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Spatial organisation and intra-specific relationship of the raccoon dog *Nyctereutes procyonoides* in Central Europe

Frank Drygala, Norman Stier, Hinrich Zoller, Henry M. Mix, Kathrin Bögelsack & Mechthild Roth

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During October 1999 - October 2003, we monitored 26 adult raccoon dogs *Nyctereutes procyonoides* using radio-telemetry in an area of Germany which has been occupied by this invasive alien species since the early 1990s. 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 for males (N = 32 seasonal home ranges). Paired raccoon dogs had home ranges of similar size ($P = 0.203$), with pairs sharing the same area all year round ($P < 0.001$). 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, based on the results of home-range overlap analysis and interaction estimations, it can be assumed that the raccoon dog in Central Europe is monogamous without exclusive territories.

Key words: Central Europe, home range, monogamy, raccoon dog, social system, territoriality

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The raccoon dog *Nyctereutes procyonoides* was introduced from eastern Asia into several areas of the former USSR (mainly the European part) during 1929-1955. Approximately 9,100 animals were released, and they expanded their range at an average annual speed of about 40 km. They soon began to

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colonise neighbouring countries (Lavrov 1971). The first recorded sighting in Poland was in 1955 and by 1964 sightings were recorded in eastern Germany (Mecklenburg-Western Pomerania; Nowak & Pielowski 1964, Nowak 1973). Few raccoon dogs were recorded in Germany until the early 1990s, but thereafter an exponential increase in the hunting bag was evident (Drygala et al. 2002) and in the 2005/06 hunting season approximately 30,000 animals were shot (www.komitee.de/index.php?brdjagdstrecke).

The raccoon dog has become a permanent member of the fauna of Germany and the ever-increasing hunting bag indicates that the population has not yet reached the carrying capacity of the environment. Furthermore, as the population increases, intensively used agricultural habitats with low forest cover are being colonised (Drygala et al. 2000, 2008). In Finland raccoon dogs favour shore areas and old moist heaths with abundant undergrowth (Kauhala 1996). The diet of the species is omnivorous and generalistic in its introduced and original distribution areas, consisting mainly of small food items with a high proportion of vegetable matter (Heptner & Naumov 1974, Kauhala et al. 1993b, Drygala et al. 2000). Monogamy is the most common form of social organisation among dogs and foxes (Canidae; Kleiman 1977). A previous telemetry study of Finnish raccoon dogs (Kauhala et al. 1993a) indicated a preference for long-term pair bonding. However, because environmental conditions in Finland differ from those in Germany, these results may not be self-evidently applied to German raccoon dogs.

Our telemetry study was started in 1999 to determine which factors influence raccoon dog spatial organisation, with a view to understanding the invasion process and the ecological implications of its success in its new environment, and its potential to expand throughout western Europe. Furthermore, information on seasonal variations in home-range size and overlap, on population density and social systems (i.e. monogamy and territoriality) are important when predicting future population size and distribution area.

Material and methods

Study area

Our study area covered approximately 250 km^2 and was located in Mecklenburg-Western Pomerania approximately 50 km west of the German-Polish border (53°36'N, 13°14'E; 5-145 m a.s.l.). The climate is temperate, 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. Total annual precipitation averaged 431 mm and mean annual relative humidity was 75% (German Weather Service/Neubrandenburg 2003 Available at: http://www.wetterwarte-mv.de/).

The study area includes several protected areas and natural features such as reed beds, swamps, mixed forest, streams, ditches and a large lake (575 ha). But it is also characterised by a vast, homogeneous, agricultural landscape with cereal crops, especially maize *Zea mays*. Although the human population is sparse (49 inhabitants/km^2; Uecker-Randow-District, Residents' Registration Office 2003), it is dissected by many dirt roads, thus facilitating radio-tracking. The forests are dominated by European beech *Fagus sylvatica*, pedunculate oak *Quercus robur*, Scots pine *Pinus silvestris*, European larch *Larix decidua* and Norway spruce *Picea abies*. The swamp/marshland areas are dominated by common alder *Alnus glutinosa* and silver birch *Betula pendula*.

The area is inhabited by a diverse community of predators comprising four medium-sized carnivores, raccoon dog, red fox *Vulpes vulpes*, otter *Lutra lutra* and badger *Meles meles*. Possible predators of raccoon dogs, especially of juveniles, are white-tailed eagle *Haliaeetus albicilla*, domestic dog *Canis familiaris* and red fox.

