in the mid-50s and early-90s of the last century,

respectively. Thus, these estimates represent dispersal distances for areas where the invasion process is most probably completed.

“Long distance runners” are responsible for the colonisation of new areas in Europe. An ear-tagged individual in Russia was found to disperse 700 km in 6 years (NOWAK 1973) and for Poland; there are single reports of dispersal distances from 135 – 300 km in one year (NOWAK & PIELOWSKI 1964). In Finland raccoon dogs sometimes disperse > 200 km (KAUHALA 2008). The maximum dispersal distance in this study was 91.2 km and SUTOR (2007) recorded three dispersal distances from 80 – 100 km for raccoon dogs in Eastern Germany. Present data indicate that raccoon dogs dispersed from their natal areas while most probably trying to find a pair mate and thus continue to disperse. This is a common behaviour among canids, e.g. red foxes and wolves (*Canis lupus*) also migrate remarkable long distances while searching for a mate (HARRIS & TREWHELLA 1988, KOJOLA et al. 2006).

Dispersal distance usually correlates positively with the home range size. Thus, in areas with large home ranges and sparse population, dispersal distances are the longest, whereas in areas with high population density and small home ranges, dispersal distances are short. Furthermore in a colonizing population single individuals may disperse very far (i.e. around sub-optimal, urban areas in Western Germany). All these data illustrate the ability of the medium-sized raccoon dog to reach areas far away in a relatively short time, which contributes to the fast expansion.

The distribution area of the raccoon dog is mainly determined by climate. The longer the growing season, the better the raccoon dog manages (HELLE & KAUHALA 1991). In the former Soviet Union (Fare East), the distribution and density of the raccoon dog depends on the length of snow-free and frost-free periods (JUDIN1977), because long and harsh winters and a thick snow cover prevent the species from spreading further, northwards. The raccoon dog is the only canid that can hibernate. It spends the winter sleeping in its den in areas with harsh winters, because it has difficulties in moving and finding food in deep snow. It accumulates large fat reserves in late summer and autumn to survive the winter (KAUHALA et al. 1993b). In Finland animals usually stayed in their dens, when temperature was below -10 °C, snow depth > 35

cm and day length < 7 h. They were moving around, when temperature was >0°C, there was no snow and day length was >10h. Day length and snow depth together predicted rather well the probability of animals being active during winter (KAUHALA et al. 2006). The winter sleep makes it possible for the raccoon dogs to survive in northern areas or in harsh, extremely arid, continental climate. E.g. Eastern Mongolian with hot (35°C) summers and long (6 month) cold (-45°C) winters.

In Finland raccoon dogs stayed usually in their dens in mid-winter (December-February) but were sometimes wandering around also during the harshest months of the year and changed their winter den on average three times. Both day length and weather affected the activity of raccoon dogs in winter (KAUHALA et al. 2006).

Mean home ranges sizes of 649.9 ha from November until February in North-Eastern Germany indicate that, due to the temperate climate (mean temperature: 0.2°C in January between 2004 and 2006; German Weather Service/Laage, 2008), raccoon dogs do not hibernate in Germany. It is assumed, that juvenile and adult raccoon dogs can accumulate enough fat reserves until October to survive the winter. They even do not need to undergo winter dormancy, and just reduce their activity and home range size (see also 4.2.1; Tab.1). Thus, their energy demands in winter are low and they rely entirely on stored fat reserves. Consequently, raccoon dog females are in good conditions still in March (mating period) regardless of the weather and food availability during the winter, and they are able to invest heavily in reproduction (9 pups in average / BOGE 2006).

Climate also causes regional variation in the population density, because primary production, and hence the abundance of food is greatly affected by climate (CLUTTON-BROCK & HARVEY 1978). For the native distribution area (Far East Russia with severe winters) 0.34 ind./ km² are reported (BANNIKOV 1964). In areas where the climate is mild, the productivity of the environment is higher than in more northern areas and hence is the population density of the raccoon dog (HELLE & KAUHALA 1995). E.g. in southern Finland, the density is today > 0.75 ind./km² and can reach 1.5 ind./km² in optimal habitats. In central Finland the density is 0.2-0.5 ind./ km² and in the northern parts of the country < 0.2 ind./km² (KAUHALA 2007; KAUHALA 2008). The productivity of the population is highest in the southern and lowest in the

northern provinces of Finland (HELLE & KAUALA 1995). Ten years ago the calculated population density in North-Eastern Poland was 0.37 (GOSZCZYNSKI 1999) and has reached at present 0.7 ind./km² in the Bialowieza forest (KOWALCZYK 2008). Data from Eastern Germany absolutely confirm the increasing population density. STIEBLING (1999) calculated 0.12 - 0.22 ind./km² approx. ten years ago in Brandenburg and at present the population density is between 0.95 – 1.24 ind./km² in Mecklenburg-Vorpommern (present study, ZOLLER & DRYGALA unpubl.). It can be concluded that, regarding the highest density (1.5 ind./km²) in Southern Finland, a further increase in population density is expected for North-Eastern Germany (Tab. 4). Moreover, the combination of weak, intraspecific population pressure due to underdeveloped territoriality, carried out in the present study may facilitate a high population density throughout Central Europe.

Tab. 4 Population densities of the raccoon dog in different areas

density (ind./km ²)	area	season	method	reference
0.34	Fare East Russia	-	den estimation	BANNIKOV 1964
0.37	North-Eastern Poland	spring	den estimation/ snow tracking	GOSZCZYNSKI 1999
0.7	Eastern Poland Bialowieza	-	-	KOWALCZYK 2008
0.12- 0.22	Eastern Germany Brandenburg	spring	den estimation/ hunting bags	STIEBLING et al. 1999
1.24	Germany Mecklenburg/ Vorpommern (study area "Penzin")	mean all (adults only)	home-range estimation	ZOLLER & DRYGALA unpubl.
0.95	Germany Mecklenburg/ Vorpommern (study area "Galenbeck")	spring (adults only)	home-range estimation	present study
0.77 - 1.5 (optimal habitats)	South Finland	spring	home-range estimation	KAUHALA et al. 2006 KAUHALA 2008
0.2-0.5	Central Finland	-	home-range estimation	KAUHALA 2008
< 0.2	Northern Finland	-	home-range estimation	KAUHALA 2008

In Russia, the raccoon dog is frequently found near water or in damp meadows, swamp and alluvial soil (NASIMOVOIC & ISAKOV 1985) and it prefers moist deciduous forests with abundant undergrowth in the Ukraine (WOLOCH & ROZENKO 2007). In Finland it favors wetlands, shore areas, old moist heaths (KAUHALA 1996b) and also lives in coniferous forests, although coniferous forest is not an ideal habitat. Home range size correlates negatively with the proportion of deciduous forest and positively with that of pine forest in the home range (KAUHALA 2008).

The present study indicates that raccoon dog population also can persist in agricultural habitats with a large amount of open landscape. In such areas, raccoon dogs prefer small woods, hedges, and crop fields only to a slightly higher degree than do animals that primarily use forest covered areas. Thus, habitat composition seems to have no significant effect on the species abundance. This opportunistic and flexible habitat use is most probably decisive to ensure the further invasion to e.g. the Netherlands, Denmark and France.

