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Seasonal habitat selection of raccoon dogs (*Nyctereutes procyonoides*) in Southern Brandenburg, Germany

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Abstract. Habitat preferences of nine adult raccoon dogs were investigated during different seasons using compositional analysis after Aebischer et al. (1993). The study area (33 km²) with its mosaic landscape of forest and farmland was located in Southern Brandenburg in eastern Germany (13°56′ E, 51°37′ N). For analysis eight habitat categories were distinguished. Grassland and coniferous woods were favoured both within 95 % fixed-kernel (K95) and within core areas (K50). Grassland offered food at most times of the year and particularly after harvesting of fields. Abandoned badger dens located in coniferous woods within K50 were used by raccoon dogs all year round whereas they apparently avoided anthropogenic structures. Other habitat categories were used randomly and we detected no seasonal differences in relative usage. Such heterogeneous agricultural landscapes dominate the central and western European landscape. Furthermore, short winters and low density of top predators provide beneficial living conditions for raccoon dogs. Its flexibility in habitat use, omnivorous diet and ability to disperse over long distances facilitate a further expansion of the raccoon dog in western and southern Europe.

Key words: compositional analysis, invasive species, agricultural landscape

Introduction

The introduction of "Neobiota", especially when these are predatory mammals, is considered to be a major threat to native biodiversity (Gebhardt et al. 1996, Clout 2002, Baillie et al. 2004). Some of these alien species successfully establish themselves in their new ranges, because they satisfy essential preconditions for this process. Sufficient habitat and food resources together with a high reproduction rate and the ability for range expansion support the establishment of an alien species in a new environment (Gebhardt et al. 1996). The raccoon dog *Nyctereutes procyonoides* is an ecological generalist and is regarded as a successful invasive species.

Its omnivorous feeding habit (Sutor et al. 2010), flexible habitat use (Kauhala & Auttila 2010), high reproductive potential and dispersal behaviour (Kauhala & Kowalczyk 2011) enabled this canid to become a widespread invasive species in northern, eastern and central Europe within a few decades.

Originally the raccoon dog occurred in six subspecies distributed through much of China, as well as north-east Indochina, Korea, the Amur and Ussuri regions of Eastern Siberia, Mongolia and Japan (Kauhala & Saeki 2004). In this native range raccoon dogs live in different habitats extending from the Far Eastern temperate rain forest on the Pacific coastline to the interior plains with a continental climate that are used for agriculture (Judin 1977). Starting in the year 1928 in the Ukraine and continuing in the 1940s and 1950s a total of about 9000 individuals of the subspecies *N. p. ussuriensis* were released in the European part of the former USSR, from where the raccoon dog began its successful expansion to Fennoscandia and central Europe. The first animals in Germany were recorded in the 1960s (Nowak 1984). Ever increasing hunting-bags from throughout north-eastern Germany (Anonymous 2008), demonstrate that raccoon dogs are able to live in a wide range of lowland habitats and indicate that agricultural landscapes offer suitable conditions for this invasive predator.

Identifying habitat types favoured by raccoon dogs in a farmland landscape will help conservation managers to assess potential negative effects on native species.

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Particularly in landscapes with agricultural use an increasing loss of egg clutches and chicks of ground-nesting birds mainly caused by nocturnal mammalian predators is documented (Bellebaum 2002, Litzbarski 2002, Engl et al. 2004, Melter & Südbeck 2004).

A study in Mecklenburg-Western Pomerania showed that raccoon dogs living in an open agricultural landscape used different habitat types opportunistically, and in contrast to other studies no clear habitat preferences were detected (Drygala et al. 2008a). Another study conducted in a similar landscape in the same German federal state confirmed that structures with a high degree of coverage were favoured by raccoon dogs (Zoller 2010).

The purpose of our telemetry study was to analyse habitat preferences of raccoon dogs in a diversified agricultural landscape in southern Brandenburg, applying the compositional analysis after Aebischer et al. (1993). This method, not previously adapted to German telemetry data of raccoon dogs, has the advantage of dealing with the data as independent (Kaartinen et al. 2005). In addition, the results obtained are comparable with recent international studies.