Telemetry and data analyses

We live captured 104 raccoon dogs using wire-box traps and fish bait, (raccoon dogs are easy to handle and do not require immobilisation). We fitted 74 of the 104 raccoon dogs with radio-collars (Wagener, Cologne) which produced sufficient locations for the home-range calculations of 26 adults (12 males and 14 females). Resident animals were monitored during October 1999 - 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 (< 1 year) by noting body weight, fur and the attrition of teeth, especially incisors. Resident raccoon dogs were identified as the animals that showed no home-range shift after being fitted with a radio-collar. Locations for dispersing animals were not included in our study. Two raccoon dogs were monitored for at least 3.5 years (one for a 4-year period), two animals for 1.5-2 years, eight animals

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for 1-1.5 years, 10 animals for 6-12 months and four animals for 1-6 months.

Raccoon dogs were located with a handheld H antenna (HB9CV) or a 3-element Yagi at different times of the night and day (point method) as often as practically possible (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 <1 km. Bearings were taken from at least two points (often triangulation or more), the angle between the bearings being as close to 90° as possible.

Location error was estimated to be about 100 m (91 m $\pm$ 125 SD) by locating hidden transmitters ($N=52$). Radio-tracking was supplemented by visual observation of collared animals, carried out as often as practically possible to improve the accuracy of fixes. For tracking with a 2-3 element Yagi antenna, a 1-in-10 rule is acceptable (Kenward et al. 2003). Thus, our tracking resolution (100 m) and observer-animal distance ($<1{,}000$ m) were in a ratio of 1:10. However, location error may be greater if locating moving animals instead of using hidden transmitters. We grouped animal locations into four different seasons: oestrous and gestation (March-April), parturition and cub 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 1985a, 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, we used this method to estimate raccoon dogs' home-range size and utilisation distribution to investigate spatial use.

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

Using Schoener's index ($S = t^2/r^2$; Swihart & Slade 1985b), we 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 we arbitrarily excluded seasonal home ranges corresponding to a Schoener's index of <0.92.

Core areas were determined for seasonal home ranges by plotting utilisation distribution graphs with RANGES 6 version 1.2. The slope discontinuity was taken as an indicator of how many fixes constituted the core (Kenward et al. 2003). We 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. We examined how the core areas changed as successive locations were added and found stable home ranges from the mean of 28.40 $\pm$ 20.96 SD locations. Hence, all seasonal home ranges with <29 fixes were excluded, resulting in 62 (average Schoener's Index 1.52 $\pm$ 0.38 SD) independent and stable seasonal home ranges (6,158 total locations; Fig. 1).

Mean stability of MCP 100 home ranges was at 47.88 $\pm$ 31.21 SD locations resulting in 61 stable home ranges with a minimum of 48 bearings for further analysis. For map representation we 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 mean percentages of home-

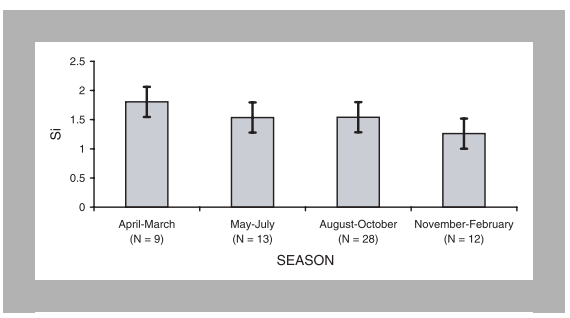


Figure 1. Schoener's Index (Si $\pm$ SD) reflecting the autocorrelation of locations of 62 stable home ranges estimated using fixed Kernel analysis in four different seasons with N = seasonal home ranges, and Si = 2 equaling independent locations.

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range overlap of two animals were used. We 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. We calculated one pair (two adults) for the mean home-range size during the breeding season, when home ranges of adjacent raccoon dogs only overlap slightly (11.7% ±3.0 SD). 'Helpers' have not been observed in raccoon dogs (Kauhala & Saeki 2004).

Because the raccoon dog is more of a gatherer than a hunting predator (Kauhala et al. 1993a, Drygala et al. 2000) and roams at a low mean speed of 1.86-6.96 m/minute (Saeki 2001), we defined a 15-minute input threshold as same-time observations. The observed and possible distances between animals (a random sample of 500 fixes) were compared using Jacobs' index (Ji) 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). We were able to use all 11,261 fixes regardless of their independence because RANGES 6 version 1.2 avoids assumptions about autocorrelation and distribution of locations between single pairs of individuals (Kenward et al. 2003).