Raccoon dogs have a very high reproductive potential which supports the fast expansion in Europe. The mean litter size is 9 pups in southern Finland and Eastern Germany (HELLE & KAUHALA 1995, BOGE 2006). Large litters have been found also in the original distribution area in South-East Russia (JUDIN 1977). Besides, the status of the population may also affect the reproductive strategy of individuals, e.g. expanding populations may display higher productivity than other populations of the species (WESTERN 1979).

The high mortality rate of juvenile raccoon dogs (69.5%) in North-Eastern Germany reflects the high proportion of juveniles in the population. This is basically a consequence of the high reproductive potential of the species, but also may be affected indirectly by high hunting pressure. If the population density is pressed under the carrying capacity of the environment by high hunting pressure, intraspecific competition between females is reduced and productivity may increase, because there are fewer females to share the resources. Thus, the more they are hunted, the larger litters they have. It is difficult to control the raccoon dog population due to the high reproductive potential of raccoon dogs and their tendency to disperse far. To be effective the hunting pressure should be so high that – in spite of the increased litter

size – the breeding population would decline. The practice of moderate hunting pressure in Germany just ensures that the reproduction rate is high and the population is healthy and viable. Hunting should also take place in a large area and from year to year, otherwise the population will recover quickly. In Finland, the hunting bag has increased during the last decade in spite of several campaigns arranged to control small predators. About 50% of the autumn population is hunted each year (KAUHALA 2007). In the present study hunting (55 %) was the major mortality factor and it is most likely that, the population is still increasing in North-Eastern Germany and expanding further to South and West, anyway.

Traffic (27 %) was the second important mortality factor in Mecklenburg-Vorpommern. Regarding the low developed road network in North-Eastern Germany, compared to Western and Southern Germany, a percentage increase in roadkills is probable in the future. However, in Japan 110.000 – 370.000 raccoon dogs are killed each year and the number of roadkills increases as traffic volume increases. There was no evidence that the rate of roadkills was declining as traffic density increased, as would be expected if this mortality was having an effect on population size (SAEKI & MACDONALD 2003). These results indicate that also dense traffic will have no significant impact on the fast growing population in Europe.

Furthermore the almost complete lack of effective natural predators in Central and South Europe is surely facilitating the further expansion of the raccoon dog. Only domestic dog, red fox, badger, white tail eagle and Goshawk (*Accipiter gentilis*) might have a slight impact on the population (esp. on juveniles). Against predation from red fox and badger on raccoon dog pups, the monogamous social system with intensive share of labor between pair mates ensures that the pups always guarded by one parent (mostly the male) in their first two months after birth. Raccoon dogs are absolutely able to chase a badger away from the breeding den (pers. obs. through video recording).

8.2 Competition with other semi-sized carnivores

The raccoon dog potentially competes with the native red fox and badger throughout Europe. Additionally there might be competition with the introduced raccoon in Germany, France and various parts of the former Soviet Union (e.g. Caucasus) (NOWAK 1999). In general, competition for food between the species is eased by their omnivorous character and by dietary differences (VIRO & MIKKOLA 1981).

Raccoon dogs, badgers and red foxes are partly sympatric in the original distribution area (Far East Russia). Hence, they may have adapted to coexistence with the other carnivores, which may reduce competition.

In Northern Belarus, the native, generalist predator populations began to decline after the raccoon dog reached a high population density. Competition with in particular polecat (*Mustela putorius* L. 1758) but also to lesser degree, red fox and pine marten (*Martes martes* L. 1758) on carcasses in winter was proposed as a factor in the observed decline (SIDOROVICH 2000). In contrast, a rapid raccoon dog population increase during the 1970s and 1980s coincided with a badger population increase in Finland (Kauhala 1995). This may lead to the conclusion that no cruel competition takes place between the badger and the raccoon dog in Finland and thus, most probably also in Central Europe. Furthermore, one of the reasons behind the expansion of badger distribution in Scandinavia may have been warming of the climate and lengthening of the growing season (BEVANGER & LINDSTROEM 1995). Also no evidence of negative impact of the raccoon dog on native predators was reported in Poland (KOWALCZYK 2008).

However, within areas where raccoon dog density is high, raccoon dogs may compete with badgers for the best habitat patches. Preliminary results from the South-West coast of Finland indicate that both, badgers and raccoon dogs prefer deciduous forests. Both species avoid fields, but the use of all other habitats differs between the species: when one of them prefers, the other one avoids a certain habitat type. In another area with lower raccoon dog density the habitat preferences of both species were very similar, indicating that competition may occur in an area with very high raccoon dog density (KAUHALA 2008).

In Northern Europe (Scandinavia) and North-Eastern Europe (Russia, Belarus, Eastern Poland), winter is the critical season when food is scarce and competition most severe, therefore raccoon dogs and badgers are dormant in winter; this probably prevents them from competing severely with each other and with the red fox. In contrast, in the temperate climate of Central Europe all omnivore, semi-sized predators face no bottleneck in terms of food availability in winter. E.g. rodents, carrion (esp. innards from game), vegetable matter (fruits, maize from bait stations) are supposed to be abundant.

The diet of the raccoon dog, the badger and the raccoon is quite similar. However, only minor competition is assumed since some differences in diet do exist: the badger consumes more invertebrates (esp. earthworms *Lumbricus spec.* L. 1758) and the raccoon more invertebrates and less carrion than the raccoon dog. Furthermore, the arboreal habits and different food intake (e.g. groping for food items) of the raccoon makes a severe competition with the raccoon dog most unlikely (CLARK 2001, DRYGALA et al. 2002, HOHMANN & BARTUSSEK 2001, KOWALCZYK 2003, SCHWAN 2004). All three species are able to store fat reserves in autumn and need minor food intake from approx. November – March. Hence, these opportunists neither do compete significantly for food during the most critical season nor during the vegetation period, when food is abundant.

The red fox is a more active predator and consumes more vertebrates prey (mammals and birds), whereas the raccoon dog feeds more frequently on shrews, invertebrates, carrion and plants (KAUHALA 1996c, KAUHALA et al. 1998b, WERNER 2007). It has, as a successful generalist and opportunist the largest distribution range of all canids and is adapted to a high variety of habitats (from arctic to subtropical regions) (NOVAK 1999). Therefore it is evolved to concur with a large number of different predators and i.e. also with the raccoon dog.

According to HEPTNER & NAUMOV (1974) red foxes predate on juvenile raccoon dogs and there were also cases where raccoon dogs were killed by foxes and badgers in the den. Predation from red fox on juvenile raccoon dogs was also recorded for the present study. Moreover, an adult female raccoon dog was deadly injured on the back part, most probably through badger bites in the den (pers. obs.).

Indirect competition may take place as raccoon dogs often use burrows that were dug by foxes or badgers (YAMAMOTO 1994). In Poland raccoon dogs usually settled in nonnative badger dens (12.9% of cases) for wintering and/or reproduction. Joint utilization of setts by badgers and raccoon dogs was observed in 5.3 % of cases (KOWALCZYK 2002). For the present study one large badger sett (breeding den / pair 2, Fig.3) was used for pup-rearing and as a winter den from both species in consecutive years, without signs of competition. The raccoon dog regularly uses dens from red fox and badger, often in the close vicinity to the other predators, without obvious intraspecific, negative impact (KOWALCZYK 2002, pers. obs.).