Material and Methods

Study area

The 33 km² sized study area is part of the "Lug" (13°56′ E, 51°37′ N), a basin plain at an average 110 m a.s.l., accessible by a network of gravel roads and located in the county "Oberspreewald-Lausitz" in the southern part of the Federal State of Brandenburg in eastern Germany (Fig. 1). The central part of "Lug" is mainly used for grassland farming – both pastures and meadows – and is crossed by a network of 2 m wide drainage ditches with a total length of 91 km. For compositional analysis, pastures and meadows were merged in the category grassland. The adjoining agricultural fields (= arable land) and villages (= anthropogenic structures) are located at 115 m a.s.l. (Möckel et al. 2000). In the study area we distinguished eight main habitat categories as listed in Table 1. Farm roads, hedges and ditches are linear structures and with respect to the location error were not classified as separate habitat categories. Shallow areas of standing water are possibly frequented by raccoon dogs as foraging sites, because they offer preferred food items such as amphibians (Kauhala 1996, Sutor et al. 2010). Therefore we considered this habitat type in the compositional analysis, too. The habitat structure of the study area is typically representative of the East German agricultural landscape.

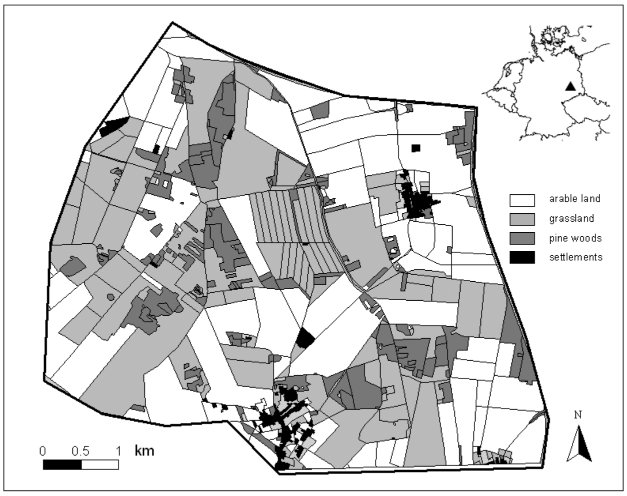

Fig. 1. Location and land-use of the study area "Lug" in eastern Germany (13°56′ E, 51°37′ N).

Table 1. Percentages of main habitat categories in the study area "Lug" in Southern Brandenburg, Germany. Listed habitat categories used for compositional analysis.

Habitat category	%	Abbreviation in tables and figures
grassland	35.11	grassl
moist grassland	0.09	moist_gras
arable land	47.31	arab_land
standing waters	0.15	stand_water
deciduous wood	0.43	dec_wood
coniferous wood	13.19	con_wood
anthropogenic structures	0.76	antr_struc
outlying holding facilities	2.96	out_fac

Coniferous woods occur in several isolated parcels and consist of pine trees (*Pinus sylvestris*) with a small proportion of oak (*Quercus robur*) and birch (*Betula pendula*) mainly at the edges of the forest. Drainage ditches and standing waters are predominantly surrounded by deciduous trees (alder *Alnus glutinosa*, willow *Salix* spp., ash *Fraxinus excelsior*, birch) and shrubs. These groups of trees and small woods form the habitat category deciduous woods. Maize and winter crops were frequently grown, with some fields of sunflowers or potatoes. Grassland is used extensively, mainly as cattle pasture; moist grassland adjoins drainage ditches and standing waters. Both water types are mainly shallow and raccoon dogs were able to swim through them (pers. observation).

Outlying holding facilities, two to four kilometers away from villages, are still used for pig fattening and some of them formerly as milking parlours for cattle.

In the study area "Lug" the presence of raccoon dogs was first proved in 1988. Reliable evidence for reproduction in this area already existed for the years 1988, 1989, 1993 and 1998, and hunting bags increased throughout the 1990s and 2000s (Möckel 2000). Medium-sized carnivores in the study area other than raccoon dogs were red fox *Vulpes vulpes* and European badger *Meles meles*. Throughout the study period, we searched the study area for dens and identified the occupying species by tracks at the sandy entrances. During our study (2001-2004) the annual average temperature was 8.9 °C and ranged from a mean of –0.3 °C in January to a mean of 18.9 °C in July. The average annual precipitation was 666.7 mm (German Weather Service; weather station: Dresden-Klotzsche: 2001-2004 http://www.dwd.de/bvbw/appmanager/bvbw/dwdwwwdesktop?; 13.2.2009, 10:40).