We only used single pairs of animals with > 20 locations (mean 162±224 for pair mates; mean 39.6±22.3 for neighbours). We 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 (F. Drygala, 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 cub tracks. We 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 pseudoreplication for home-range sizes, home-range overlap and interaction analysis was low because sufficient seasonal data existed only for six animals radio-tracked for >1 year. Thus, we used all 62 calculated seasonal home ranges.

For statistical analysis, we removed pseudoreplication by the calculation of means for seasonal home-range sizes of 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. We tested significance of seasonal shifts in home range and variations in home range overlaps towards partner and neighbour with the related samples with missing values test, reflecting the sum of absolute differences between treatments (here seasons = 'D'). We tested correlation of home-range sizes for paired mates using Spearman correlated coefficient test (r_s).

Results

Home ranges

MCP 100 estimation

The mean annual home-range size was 583.0 ha± 398.0 for females (N = 28 seasonal home ranges) and 551.6 ha±418.6 for males (N = 33 seasonal home ranges) with no significant difference (T = 25, N = 9, P = 0.82) between the sexes. We 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 ±441.3) for both sexes was observed during August-October. Even in the winter den associated season (November-February), raccoon dogs had large home ranges (647.1 ha±427.5). With a mean size of 314.1 ha±112.6 females had the smallest home ranges during the oestrous and gestation period in spring. There was a distinct difference between the sexes during the cub-rearing season when males (N = 8) had the smallest (240.0 ha±96.2) and females (N = 8) the largest (444.1 ha±260.3) home-range sizes (Table 1). Among males there were significant MCP 100 (N = 33) differences between seasons (D = 1598.14, P = 0.04), but no such differences were 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 1-4) 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 in the long term (probably lifelong) but some changed their breeding den every year. The breeding den of pair 1 was located within 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

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Table 1. Home-range and core-area sizes (mean in ha ± SD) of raccoon dogs in different seasons estimated using three different methods with N = number of seasonal home ranges.

	MCP 100				Kernel 85 distribution (core area)				Kernel 95 distribution			
Season (months)	Female	N	Male	N	Female	N	Male	N	Female	N	Male	N
Oestrous and gestation (March-April)	314.1 ± 112.6	3	284.1 ± 186.8	4	83.4 ± 44.2	4	101.0 ± 49.8	5	157.7 ± 81.1	4	159.2 ± 69.5	5
Cub rearing (May-July)	444.1 ± 260.3	8	240.0 ± 96.2	8	122.2 ± 79.2	7	93.4 ± 75.0	6	225.3 ± 179.5	7	194.1 ± 181.0	6
Weight gain (August-October)	706.6 ± 401.2	12	766.4 ± 486.4	14	352.3 ± 227.8	15	319.0 ± 229.8	13	554.6 ± 334.8	15	528.0 ± 378.7	13
Reduced activity (November-Febuary)	669.8 ± 594.8	5	630.0 ± 313.8	7	191.8 ± 98.3	6	191.0 ± 141.4	6	283.1 ± 127.0	6	291.4 ± 190.5	6
Mean for all seasons	583.0 ± 398.0	28	551.6 ± 418.6	33	238.3 ± 198.1	32	212.0 ± 192.0	30	382.0 ± 297.4	32	352.4 ± 313.3	30

area throughout the year. Home ranges of adjacent animals overlapped to varying degrees (Fig. 2).

The average annual home-range size did not differ between sexes, being 382.2 ha ± 297.4 SD for females and 352.4 ha ± 313.3 for males (Wilcoxon signed ranks T-test: T = 34, N = 9, P = 0.203), neither were there significant seasonal differences in home-range sizes among males (N = 26; 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 ha ± 69.9, N = 9). The largest home ranges were recorded during autumn (August-October; 542.2 ha ± 349.4, N = 28; see Table 1), with no significant difference between males and females (T = 18, N = 7, P = 0.58); the second largest home range was recorded during winter (November-February, 287.2 ha ± 154.4, N = 12).