However, it is suggested that raccoon dogs predate on badger cubs which are left alone by parents, while raccoon dogs always guard their cubs (KOWALCZYK 2008). Red foxes are, different to badgers strictly related to the den only during pup-rearing and can dig a breeding den in suitable soil, in just one – two nights (pers. obs). Furthermore, STIER (2007) believes that only 10% of existing dens are used by badger, red fox and raccoon dog in Northeastern Germany. In general, this makes, a stiff competition for dens among this three, ground dwelling, semi-sized carnivores very unlikely. Competition between the clumsy raccoon dog and the more arboreal raccoon for breeding dens and sleeping places can be excluded (KOEHNEMANN 2007).

It can be concluded, that competition between raccoon dog, raccoon, red fox and badger might take place in Central-Europe, but it is unlikely that it is very severe leading to the significant decrease of either of the species.

8.3 Predation on native species

Raccoon dogs are slow and clumsy, have small canine and carnassial teeth and a long intestine (NOVAK 1993). All these are features of omnivore – not carnivore – mammals.

The diversity and composition of food items indicates that it is more of a scavenger and gatherer than an active predator (KAUHALA et al. 1993b, DRYGALA et al. 2002, SUTOR 2005, SCHWAN 2004, WERNER 2007, SIEGERT 2007). Moreover, it is a true omnivore, eating anything it can find and catch (e.g. IKEDA 1985, NASIMOVIC & ISAKOV 1985, KAUHALA et al. 1998b, KAUHALA & AUNIOLA 2001, BALTRUNAITE 2002, 2003, WOLOCH & ROZENKO 2007, SIDOROVICH et al. 2000, 2008) and the generalistic diet certainly promotes its colonizing of new ranges.

Stomachs analyses (n = 79) from Eastern Germany (Brandenburg) indicate that plants (75.5%), insects (67.7%), small mammals (41.0%), and carrion (35.1%; mostly guts from hunting bags) were most frequently consumed. Other common food items included amphibians (15.6%) and birds (esp. Passeriformes; 23.3%) (DRYGALA et al. 2000). Scat analyses (n = 684) from the study area “Galenbeck” (Mecklenburg-Vorpommern, see also Fig. 1) show that mainly small rodents and shrews (35.3 % biomass) and plants (33.5 %; mostly maize (*Zea mays*) and fruits) were the important food sources for raccoon dogs. Amphibians and birds were consumed to 8.0% and 4.6% biomass share, respectively (SIEGERT 2007). Because fruits and cereals (e.g. maize) are an important source of carbohydrate in the diet of the raccoon dog, and carbohydrates can be used to synthesize fats (MAYNARD & LOOSLI 1969), the availability of plants affects the amount of fat reserves during winter. These results completely confirm those of other studies, i.e. the raccoon dog is omnivorous and the food composition varies somewhat with the area.

However, small mammals and plants seem to be among the commonly consumed food items in most of the distribution range (BANNIKOV 1964). Frogs are also an important prey in some areas (BARBU 1972, VIRO & MIKKOLA 1981). E.g. in Finland the diet mainly consisted of small mammals (in 64.3% of the stomachs), plants (60.7%) and amphibians (50.0%) during the snowless period of the year. In winter carcasses

(92.9%), small mammals (50.0%) and plants (42.9%) were the most frequently eaten (KAUHALA et al 1993b). Therefore the raccoon dog is considered as a true omnivore. The availability of different food items affects both seasonal and annual composition and diversity of the diet. Hence, the raccoon dog probably does not have strong preference for any food items, except possibly small mammals and vegetable matter (KAUHALA et al. 1993b, VIRO & MIKKOLA 1981). The Finish study (KAUHALA et al. 1993b) provides no evidence that the raccoon dog is highly harmful to game bird populations. However, there were some remains of waterfowl in the scats, so the raccoon dogs may have killed incubating females, because they are most likely unable to catch other healthy birds. In a study from Eastern-Germany, based on the analyses of 70 raccoon dog stomachs only 4.8% contained birds (SUTOR 2005) and for the area of the present study ("Galenbeck") 13.3 % of the raccoon dog scats contained birds (SIEGERT 2007).

There is not much knowledge of egg predation by the raccoon dog, in general. However, pers. obs. on a captive animal indicate, that raccoon dogs usually do not take in egg shells from domestic chicken (*Gallus gallus domesticus* L. 1758) and quail (*Coturnix coturnix* L. 1758) accidentally when eating eggs. Furthermore, egg shells from domestic fowl, feed with scrambled meet is not digestible by raccoon dogs. I.e. that diet analyses, estimated through stomach or scat analyses may under represent the amount of eggs consumed and thus bias towards the predation pressure on ground nesting birds.

Raccoon dogs have caused damage to waterfowl colonies in Estonia. In some areas raccoon dogs robbed up to 85% of the nests. In a reserve area at the seashore, birds occurred in 31% and egg shells in 33% of the scats in spring (NAABER 1971, 1984). IVANOVA (1962) found remains of birds (mainly waterfowl) in 45% of the faeces collected in a river valley in European Russia.

However, excluding waterfowl colonies, the raccoon dog seems to be rather harmless to game birds: in Finland only 1% of the raccoon dog faeces collected in May and June contained remains of gallinaceous birds (KAUHALA et al. 1993b).

In Poland, REIG & JEDRZEJEWSKI (1988) found that while the red fox frequently prey on birds, the raccoon dog does so only occasionally. NAABER (1971) concluded that

raccoon dogs are not harmful to grouse or hare populations in Estonia. In Latvia, a study of natural duck nests destroyed by predators revealed that the most important predator was the marsh harrier (*Circus aeruginosus* L.) destroying 54% of the depredated nests (OPERMANIS et al. 2001). The study was carried out in a wetland area and lasted for 13 years. It included > 1000 destroyed nests. Corvids and the American mink (*Mustela vison* SCHREBER 1777) were among the important predators, whereas raccoon dogs destroyed only 0.6% of the depredated nests. In contrast, recently published data indicate that the main biomass share (24.8%) of raccoon dog diet in Northern Belarus were birds and their eggs (SIDOROVICH 2008).

Nevertheless, in general it is assumed that, the raccoon dog does not impact game animal populations, including Gallinaceous birds, waterfowl, and hares. E.g. in a predator removal study (Finland), no impact of the elimination of red fox, raccoon dog, pine martens and stoat (*Mustela erminea* L. 1758) on mountain hare (*Lepus timidus* L. 1758) were evident, and trends in hare populations were similar in predator removal and -protection areas (KAUHALA et al 1999). In fact, the raccoon dog is very clumsy and most probably has great difficulties in catching an adult bird or hare.

In another predator removal/protection study from Southern Finland 280 raccoon dogs, 49 red foxes and 40 pine martens were removed from a 55 km² area and compared with a 48 km² protection area. Predator removal/protection affected the reproductive success of grouse, but the impact of control on adult grouse population (black grouse / *Tetrao tetrix* L. 1758 and capercaillie / *T. urogallus* L. 1758) was not evident (KAUHALA et al. 2000).

In a third predator removal study in Southern Finland, the breeding success of ducks decreased in the predator removal area during the 4th and 5th year of removal. Most removed predators were raccoon dogs but also some red foxes, pine martens and American minks were removed. The raccoon dog population started to decrease after 3 years of removal. At the same time, the fox population started to increase. Thus, there was a positive correlation between the breeding success of ducks and raccoon dog abundance but a negative correlation between the breeding success of ducks and fox abundance. This point to the conclusion, that the interactions between the

predators – raccoon dog and fox – played an important role in this area (KAUHALA 2004).