Radio tracking

Raccoon dogs were caught in wooden box traps and metal cage traps distributed in the centre of the study area. These box traps were large enough (l = 140 cm × h = 26 cm × w = 26 cm) for adult raccoon dogs. Traps were operated all year except from mid March to the end of April. During this period night temperatures were usually low and trapping might have resulted in the death of fox and raccoon dog pups if parent individuals had been unable to return to them at night. The box traps were operated for a total of 369 trap-days. Traps were checked once every day, early in the morning. Trapped animals were immobilized with the "Hellabrunner mixture", at a dose of 0.1 ml Rompun/kg body weight and 0.07 ml Ketamin/kg body weight (Hatlapa & Wiesner 1982). Trapping and handling of the raccoon dogs was carried out with minimal stress for the animals and according to German laws.

All trapped raccoon dogs were marked with consecutively numbered circular plastic eartags (diameter 180 mm). Those individuals with a minimum body mass of 4.5 kg were additionally fitted with radio collars (Biotrack, UK, 151-152 MHz). An acceptable ratio between body mass and the weight of the radio collar (150 g; i.e. 2-4 % of body weight) was thus maintained. The presence of permanent dentition and the abrasion of teeth enabled us to classify individuals as adult. Battery life of radio collars, was about 1.5 years. Radio tracking was done by following the animals by vehicle, occasionally on foot, using a flexible three-element Yagi antenna and a "Mariner 57" (Biotrack, UK) receiver. Animals in motion were located from at least two points resulting in an angle between the two bearings as close as possible to 90°. Slowly roaming or inactive raccoon dogs were located using triangulation (White & Garrott 1990). Activity or resting of an individual could be detected by amplitude fluctuation of the signal. Lost signals were searched for by aircraft. Following a Finnish study (Kauhala et al. 1993) we considered 36 locations (± 6 SD) to be sufficient for determination of a seasonal home range. Estimation of location error was done by detection of hidden transmitters and the location error ranged from 48 to116 m with a mean of 82.00 m ± 30.17. Clear signals were received at an average distance of 500 m. Therefore, our location error and observer-transmitter distance were acceptable following the 1:10 rule proposed by Kenward (2001).

Analysis of habitat use

Between February 2001 and July 2004 we radio-collared 12 (4 males, 8 females) adult raccoon dogs. On average ten individuals per year were observed and we collected 1462 telemetry points in total. Habitat use during different seasons was investigated only for resident adult raccoon dogs (1 male, 8 females).

We compared our results only with those of other studies dealing with *N. p. ussuriensis*, because Europe is exclusively colonized by this subspecies (Nowak 1973, Nowak 1984). Furthermore, the Japanese subspecies, *N. p. viverrinus* and *N. p. alba*, differ clearly in genetics and morphology from the mainland subspecies (Kauhala & Saeki 2004).

Home ranges were calculated as fixed kernel-density estimation (KDE; Worton 1989) and we distinguished the 95 % Kernel isopleth (K95; total home range) and the 50 % Kernel isopleth (K50; core area). Mean annual home range sizes were calculated as 1.83 km² ± 1.54 (K95) and 0.50 km² ± 0.49 (K50). A comprehensive description of the calculation of home range sizes is given in Sutor & Schwarz (2012).

Spatio-temporal analyses were done in ArcView Gis 3.3 (© 1999, ESRI Environmental Systems Research Institute, Redlands-California, USA), with the extensions spatial analyst and animal movement (Hooge & Eichenlaub 1997) and the home range extension for ArcView (Rodgers & Carr 2002). We applied Microsoft Excel (2000) for calculations, followed by compositional analysis according to Aebischer et al. (1993) using the program Compos Analysis Version 6.3 for Microsoft Excel (Smith 2010).

As has been shown in other studies, there are no significant differences in home range sizes and habitat use between female and male raccoon dogs (Kauhala et al. 2006, Drygala et al. 2008b), therefore data can be pooled. According to the raccoon dog's biology and behaviour we divided the year into four time periods:

February to April (season 1): rut and birth, May to July (season 2): pup rearing, August to October (season 3): dispersal time and fat storage, November to January (season 4): limited winter activity. In total 37 data sets of seasonal home ranges provided the basis for the investigation of habitat use during these four seasons. Those raccoon dogs which were tracked longer than one year, provided more than four seasonal home ranges. Home ranges of the same season in different years for the same individual were pooled, because they did not differ. In addition to data pooling we used individual animals as sample units in this study.