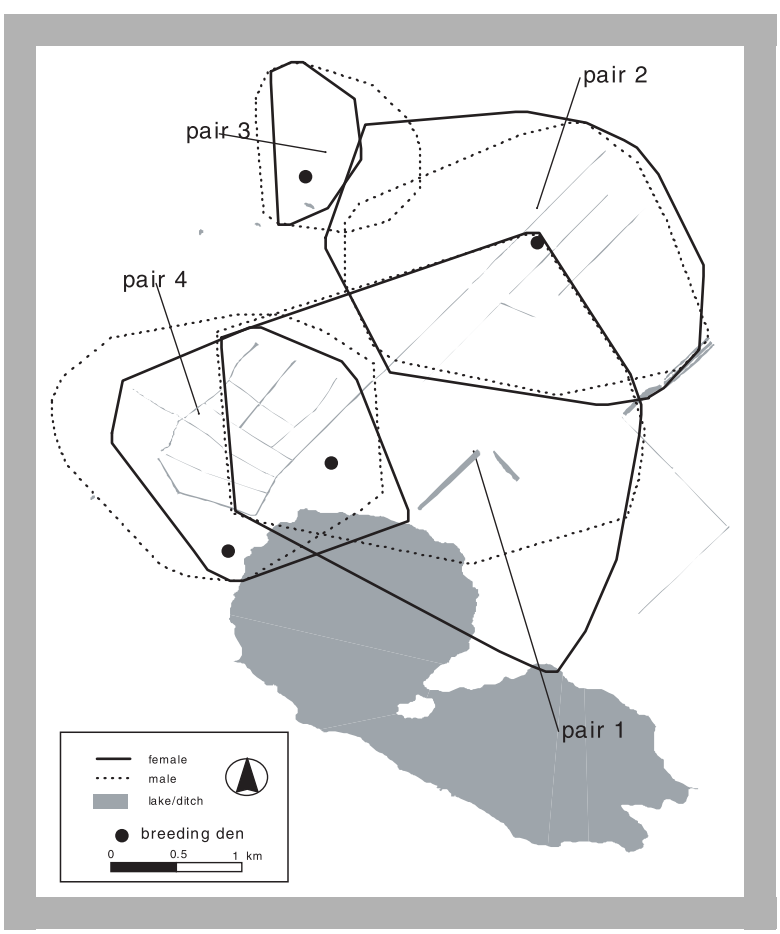


Figure 2. Mean annual home-range distribution pattern based on 95% MCP of raccoon dog pairs 1-4 which were radio-tracked in 2003.

After parturition in the cub-rearing period (May-July) female home ranges (225.3 ha ± 179.5, N = 7) were slightly larger than those of males (194.1 ha ± 181.0, N = 6; see Table 1). We 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; see Fig. 2). The calculated population density based on kernel 95 estimation (breeding season) was 0.95 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 ha ± 198.1 for females and 212.0 ha ± 192.0 for males. Annual comparisons showed a clear relation between the sizes of core areas of pair

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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 ha ± 45.5) and parturition and pup rearing (May-July; 108.9 ha ± 75.5). In winter (November-February), the average core area was 191.0 ha ± 116.1. The largest core areas (336.9 ha ± 225.1) were recorded during August-October with no significant difference in size between the sexes (T = 30, N = 9, P = 0.43; see Table 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 ha ± 44.2 in spring and 352.3 ha ± 227.8 in autumn.

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% ± 4.7 SD) in March-April. During May-June in the cub-rearing season, the paired mates had smaller home-range overlaps (68.9% ± 10.0). During August-October, there were large overlaps (90.5% ± 5.3) and during winter (November-February) paired males and females shared 85.4% ± 5.5 of their home ranges (Fig. 3).

Adjacent raccoon dogs had moderate home-range overlaps for every season. The maximum seasonal overlaps occurred during August-October (29.2% ± 19.8). During oestrous and gestation (March-April), home ranges of neighbours overlapped by 16.3% ± 11.8. In the cub-rearing period (May-June) ranges overlapped by 11.7% ± 3.0, but during winter (November-February) the overlap decreased to 2.6% ± 9.1 (see Fig. 3). We 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

We considered seasonal effects by comparing overlap of core areas for adjacent raccoon dogs. The maximum overlap (20.9% ± 18.7) was observed during the intensive foraging period (August-October). In the cub-rearing season (May-July), core areas overlapped by no more than 3.0% ± 1.0. Core areas of pair mates overlapped significantly (mean 83.5% ± 9.2) all year (see Fig. 3).