Raccoon dogs may, especially on small islands, threaten frog populations. Frogs have vanished from some islands of the southwest coast of Finland after raccoon dogs arrived in the 1970s, but frog populations have not declined on the outer islands where raccoon dogs are not found (KAUHALA 1996a). It is also imaginable, that future high population density of raccoon dog can have a negative impact on the endangered moor frog populations (*Rana arvalis* NILSSON 1842) in Central-, West- and South Germany, which may even lead to local extinction. Furthermore, a high predation pressure on grass snakes was evident for the present study area (see also Tab. 3).

Raccoon dogs are scavengers and can relay on carrion to high amounts depending on the season. E.g. from late November to April ungulate carcasses (55.1 % biomass share) were the main food in Northern Belarus (SIDOROVICH 2008). Raccoon dogs in Poland (Bialowieza) scavenge in 50% of all available ungulate carcasses (KOWALCZYK 2008) and in North-Eastern Germany (Mecklenburg-Vorpommern) the mean biomass share of carrion was 31.86 % in winter (WERNER 2007). The high availability of carrion, through hunting (esp. guts of hunting bags) and roadkills may reduce the predation pressure on native species and surely supports the further expansion throughout Central-Europe.

In conclusion, the principle prey of the raccoon dog in many areas is, however, small rodents (e.g. NAABER 1974, KAUHALA et al. 1993b, DRYGALA et al. 2000, SCHWAN 2004, SUTOR 2005, SIEGERT 2007). Thus, the raccoon dog may be locally (mainly on islands or for isolated populations) harmful to native birds and frogs, but most probably its overall impact on native fauna is insignificant.

8.4 Spread of zoonosis and diseases

During recent years the role of the raccoon dog as a vector of rabies has increased in northeast Europe and today it is a more common victim as the red fox, at least in Estonia (WHO 2004). Current studies about rabies in Europe indicate a high risk of distribution of this disease by dispersing juveniles, both 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 dispersed (KAUHALA et al. 1993a, KAUHALA et al. 2006, KAUHALA et al. 2007). Because of oral vaccination there were only 12 records for rabies in 2004 for Germany (<http://de.wikipedia.org/wiki/Tollwut#Deutschland>). Regarding open borders and uncontrolled transmission of pets (esp. 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. Scavenging on red foxes and badgers may also facilitate the spread of the disease. Moreover, raccoon dogs are potential vectors of *Echinococcus multilocularis*, a tapeworm that also infects humans. Unlike rabies, which is transmitted in direct contact, *E. multilocularis* 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, intraspecific infection is likely. Thus, the raccoon dog is an important reservoir and vector of this dangerous zoonosis and an expansion of risk areas are probable. Raccoon dogs are also known to be infected by *Trichinella* sp. (L.). In Finland 72% of the examined adult males and 53% of adult females were infected (Mikkonen et al. 1995) and in Eastern Germany (Brandenburg) 5.8% of examined raccoon dogs were contaminated (THIES 2004). Raccoon dogs face a serious problem with infestation of scabies or sarcoptic mange (*Sarcoptes scabies* L. 1758), which seems to be widespread in many parts of Japan and Europe (KAUHALA K. & SAEKI M. 2004a; SHIBATA & KAWAMICHI 1999, pers. obs.). Mass deaths of the infested animals can occur in winter but raccoon dogs may also

recover from the disease in Japan (M. SAEKI, IUCN/SSC Canid Specialist Group, pers. comm.).

In England, where there is no rabies, like in Central and Western Europe (due to bait vaccination), mange is the most important regulative factor of the fox population (HARRIS & BAKER 2001). Due to a supposed dense population, the raccoon dog will most probably play an important part for the spread of the disease in the future.

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10. Zusammenfassung (German Summary)

Zwischen Oktober 1999 und Oktober 2003 wurden 30 Adulte und 48 „junge“ (< ein Jahr) Marderhunde (*Nyctereutes procyonoides* GRAY 1834) in einem Gebiet in Nord-Ostdeutschland (Mecklenburg-Vorpommern) telemetrisch untersucht, dass seit Anfang der 1990er Jahre von der invasiven Art besiedelt wird. Zusätzlich wurden 2003, in den ersten sechs Wochen nach der Geburt der Welpen drei Marderhundpaare mittels 24 Stunden Peilserien überwacht. Weiterhin konnten zwischen Juni 1999 und August 2006 136 Marderhundwelpen mit Ohrmarken versehen werden.

Während des gesamten Untersuchungszeitraumes wanderten keine Alttiere aus dem Untersuchungsgebiet ab und die Aktionsräume wurden über lange Zeiträume, (vermutlich lebenslang) genutzt. Die mit dem Kernel 95% berechnete, durchschnittliche Aktionsraumgröße war $382,2 \text{ ha} \pm 297,4 \text{ SD}$ für Fähen ($n = 30$ saisonale Aktionsräume) und $352,4 \text{ ha} \pm 313,3 \text{ SD}$ für Rüden ($n = 32$ saisonale Aktionsräume). Verpaarte Tiere beliefen Aktionsräume von identischer Größe, wobei die Partner dieselben Flächen im gesamten Jahresverlauf nutzten.

Die großen Kernzonen (Kernel 85%) bedeckten 81,2% des Gesamtaktionsraumes. In der Paarungszeit hatten die Aktionsräume ihre geringste Ausdehnung. Die etwas größeren Aktionsräume im Winter deuten darauf hin, dass Marderhunde in Deutschland keine Winterruhe halten. Rüden und Fähen zeigten eine lang anhaltende (vermutlich lebenslange) Paarbildung.

Gleichgeschlechtliche Nachbarn ignorierten einander und sogar angrenzende Rüden / Fähen zeigten weder Präferenz noch Meidung. Daher kann, auf der Grundlage der Analyse von Aktionsraumüberlappungen und der Berechnung von Interaktionen angenommen werden, dass der Marderhund in Mitteleuropa monogam ist, ohne exklusive Territorien zu bilden.

Die Habitatzusammensetzung innerhalb der Aktionsräume und des gesamten Untersuchungsgebietes war nahezu identisch. Jedoch war innerhalb der

Aktionsräume der prozentuale Anteil von Ackerland 16,35% geringer und von Weideland 12,06% höher. Alle neun Habitatkategorien (Ackerland, Wald, Siedlung, Wasser, Weideland, Maisfelder, Feldgehölze, Schilf und Hecken) wurden opportunistisch genutzt. Zwischen den Jahreszeiten zeigten Marderhunde keine signifikant unterschiedlichen Habitatpräferenzen. Das Habitatpräferenzmuster weiblicher und männlicher Marderhunde war identisch. Ein Vergleich der Peilungen von aktiven und inaktiven Tieren in den jeweiligen Habitaten wies keine bemerkbaren Unterschiede auf. Die Habitatzusammensetzung der individuellen Aktionsräume wurde zur Kategorisierung von Marderhunden genutzt. Wenn der prozentuale Waldanteil innerhalb eines Aktionsraumes 50% überstieg, wurde das Tier als „Waldtyp“ eingestuft. Wenn der prozentuale Waldanteil eines Aktionsraumes unter 5% lag, resultierte dies in einem durchschnittlichen Flächenanteil von $81,82\% \pm 16,92$ SD Weideland. Folglich wurde das Tier als „Agrartyp“ eingestuft. Weder Habitatpräferenz noch Habitatauswahl differierten zwischen beiden „Typen“. Habitatnutzung und –präferenz wird bezüglich des weiteren Ausbreitungspotentials nach Westeuropa diskutiert.