The compositional analysis after Aebischer et al. (1993) is based on the comparison of utilized with available habitats. Sets of proportions of different habitat categories within an individual seasonal home range (= used habitat) and within the study area (= available habitat) are calculated. For analysing the proportion of each habitat category within the individual home range area and the available corresponding habitat category in the study area, transformation to log-ratios is required. According to the results of this calculation all habitat types are ranked in order of use, which indicates their preference.

Compositional analysis is a method which overcomes certain problems in analyzing data in habitat utilization, such as invalid sampling units or sample sizes and non-independence of proportions (Aebischer et al. 1993). Within an individual home range the core area is used most intensively and as already shown in a similar study on raccoon dogs, this method indicated habitat preferences better than the application of location points (Kauhala & Auttila 2010). If habitat patches are too small, utilization of tracking fixes for an use-availability analysis might lead to inaccurate results, because the position of fixes in specific habitat categories could involve location error (Kauhala & Tiilikainen 2002).

Results

Both in K95 and K50 significant differences between various habitat categories according to their use within each season – except in season 4 in K50 – were detected. Ranking of eight habitat categories indicated preferences (Table 2, Table 3).

Habitat preferences within K95

In four different seasons habitat categories appeared in similar ranked sequences, whereas in three seasons significant differences between two consecutively ranked categories occurred (Table 2). Grassland and coniferous woods were ranked highest throughout the year and in season 4 the category coniferous woods was even more important than grassland. Anthropogenic structures and outlying facilities were ranked lowest throughout the year and in season 2 even a significant difference between these categories appeared (Table 2). In all seasons the relative use of grassland was higher than its availability. With respect to the habitat category,

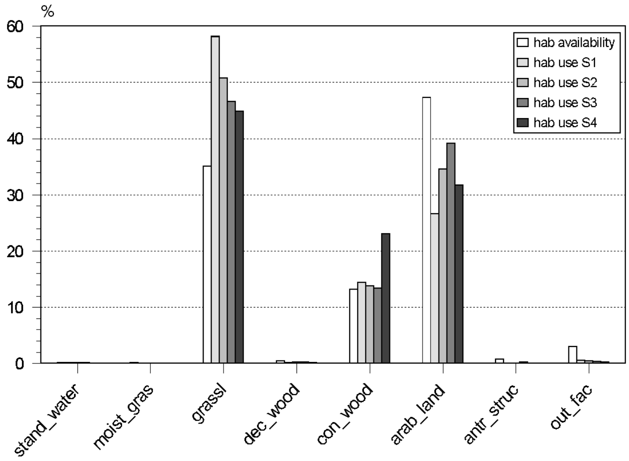

Fig. 2. Availability in the study area (%) and use (%, mean value of radio tracked individuals) of eight habitat categories within home ranges (K95) of raccoon dogs during four seasons (S1: February to April, S2: May to July, S3: August to October, S4: November to January).

Table 2. Habitat preferences of raccoon dogs within K95 during different seasons (S) determined by compositional analysis according to Aebischer et al. (1993). Habitat ranking, test statistics lambda (λ), χ^2, *p* and randomised *p* are given.
>>> denotes a significant difference between two consecutive ranked variables. February to April (S1): rut and birth, May to July (S2): pup rearing, August to October (S3): dispersal time and fat storage, November to January (S4): limited winter activity.

S	Ranked habitat sequence	λ	χ^2	*d.f.*	*p*	*Rand p*
1	grassl>>>con_wood>>>arab_land>moist_gras> dec_wood >stand_water>out_fac>antr_struc	0.0019	56.2249	7	P < 0.0001	0.0261
2	grassl>con_wood>arab_land>moist_gras> stand_water>dec_wood>out_fac>>>antr_struc	0.0296	35.2113	7	P < 0.0001	0.0233
3	grassl>con_wood>arab_land>moist_gras> stand_water>dec_wood>out_fac>antr_struc	0.0616	27.8750	7	P < 0.001	0.0187
4	con_wood>grassl>>>moist_gras>arab_land> dec_wood>stand_water>out_fac>antr_struc	0.0011	54.7120	7	P < 0.0001	0.0723

use of coniferous woods was high in all seasons, but especially during season 4 (Fig. 2).