Interaction analysis

Pair mates

We used data for 10 raccoon dog pairs and 26 seasonal home ranges for interaction analyses. Males

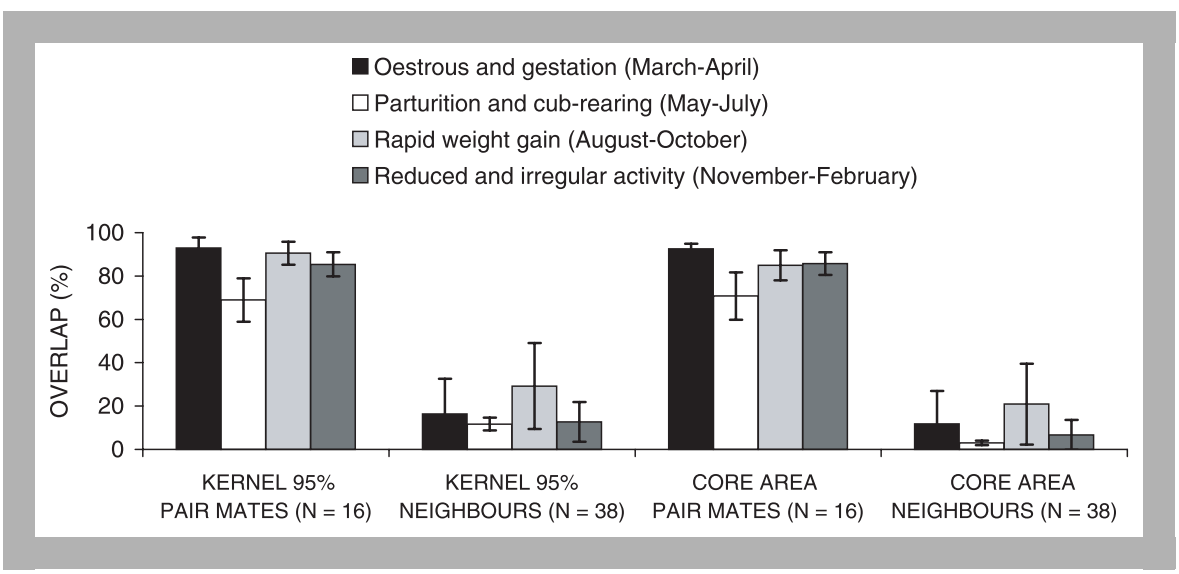


Figure 3. Home-range overlap (± SD) of pair mates and adjacent (neighbour) raccoon dogs based on Kernel 95, core area (Kernel 85) utilisation and MCP estimation with N = number of pairs of home ranges examined in the four different seasons.

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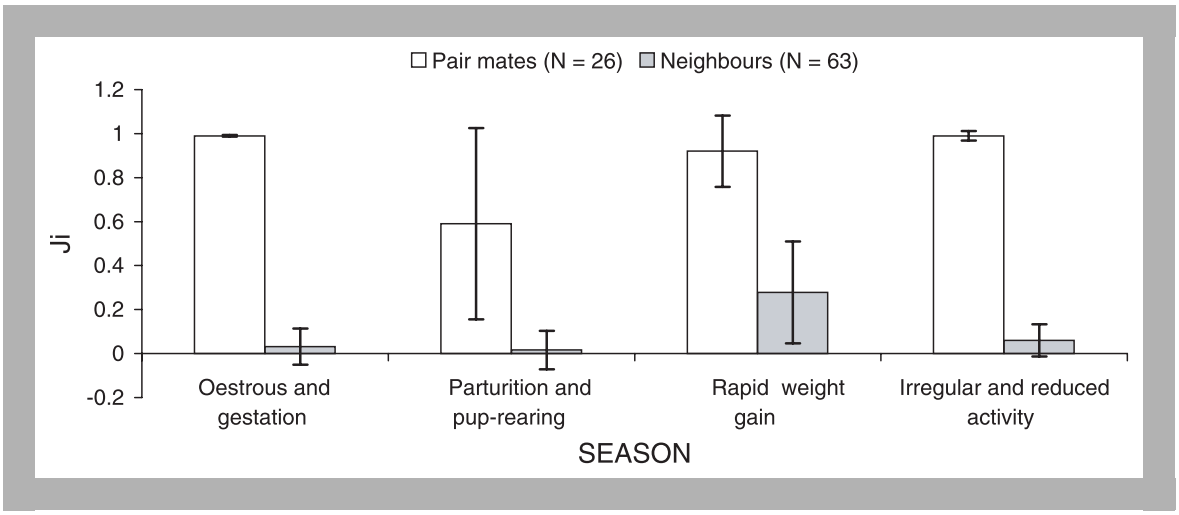


Figure 4. Jacobs' index (Ji ± SD) among raccoon dogs according to season with N = number of seasonal home ranges.