Männliche Marderhunde verbrachten deutlich mehr Zeit ($40,5\% \pm 11,7$ SD) alleine mit den Welpen als weibliche Marderhunde ($16,4\% \pm 8,5$ SD). In den ersten sechs Wochen nach der Geburt der Welpen hatten Fähen deutlich größere Aktionsräume ($98,24 \text{ ha} \pm 51,71$ SD) als Rüden ($14,73 \text{ ha} \pm 8,16$ SD) und legten innerhalb von 24 Stunden wesentlich längere Distanzen ($7.368 \text{ m} \pm 2.015$ SD) zurück als Rüden ($4.094 \text{ m} \pm 2.886$ SD). Die untersuchten Alttiere verließen den Wurfbau in der sechsten Lebenswoche der Welpen. *In situ* Videoaufzeichnungen belegen, dass der Rüde die Welpen und die Fähe mit Nahrung versorgt.

In der Lakatationsphase zeigten die Elterntiere eine ausgeprägte Arbeitsteilung: Während die Rüden die Welpen im Bau oder seiner unmittelbaren Umgebung bewachten, gingen die Fähen auf Nahrungssuche um ihren steigenden Energiebedarf zu decken.

Von 59 (43,4%) mit Ohrmarken versehen Marderhunden lagen Rückmeldungen vor, wobei die durchschnittliche Distanz zum Markierungsort $13,5 \text{ km} \pm 20,1$ SD war. Die Mortalitätsrate für abwandernde Jungtiere lag bei 69,5%. Die meisten Tiere (55,9%)

wurden innerhalb von 5 km vom Markierungsort nachgewiesen, wohingegen nur 8,5% der Rückmeldungen weiter als 50 km vom Markierungsort realisiert wurden. Zwischen männlichen und weiblichen Marderhunden gab es keinen Unterschied in der Dismigrationsdistanz. Die meisten markierten Tiere (53,7%) wurden zwischen August und September nachgewiesen, zwischen Juli und September wurden nur 34,1% zurückgemeldet. Die Welpenaktionsräume (MCP 100%) hatten eine durchschnittliche Größe von 92,1 ha \pm 66,4 SD (n = 17). Bei Berücksichtigung der Exkursionen ergab sich ein deutlich größerer Aktionsraum von 502,6 ha \pm 66,4 SD (n = 9). Bezüglich des Abwanderungsmonats gab es zwischen Rüden und Fähen keinen Unterschied. Die Abwanderungsrichtung scheint bei Marderhunden, mit Abwanderungsdistanzen zwischen 0,5 km bis 91,2 km zufällig gewählt zu werden. Die hohe Flexibilität im Abwanderungsverhalten ist sicher ein Grund für den großen Ausbreitungserfolg der Art.

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12. Appendix

12.1 Abbreviations

approx.	approximately
a.s.l.	above sea level
°C	degrees Celsius
cm	centimetre
D	sum of absolute Differences between
treatments	
DMD	Daily Movement Distance
df	degrees of freedom
'E	east
e.g.	exempli gratia
et al.	(et alii)
esp.	especially
Fig.	figure
GIS	Global Information System
ha	hectare(s)
h	hr hour(s)
IAS	invasive Alien Species
i.e.	id est
ind.	individuals
JI	Jacobs' Index
K	kernel estimations
km	kilometre(s)
km ²	square kilometer
m	metre(s)
MCP	minimum convex polygon
min	minute(s)
'N	north

n	number	sample size
p		statistical probability value
pers. obs.		personal observation
pers. comm.		personal comment
Pi		reference index
R		correlation coefficient
r_s		Spearman correlated coefficient test
SD		Standard Deviation
Si		Schoener's Index
Tab		table
unpubl.		unpublished
Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec – for months in the text, tables and figures		



12.2 raccoon dogs / study area "Galenbeck"

No.	capture- date	sex	age	location/ capture	weight	ht	tail	hf	ear	time span	status/ mortality factor	recovery	location/recovery
1	25.06.1999	f	juv	Johbg	1,7	37,5	12	7,3	3,9	25.06.99- 18.08.99	dispersal	02.06.2002	Borken(PW-Krugsdorf)
2	26.06.1999	m	juv	Johbg	1,8	39,2	13,3	9	4,2	26.06.99- 28.07.99	dispersal		
3	26.06.1999	m	juv	Johbg	2	43	12,2	9,3	4,2	26.06.99- 09.08.00	collar expire		Klepelshagen
4	27.06.1999	m	juv	Johbg	1,7	38,5	13	8,9	4,2	27.06.99- 15.09.99	dead/gunshut	15.09.1999	Brohm/Charlottenhof
5	28.06.1999	f	juv	Schwbg	1,8	43,2	11,5	9,2	4,2	28.06.99- 11.08.99	dead/traffic	11.08.1999	Eigentum
6	28.06.1999	f	juv	Johbg	1,7	40	12,1	8,9	3,9	ear tagged only	dead/gunshut	15.03.2000	Brohm/Cosa
7	13.07.1999	m	2-3	Johbg	6,2	59,8	20,3	12,9	5,7	13.07.99- 19.08.00	collar expire		

8	14.07.1999	f	juv	Johbg	2,9	45	15,6	9,8	4,2	14.07.99- 08.11.99	dead/gunshut	16.08.1999	Rev.Schwarzensee
9	21.07.1999	f	4-5	Schwbg	6,7	63	20,5	12,5	5,3	21.07.99- 14.09.99	dead/gunshut	14.09.1999	Lübkowsee
10	22.07.1999	f	juv	Eigt	2,8	41,2	18,9	10	4,7	22.07.99- 01.10.99	dead/gunshut	29.04.2000	Waldteil Brohm
11	23.07.1999	m	juv	Schwbg	2,3	44,5	13,1	10,5	4,3	23.07.99- 24.02.00	dead/traffic	24.02.2000	Friedl.Wiese
12	27.07.1999	f	juv	Eigt	3	45,7	19,1	10,3	4,8	27.07.99- 10.10.99	dispersal		
13	28.07.1999	m	juv	Eigt	3,3	54	14,2	10,5	5,1	28.07.99- 29.08.99	dead/gunshut	29.08.1999	Friedl.Wiese
14	29.07.1999	f	juv	Eigt	2,4	48,3	15	9,5	4,5	eartagged only ?			
15	17.08.1999	f	juv	Rohrk-Heinrw	3,5					eartagged only ?			
16	18.08.1999	m	juv	Rohrk-Heinrw	4,8	59,6	22,2	12,1	5	eartagged only 12.09.99- 06.10.99	dead/gunshut	26.09.1999	Rohrkrug
17	01.09.1999	m	juv	Johbg	4,5	52,5	18,2	11,1	5	02.09.99- 18.03.2000	dead/traffic	06.10.1999	AlteMühleWittenborn
18	02.09.1999	f	3	Johbg	9,4	58,2	21	12,2	5,9	30.09.99- 06.10.99	dead/gunshut	18.03.2000	Gehren
19	02.09.1999	f	juv	Johbg	3,9	52,3	22,7	10,7	4,3	06.10.99	dead/traffic	06.10.1999	AlteMühleWittenborn
20	09.09.1999	f	juv-1	Eigt	6,1	63,2	19	13	5,1	09.09.99-	dead/gunshut	29.02.2000	Bredenfelde