Habitat preferences within K50

In K50 (= core areas) coniferous woods was the highest ranked category in seasons 1, 2 and 4. During season 3 grassland was the most favoured category (Table 3). Similarly to K95, outlying facilities and anthropogenic structures were ranked lowest in seasons 1 to 3. In season 4 the smallest core areas were detected and observed raccoon dogs did not use moist grassland and anthropogenic structures, hence these habitat types did not appear in the ranking (Table 3). Year-round habitat use of both grassland and coniferous woods was higher than the availability of these habitat categories (Fig. 3).

Discussion

Comparable to other studies we detected preferences in habitat use of raccoon dogs (Table 4). The distribution of essential supplies is the primary cause of animals' distribution (Brown & Orians 1970). The analysis of habitat use allows researchers to determine selection and preference of a species (Boitani & Fuller 2000). However, the classification of habitat types fundamentally influences the analysis of habitat use and may therefore cause difficulties when comparing studies (Kauhala & Auttila 2010). For instance, in our study area coniferous woods were composed of pine trees with little undergrowth, whereas in southern Finland the same habitat category consists of mixed pine and spruce forest with more undergrowth, especially dwarf shrubs (pers. observation).

A further problem in analyses of habitat use results from the application of different methods. In our study we identified habitat categories favoured by raccoon dogs by applying compositional analysis according to Aebischer et al. (1993). Due to different analytical methods on habitat use of raccoon dogs in two German studies (Drygala et al. 2008a, Zoller 2010) which applied a modified index after Jacobs (1974), comparison with our results may be difficult.

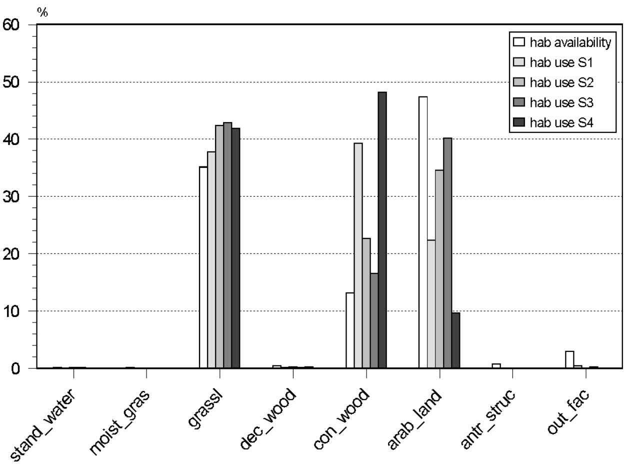

Fig. 3. Availability in the study area (%) and use (%, mean value of radio tracked individuals) of eight habitat categories within home ranges (K50) of raccoon dogs during four seasons (S1: February to April, S2: May to July, S3: August to October, S4: November to January).

Habitat preferences in K95

The sequential ranking of habitats resulting from the compositional analysis is similar in all seasons: grassland and coniferous woods are preferred most, whereas outlying facilities and anthropogenic structures are less favoured habitat categories.

Within home ranges feeding places have an important impact on habitat use (Saeki 2001) and we assume food to be a key factor in habitat use. Small mammals, invertebrates, amphibians and birds have been identified as main food items (Sutor et al. 2010). Obviously grassland offers good living conditions for these species groups and consequently represents a favourable habitat type for raccoon dogs. In north-eastern Germany smaller home range sizes of raccoon dogs living in an agricultural landscape indicated higher

Table 3. Habitat preferences of raccoon dogs within K50 during different seasons (S) determined by compositional analysis according to Aebischer et al. (1993). Habitat ranking, test statistics lambda (λ), χ^2, *p* and randomised p are given.
>>> denotes a significant difference between two consecutive ranked variables. February to April (S1): rut and birth, May to July (S2): pup rearing, August to October (S3): dispersal time and fat storage, November to January (S4): limited winter activity.

S	Ranked habitat sequence	λ	χ^2	*d.f.*	*p*	*Rand p*
1	con_wood>grassl>dec_wood>stand_water> arab_land>moist_gras>out_fac>antr_struc	0.0010	62.2657	7	P < 0.0001	0.0220
2	con_wood>grassl>>>moist_gras>stand_water> arab_land>dec_wood>>>out_fac>antr_struc	0.0104	45.6915	7	P < 0.0001	0.0274
3	grassl>con_wood>arab_land>stand_water> moist_gras>dec_wood>out_fac>antr_struc	0.0007	72.9736	7	P < 0.0001	0.0036
4	con_wood>grassl>dec_wood>stand_water> out_fac>arab_land	0.0905	19.2192	5	P < 0.01	0.1586

Table 4. Habitat structures used and preferred by raccoon dogs (*Nyctereutes procyonoides*) living in European colonization areas.