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 Ji = 0.87 ± 0.27 SD). No mate changes were observed. During the periods of winter (Ji = 0.99 ± 0.02) and oestrous and gestation (Ji = 0.99 ± 0.004), the paired mates were exclusively located at the same point. Partners also roamed closely together from August to October (Ji = 0.92 ± 0.16). Only after parturition, during the cub-rearing period, did pair members show different spatial allocation (Ji = 0.59 ± 0.43; Fig. 4).

Neighbours

We used 63 seasonal home ranges (444.1 ha ± 260.3) from 23 adjacent raccoon dogs (mean annual Ji = 0.12 ± 0.29) for interaction analysis. During periods of oestrous and gestation (Ji = 0.03 ± 0.08), parturition and cub rearing (Ji = 0.02 ± 0.09) and winter (Ji = 0.06 ± 0.07), the observed adjacent animals ignored each other. Only in autumn, was a slight preference shown among neighbours (Ji = 0.28 ± 0.23) compared to the other seasons (see Fig. 4). We 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; Ji = 0.10 ± 0.18) and females (N = 13; Ji = 0.10 ± 0.15) were almost neutral and even neighbouring males and females (N = 34) ignored each other (Ji = 0.12 ± 0.19).

Discussion

Accuracy 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, we divided our 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 home-range size (Swihard & Slade 1985a), whereas data subsampled 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 autocorrelated (Robertson et al. 1998, Rooney et al. 1998, DeSolla et al. 1999).

However, ignoring autocorrelation may result in underestimated range sizes (Cresswell & Smith 1992). 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 we excluded all seasonal home ranges with Schoener's Index of <0.92 for kernel distribution analysis. MCP 100 home-range analysis is not affected by autocorrelation of successive fixes (Harris et al. 1990), so we used all locations. Seaman

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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, Kauhala et al. (1993a) identified a minimum of 35 relocations as stable home ranges for raccoon dogs in southern Finland. We found stable home ranges with a mean of 29 locations for fixed kernel estimates and a mean of 48 fixes for 100% MCP analyses.

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 estimates. 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) reported from southeastern Finland (Kauhala et al. 2006). However, environmental conditions in Finland and Japan differ essentially from those in Germany, so results obtained in these two countries may not be comparable with our data. The Japanese raccoon dog belongs to another subspecies, *N. p. viverrinus*, which has adapted to a variety of different (inter alia subtropical) habitat types. Moreover, it can be assumed that food availability is higher 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/km^2) in Germany was comparable to the density recently estimated in southeastern Finland (minimum 0.38 adults/km^2 and maximum 0.77 adults/km^2; Kauhala et al. 2006).

Raccoon dogs expanded their home ranges during August-October to feed especially in maize 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. The 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 2002/03 when temperatures fell to below -20°C. The two 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 may occasionally be active in mild winters (Heptner & Naumov 1974, Kauhala et al. 1993a).

Social organisation

Canids have developed omnivorous food habits and produce large litters, 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 our study. However, exceptional among canids is the low developed territoriality and bipaternal breeding system, we 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 (Ji = 0.89; Kauhala et al. 1993a, Kauhala & Saeki 2004, Kauhala & Holmala 2006). We 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 (Ji) 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, 1998).

Core areas covered 81.2% of raccoon dogs' home ranges in our study area, indicating that they use their home ranges evenly. The almost neutral Jacobs' index (Ji) throughout the year between adjacent individuals is also confirmed by high intraspecific 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 (Ji = 0.04; Kauhala & Holmala 2006). However, core areas of most adjacent individuals or pairs did not overlap in the cub-rearing season, which suggests a degree of avoidance, if not territoriality and defence, of the breeding den vicinity when the cubs are small. These results also agree

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with what Kauhala et al. (1993a, 2006) found in Finland.

In all other seasons we found a combination of weak, intraspecific population pressure due to underdeveloped 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, we conclude that the raccoon dog in Germany is monogamous without defending an exclusive territory.

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