											18.11.99			
											30.09.99-	dead/bite		
21	30.09.1999	f	2-3	Johbg	8,6						04.10.99	carniv.	04.10.1999	Wittenborn
											16.11.99-			
22	01.10.1999	m	juv	Eigt		62,2	16,5	12	5,3		18.11.99	dispersal		
											14.11.99-			
23	14.11.1999	m	juv	Johbg	8,8	64,3	22	13	5		26.04.00	dead/traffic	09.07.2000	Str.Schwbg-Ferdihof
											15.11.99-			
24	15.11.1999	m	2-3	Galenb	8,5	57,5	18	11,9	5,3		18.11.00	dead/gunshut	18.11.2000	Rohrkrug
											15.11.99-			
25	15.11.1999	f	2-3	Galenb	8	59,2	21	11,2	5,2		06.08.00	collar expire		
											30.01.00-			
26	30.01.2000	f	1	Eigt	6,8	61	22	12,6	5,5		18.12.03	dog	18.12.2003	Fleetholz
											26.02.00-			Str.Schwbg-
27	26.02.2000	m	1	Friedl.W.	5,7	61	23	11,7	5,1		26.5.00		15.09.2000	Ferdihof/Kalkloch
											30.04.00-			
28	30.04.2000	m	3-5	Johbg	6,2	55,8	24,2	11,6	6,2		9.7.01	collar expire		
											01.05.00-			
29	01.05.2000	f	3-5	Johbg	5,8	64,5	19	11,2	5,1		04.02.01	collar expire		
											06.05.00-			
30	06.05.2000	f	1-3	Johbg	4,3	58,5	21	11,7	5,1		16.09.00	dead/gunshut	16.09.2000	Gehren-Ausbau
											13.06.00-	dead/bite		
31	13.06.2000	m	juv	Johbg	1,2	37,5	10,4	7,8	3,3		01.08.00	carniv.	01.08.2000	Johannisberg
											14.06.00-			
32	14.06.2000	f	juv	Johbg	1,3	36,5	12	7,5	3,6		09.08.00	dispersal		

33	15.06.2000	f	juv	Johbg	1,4	32,7	10,7	8	3,1	15.06.00- 27.08.01	dead/gunshut	27.08.2001	Rattey
34	15.06.2000	m	juv	Johbg	1,1	31,3	8,6	7,1	3,6	15.06.00- 29.07.00	dead/injury	29.07.2000	Johannisberg Todfund
35	18.06.2000	f	juv	Johbg	1,1	33,2	10,3	7	3,6	24.6.00- 10.1.01	dead/gunshut	10.01.2001	Annenhof,Lübbs
36	19.06.2000	m	juv	Eigt	1	32	10	7	3,4	19.06.00- 28.11.00	dispersal		
37	20.06.2000	m	juv	Johbg	1,1	34,5	11	7,5	3,7	20.06.00- 24.08.00	dead/Verletzung	24.08.2000	Johannisberg
38	24.07.2000	f	juv	Eigt	2,8	48	17	11	4,7	24.07.00- 10.7.01	Sender verloren		Angelteich/Fang9.7.01
39	28.07.2000	m	1	Eigt	6,6	59,2	19,5	12	5	28.7.00- 18.12.03	dog	18.12.2003	Fleetholz
40	29.07.2000	f	3	Eigt	7,2	64,7	17,5	11,7	5,2	29.07.00- 18.04.01	dead/injury	18.04.2001	Eigentum
41	29.07.2000	m	5	Eigt	6,8	56,3	18,3	11,7	5	29.07.00- 1.8.01	found dead	01.08.2001	Eschholz/Graben
42	29.07.2000	f	juv	Eigt	3,2	49,2	16,3	10,7	4,9	29.07.00- 13.08.00	dispersal		
43	29.07.2000	m	juv	Johbg	3	52	15,4	10,5	4,2	29.07.00- 22.09.00?	collar expire		Klepelshagen
44	30.07.2000	m	2	Eigt	7,9	67	20,5	12,5	6,1	30.07.00- 25.04.01	dispersal		
45	30.07.2000	m	juv	Johbg	3,4	56,5	16	10,5	4,3	30.07.00-	collar expire		Neddemin/Rev. Barnekow

										23.09.00			
										30.7.00-			
46	30.07.2000	f	juv	Eigt	3,4	50,3	16,5	10,7		01.08.03	dead/Vehrkkehr	01.08.2003	neue Strasse bei Fleethof
47	01.08.2000	f	juv	Eigt	3,8	46,5	16,5	11	4,8	eartagged only	?		
										02.08.00-	dead/bite		
48	02.08.2000	m	juv	Eigt	3,6	48	17,5	10,5	4,4	12.08.00	carniv.	12.08.2000	Friedland
49	06.08.2000	f	juv	Eigt	3,3	51,5	18	10,5	3,8	eartagged only	?		
50	08.08.2000	m	juv	Eigt/Fleethof	3,8	54	17,5	10,5	4,8	8.8.00-Jan 03	dead found	15.01.2003	Feld bei Klockow
										10.8.00-			
51	10.08.2000	f	3	Eigt	8,2	56,5	19,5	12	5,1	7.11.01	collar expire		
													Mühlgraben/ca. 1km vom
52	11.08.2000	f	juv	Mühlgr	4	53,5	15	10,5	4,2	eartagged only	gunshut	05.09.2000	Fangpl.
										11.08.00-			
53	11.08.2000	f	4-5	Eigt	6,7	65,3	22	12	4,6	06.04.01	dead/gunshut	06.04.2001	Eigentum/Eschholz
54	12.08.2000	m	juv	Mühlgr	3,9	56,5	15,1	11,1	5	eartagged only	dead/gunshut	04.06.2001	Eikstädt/Prenzlau
55	13.08.2000	f	juv	Mühlgr	3,5	52,8	16	10,5	5	eartagged only	dead/gunshut	04.08.2001	Daberkow/Tollense
56	22.08.2000	m	2	Johbg	4,9	61	18,5	11,9	5	eartagged only	?		
57	22.08.2000	f	juv	Johbg	4,1	52	18,8	11,1	4,9	eartagged only	?		
58	30.09.2000	f	juv	Eigt	6,5	59	16,5	11,4	4,6	30.09.00-	dispersal		

27.11.00

59	08.07.2001	f	juv	Eigt	3	47	17,6	10,8	2,9	eartagged only	?		
60	09.07.2001	m	juv	Eigt	2,5	49,2	17,8	10,6	4,7	eartagged only	?		
61	09.07.2001	m	juv	Mühlgr	2,35	47,5	14,2	9,9	3,9	eartagged only	?		
62	09.07.2001	f	juv	Mühlgr	2,4	46,2	13,8	9,9	4,1	eartagged only	?		
63	11.07.2001	m	juv	Eigt	2	44,5	16,3	9,9	4,1	eartagged only	?		
64	12.07.2001	f	juv	Fleethof	1,5	42,2	10,3	8,2	3,8	eartagged only	?		
65	12.07.2001	f	juv	Eigt	2,7	46,5	14,9	10,7	4,2	eartagged only	dead/traffic	26.7.02	Gr.Müritz/Löwenberg
66	30.07.2001	f	juv	Eigt	3,1	51,5	18,1	10,8	4,4	eartagged only	?		
67	31.07.2001	f	juv	Eigt	3,7	53	18	10,9	4,8	eartagged only	?		
68	31.07.2001	m	juv	Angelteich	3,2	50,7	17,6	11	4	eartagged only	?		
69	31.07.2001	f	juv	Eigt	2,6	47,5	15,7	10,1	4,3	eartagged only	dead/traffic	13.08.2001	Eigt
70	17.08.2001	f	juv	Angelteich	4,2	53,5	17,4	10,2	4,9	eartagged only	?		