Study area	Used habitat structure	Preferred habitat structure	Analyzing method	Reference
Finland	Periurban area, rural area	mixed forest, meadow field, garden	Compositional analysis	Kauhala & Auttila 2010
Finland	Agricultural areas and commercial forest	deciduous forest, fields, watersides	Compositional analysis	Holmala & Kauhala 2009
Germany	Agricultural landscape	no seasonal habitat preferences	Preference-Index	Drygala et al. 2008a
Germany	Agricultural landscape	structures with high degree of coverage	Preference-Index	Zoller 2010
Germany	Agricultural landscape	coniferious woods, grassland	Compositional analysis	present study
Lithuania	Nationalpark Dzūkija: 85 % forest cover	mixed forest, swamps (during winter)	Selection Index	Baltrūnaite 2006
Poland	National park Białowieża: deciduous and mixed forest	Sedge marshes, wet deciduous forest	Survey of dens, snow tracking and radio tracking in combination	Jedrzejewska & Jedrzejewski 1998
Romania	Danubian delta	reeds, lowland riparian forest	Observation data and hunting bags	Barbu 1972
Sweden	Forest mixed with open natural and agricultural areas	forest, wetland	GPS-locations buffered and tested against random points	Herfindal et al. 2012
Ukraine	River deltas and rural areas	forest, wetland	Observation data and den use	Woloch & Roženko 2007

food abundance in grassland (Drygala et al. 2008a).

Especially during periods when arable land is not covered with crop plants – in spring (season 1) and after harvest (season 3) – grassland is very attractive. In a study area in southern Finland with a comparable proportion of open habitats raccoon dogs preferred meadows most (Kauhala & Auttila 2010).

In season 4 coniferous forest was ranked highest. This observation results from an enormous decrease in home ranges (K95: 0.85 km² ± 0.89), which were mainly located in coniferous forests (Sutor & Schwarz 2012). During the cold season raccoon dogs showed reduced activity and used their body fat reserves (Asikainen et al. 2004). This behaviour presumably caused a preference for coniferous forest and for dens located in these woods, which were used as resting places. A Finnish study indicated that the location of the winter den influenced the preference for the habitat type (Mustonen et al. 2012).

In our study area grassland provided food, while abandoned badger dens within coniferous woods provided safe shelters, therefore both habitat types were ranked highest. In Finland meadows, open woodlands, deforested areas and sapling stands were favoured habitat types, because these habitats offered cover and diverse food items (Kauhala & Auttila 2010). In a Lithuanian study area with 85 % forest cover, raccoon dogs favoured mixed forest but also used open habitats, mainly swamps (Baltrūnaitė 2006). Similar behaviour was observed in Białowieża National Park in Poland: raccoon dogs preferred mixed deciduous forest and sedge marshes along rivers (Jedrzejewska & Jedrzejewski 1998). A preference for humid habitats as observed in other studies (Barbu 1972, Judin 1977, Jedrzejewska & Jedrzejewski 1998, Baltrūnaitė 2006, Woloch & Roženko 2007) was however not indicated by our results. Presumably the numerous drainage ditches in our study area were frequented by raccoon dogs, but the tracking method described above did not provide clear evidence of this.