71	26.10.2001	m	ad	Hammelstall	7,3	-	-	-	-	26.10.01- 10.9.03	gunshut	10.09.2003	Waldrand/Waldeshöhe
72	23.06.2002	f	juv	Fleetholz	2,5	43	15,6	9,5	4,1	23.06.02- 22.07.02	dead/traffic	22.07.2002	Lübbersdorf/ Mühle
73	04.07.2002	f	juv	Fleetholz	2,9	52,5	17,6	10,1	3,8	4.7.02-11.7.02	dispersal		
74	05.07.2002	f	juv	Fleetholz	2,6	45,4	15,2	9,6	3,9	05.07.02- 22.08.02	dead/gunshut	22.08.2002	Dennin
75	09.07.2002	f	juv	Fleetholz	3,2	40,2	19,7	9,7	4,4	09.07.2002- 22.07.02	dead/gunshut	22.07.2002	Fleethof/ Schilfloch
76	22.07.2002	m	juv	Fleetholz	2,7	51,3	15,2	10,8	4,2	22.07.02- 24.07.02	dispersal		
77	24.07.2002	f	juv	Fleetholz	3,05	52,8	17	11,2	3,8	24.07.02- 26.07.02	dispersal		
78	24.07.2002	f	juv	Fleetholz	3,25	52,3	18,9	11,1	4,8	24.07.02- 31.07.02	dead/gunshut	31.07.2002	Blumthal/ Deponie
79	26.07.2002	m	ad	Fleetholz	7,65	64,4	20,9	12,2	4,9	26.7.02- 30.11.03	under control		
80	04.08.2002	m	juv	Fleetholz	3,55	52,2	19,5	10,9	4,4	4.8.02-1.10.03	gunshut		
81	01.11.2002	f	ad	Fleetholz	9,2	62,3	17,9	12,3	5,7	1.11.02- 1.10.03	gunshut		
82	03.04.2003	m	ad	Angelteich	5,7	63,2	17,1	11,9	4,9	3.4.03- 30.11.03	under control		
	09.04.2003	f	ad	Angelteich	6,6	61,8	22,3	12,3	4,7	9.4.03-13.7.03	dead/traffic	13.07.2003	neue Strasse bei Fleethof

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84	25.06.2003	m	juv	Fleetholz	1,7	36,5	12,2	8,7	3,4	eartagged only	?		
85	01.07.2003	f	juv	Fleetholz	1,85	39,4	12,4	9	3,6	1.7.03-22.8.03	dispersal	10.10.2003	Ladenthin/ poln. Grenze
86	03.07.2003	m	juv	Friedl.W./Hecke	1	29,8	9,9	7,4	3,1	3.7.03-20.8.03	gunshut	01.09.2003	Mais/Heinrichswalde
87	11.07.2003	m	juv	Fleetholz	3,2	50	18,4	10,6	5,2	eartagged only 20.7.03-	gunshut	10.11.2003	Reetzow
88	20.07.2003	m	juv	Friedl.W./Hecke	1,4	38,5	13	8,1	3,7	01.10.03	dispersal		kl. Dreiecksmaisfeld bei
89	20.07.2003	m	juv	Fleetholz	2,75	46,4	16,8	10,1	4,4	20.7.03-5.9.03	gunshut	05.09.2003	Fleethof
90	20.07.2003	m	juv	Fleetholz	2,35	47,4	16,2	10,2	4,4	20.7.03- 09.10.03	dispersal		
91	23.07.2003	m	juv	Friedl.W./Str.	1,7	36,7	16	9,1	3,5	23.7.03- 20.8.03	lost collar		
92	24.07.2003	f	juv	Friedl.W./Str.	1,6	38,3	12,7	9,1	3,4	24.7.03- 15.9.03	dead/traffic	15.09.2003	Löwitz
93	24.07.2003	f	juv	Fleetholz	2,05	45,2	15,9	9,6	3,8	24.7.03-9.8.03	dog	09.08.2003	zw. Fleethof u. Klockow
94	02.08.2003	f	juv	Kamera	2,65	44,3	15,5	9,5	3,9	1.8.03-5.8.03	dispersal		
95	06.08.2003	m	juv	Mais/Heinrichswalde	3,6	54,9	18	11,5	4,7	6.8.03-16.9.03	gunshut	16.09.2003	Mais/Heinrichswalde

96	08.08.2003	m	juv	Fleetholz	3,25	54,9	19,5	11,4	4,8	eartagged only	?		
97	09.08.2003	f	juv	Maisschlag/ITorfstich	3	47,2	17,6	9,7	4,6	eartagged only	gunshut	19.09.2003	Mais/Heinrichswalde
										11.8.03-			Friedl.W. Richtg.
98	11.08.2003	m	juv	Fleetholz	4,7	56,9	20,9	11,5	4,7	11.11.03	gunshut	14.11.2003	Lübkowsee
99	13.08.2003	m	juv	am Fleetholz	3	47	18,5	9,5	4,5	eartagged only	?		
100	14.08.2003	f	juv	Fleetholz	4,5	58,5	21,5	11,6	5	eartagged only	?		
101	15..8.2003	m	juv	Friedl.W.	3,2	49	20	10,4	4,4	eartagged only	?		
										22.10.03-			
102	22.10.2003	m	ad	Friedl.W.	8,15	63,5	19	12,5	4,8	30.11.03	under control		
										27.10.03 -			
103	27.10.2003	f	ad	Friedl. W.	7,45	58,5	21	11,6	4,6	12.12.03	gunshut	12.12.2003	Klokow bei Fleethof
										27.10.03-			
104	27.10.2003	m	ad	Friedl. W.	7,5	58,2	17,8	11,2	4,7	30.11.03	under control		

12.3 raccoon dogs / study area "Penzin"

No.	date/capture	sex	age	location/capture	status	date/recovery	location/recovery	mortality factor
6	15.08.2004	m	juv	im Hals				
7	19.08.2004	m	juv	Adolfs Hecke				
8	20.08.2004	m	juv	im Hals				
10	03.09.2004	f	juv	im Hals				
11	04.09.2004	f	juv	im Hals				
12	05.09.2004	f	juv	Dresdener-Hochsitz				
13	24.09.2004	m	juv	Ende des Driftweges				
14	12.10.2004	m	juv	Teigelmeisters Bruch				
15	31.12.2004	m	juv	Reinstorfer-Tannen	dead	04.05.2005	Penzin	roadkill
16	10.07.2005	m	juv	im Hals				
18	10.07.2005	f	juv	im Hals				
19	10.07.2005	m	juv	Dresdener-Hochsitz				
20	12.07.2005	f	juv	im Hals	dead	11.10.2006	Plattenweg zw. Wokrent und hohen Lukow	gunshut
21	12.07.2005	m	juv	Schultenkoppel				
22	15.07.2005	m	juv	im Hals				
23	15.07.2005	m	juv	Schultenkoppel	dead	02.09.2005	Damm-Wolde bei Röbel	gunshut
24	15.07.2005	f	juv	Dresdener-Hochsitz				
25	16.07.2005	m	juv	im Hals	dead	22.11.2005	Belitzer Torfmoor	dog
26	16.07.2005	f	juv	Schultenkoppel	dead	30.07.2005	Tal am Rugenbach	roadkill
27	16.07.2005	f	juv	Schultenkoppel				
28	17.07.2005	m	juv	im Hals				

29	19.07.2005	m	juv	im Hals					
30	19.07.2005	m	juv	T-Stück K.					
31	20.07.2005	f	juv	im Hals					
32	22.07.2005	m	juv	Schultenkoppel					
33	25.07.2005	m	juv	Schultenkoppel					
34	25.07.2005	f	juv	im Hals					
35	13.08.2006	f	juv	Reinstorfer-Tannen					
36	22.08.2005	m	juv	T-Stück K.	dead	06.09.2005	A19 zw. Abf. Kabelsdorf und Lage (km-Stand 92,2510	roadkill	
37	31.08.2005	m	juv	T-Stück K.	dead	04.01.2006	B 105 Ortseingang Dargetzow von Rostock kommend	roadkill	
38	11.08.2005	f	juv	Wiese/Neumans Hecke					
39	27.10.2005	m	juv	im Hals					
40	01.12.2005	f	juv	Schlangenbruch	dead	06.08.2006	beim Rapsdreschen auf dem Schulacker	gunshut	
41	04.12.2005	m	juv	Wollgraswiese	dead	27.08.2006	Pasin zweites Bruch	gunshut	
42	12.12.2005	f	juv	Schlangenbruch					
43	21.12.2005	m	juv	Bau Adolfs Hecke					
44	21.12.2005	f	juv	Bau Adolfs Hecke					
47	17.02.2006	m	juv	Kurve					
48	19.02.2006	f	juv	Kurve					
51	22.07.2006	f	juv	im Hals					
52	24.07.2006	m	juv	im Hals					
53	25.07.2006	m	juv	T-Stück K.					

54	25.07.2006	f	juv	T-Stück K.				
55	25.07.2006	m	juv	Schultenkoppel	dead	12.01.2007	Ulrickenhof 100 östlich von Toorfmoor	gunshut
56	26.07.2006	m	juv	im Hals				
57	27.07.2006	m	juv	T-Stück K.				
58	27.07.2006	m	juv	Schultenkoppel				
59	28.07.2006	m	juv	im Hals				
60	31.07.2006	f	juv	im Hals	dead	28.10.2006	Waldkante Viezerhorst nach Bernitt	gunshut
61	31.07.2006	m	juv	im Hals	dead	17.09.2006	Strasse zwischen Stäbelow und Clausdorf	roadkill
62	02.08.2006	f	juv	T-Stück K.				
63	03.08.2006	f	juv	im Hals				
64	10.08.2006	m	juv	altes Toorfloch	dead	18.08.2006	Tal am Rugenbach	roadkill
65	10.08.2006	m	juv	Schultenkoppel				

12.4 Table captions

Tab. 1 Home ranges sizes (mean, ha \pm SD) of raccoon dogs in different seasons

(n = number of seasonal home ranges)

Tab. 2 Habitat composition in the total study area (254.34 km²) and in raccoon dog home ranges (n = 62) and distribution of locations (n = 6.157) in habitats

Tab. 3 Food items (n = 44) carried to the breeding den by male raccoon dog – according to video observations of a raccoon dog pair during pup rearing season

Tab. 4 Population densities of the raccoon dog in different areas

11.5 Figure captions

Fig.1 Location of the two study areas in Mecklenburg-Western Pomerania (North-Eastern Germany)

Fig. 2 Schoener's Index reflecting the autocorrelation of locations ($S_i \pm SD$) of 62 stable home ranges estimated using fixed Kernel analysis in four different seasons (n = seasonal home ranges, S_i = 2 equals independent locations)

Fig. 3 Mean annual home-ranges distribution pattern (95% MCP) of four pairs of raccoon dogs radio tracked in 2003

Fig. 4 Home range overlap (\pm SD) of pair mates and adjacent raccoon dogs based on Kernel 95, core area (Kernel 85) utilisation and MCP estimation (n = number of pairs of home ranges examined) in different seasons

Fig. 5 Jacobs' index ($J_i \pm$ SD) among raccoon dogs according to season (n = number of seasonal home ranges)

Fig. 6 Habitat preference by raccoon dogs in different seasons (n = number of home ranges)

Fig 7 Habitat preference by female and male raccoon dogs (n = number of seasonal home ranges)

Fig. 8 Habitat preference of raccoon dogs with high and low forest cover within their home ranges (n = number of seasonal home ranges)

Fig. 9 Daily range sizes (kernel 95%) of adult female and male raccoon dogs in the first six weeks postpartum calculated for the 24-h continuous radio-tracking sessions

Fig.10 Examples of daily movement distance (DMD, dashed lines) of simultaneously-located paired mates in their daily range (kernel 95%, solid lines), A

before parturition (2-3 May), B first week postpartum (14-15 May), C fifth week postpartum (12-13 June), D sixth week postpartum (18-19 June)

Fig. 11 Daly movement distance (DMD) covered by adult female and male raccoon dogs during 24-h radio-tracking sessions in the first six weeks postpartum

Fig. 12. Average distance to the breeding den of adult female and male raccoon dogs during the first six weeks after parturition

Fig. 13 Time allocation (%) of adult raccoon dog pairs ($n = 3$) at the breeding den during continuous observation (24-h/week) for the first six weeks after parturition investigated by radio telemetry

Fig. 14 Time (%) spent absent from the breeding den in weeks before and after parturition investigated by video observation (h = hours recorded, 1009.7 in total)

Fig. 15 Distance of relocations for young raccoon dogs ($n = 59$) from point of capture

Fig. 16 Month of relocations for young (< one year) raccoon dogs ($n = 41$)

Fig. 17 Dispersal distance and direction of young raccoon dogs ($n = 59$). For simplification, all marking points were standardized to one location

Fig. 18 Month of dispersal for radio-collared young (< one year) raccoon dogs (n = 48)

Fig. 19 Examples of home ranges (I natal home range, II temporary range after dispersal; Kernel 100%) and dispersal pattern (line of consecutive locations) for young raccoon dogs. **A** – male left natal area and dispersed 28.5 km as a straight line (58.1 km total distance), in 5 days in August, when it established its home range in a suitable habitat, but might disperse again. The young raccoon dog almost travelled eastwards in a straight line, until the periphery of a larger city where it turned north. **B** – male showed extremely large home-range size (> 15,000 ha) while roaming solitary in search of suitable habitat and pair mated in its 1st year. The animal lost radio-collar at one year of age and was road killed 1 km out of the displayed range in its 2nd Sept. **C** – female dispersed 16.3 km (47.9 km total distance) in 10 days (Oct./Sept.) from natal home range. The animal was shot in its 1st Jan in the new range. **D** – female showed oscillating motions by gradually extending activities into neighbouring areas, but kept returning to natal home range until August. The animal became resident in close vicinity (3.05 km) with peripheral overlap to parental home ranges. Pair mate and reproduction was recorded in its 2nd year.