The results of our study indicated that raccoon dogs apparently avoided "human" structures because outlying holding facilities and anthropogenic structures were ranked lowest. Radio-collared raccoon dogs moved not nearer than 300 m from settlements and presumably have no need to search for food in or next to villages; maybe they avoid the presence of humans and dogs. This kind of shyness towards human settlements could also be a reason for a delayed expansion of the raccoon dog into western Germany, where human structures such as roads and settlements are more frequent than in eastern Germany. At present a lower population density of raccoon dogs in western Germany is observed, documented by clearly smaller hunting bags (Grauer et al. 2008). Comparing the areas of urban settlements with respect to the total territory of different Federal States, Brandenburg with 9.07 % and Mecklenburg-Western Pomerania with 7.73 % show the lowest densities of human settlement areas in Germany. In the remaining German Federal States the percentage of the habitat category “anthropogenic structures” is clearly higher and ranges within 11-22 % (https://www.regionalstatistik.de/genesis/online/online;jsessionid=D8D222852EC40CBE5B5FDE075576C6F41 29.05.2010, 18:41:09). Because raccoon dogs invaded Germany about fifty years ago (Nowak 1984) and have good long distance dispersal ability (Kauhala & Helle 1994, Sutor 2008), we would not have expected population densities of this opportunistic canid to differ within Germany to such a degree as can be concluded from hunting bags. The majority of raccoon dogs have been successfully hunted in Mecklenburg-Western Pomerania and Brandenburg; e.g. in the year 2008 these two eastern German Federal States provided 90 % of the total German hunting bag for the raccoon dog (Goretzki et al. 2009).

Habitat preferences in K50

Comparable to K95 in core areas, K50 habitat types were ranked in a similar sequence. Except in season 3 coniferous woods was the most favoured type. During the study period radio-collared raccoon dogs inhabited six abandoned badger dens, located in small coniferous woods. These dens are important components within the home ranges throughout the year, while home range sizes varied during different seasons, as described in Sutor & Schwarz (2012). The core area is a very intensively used part within the home range (Kauhala & Auttila 2010) and therefore habitat preferences in K50 provide indications for raccoon dogs’ habitat requirements. Dens in coniferous woods were used by raccoon dogs as daytime hiding-places, as shelter during bad weather, during winter with limited activity and for pup rearing (Sutor & Schwarz 2012, Sutor unpublished data). The importance of these dens is underlined by other studies and it is assumed that the native badger accelerated the settlement of the invasive raccoon dog by providing spacious dens (Stiebling 2000, Woloch & Roženko 2007, Kowalczyk et al. 2008).

During season 3 grassland was used more than coniferous woods, and dens obviously became less important. From August to October the largest home range sizes, on average 2.37 km² ± 1.73, were observed (Sutor & Schwarz 2012). During this season raccoon dogs roamed around widely to achieve fattening, and grassland offered sufficient food. Furthermore, use of dens became marginal during this period because juveniles were gradually released from parental care and left parental home ranges (Kauhala et al. 1993, Drygala et al. 2000, Sutor 2008). Similar to K95, in K50 anthropogenic structures were ranked lowest. In season 4 this habitat type did not appear, because home range sizes were smallest and therefore this structure did not appear in ranking. Our results confirmed the avoidance of anthropogenic structures, as had already been assumed by Drygala et al. (2008a). Finally we can conclude that in our study area food is mainly available in grassland and that abandoned badger dens within coniferous woods provided safe shelters. Preference of raccoon dogs for areas with a high degree of cover, as is documented in other studies (Drygala et al. 2008a, Holmala & Kauhala 2009, Zoller 2010), was confirmed in the present study by the relatively high use of coniferous woods both in K95 and K50. Our results and those of other studies support the hypothesis that a mixed landscape structure with tree or shrub cover and open habitats offers optimal conditions of shelter and food availability for raccoon dogs. Anthropogenic changes in landscape structure resulting in a heterogeneous mix of forested and agricultural patches may enrich the food supply for raccoon dogs (Judin 1977).

Conclusion

The raccoon dog belongs to one of 33 alien mammal species in Europe which forms self-sustaining populations, and is regarded as one of the most successful alien carnivores (Kauhala & Kowalczyk 2011). So far as landscapes offer sheltered places, sufficient food supply and there is enough time for feeding and fattening for winter periods the flexible habitat selection by raccoon dogs might be a key factor enabling colonization of new areas. Heterogeneous agricultural landscapes with woodlots, meadows and arable land, comparable to our study area, are dominant in central and western Europe. In addition to this habitat structure short winter periods with little snow cover and low density of top-predators (e.g. lynx *Lynx lynx*, wolf *Canis lupus*, brown bear *Ursus arctos*), provide beneficial living conditions for raccoon dogs.

Its habitat use, the omnivorous diet and the ability for long-distance dispersal (Sutor 2008, Drygala et al. 2010) facilitate a further expansion of the raccoon dog in western and southern Europe. All this will finally cause high population densities in European lowlands, promoting intensified inter- and intraspecific interactions (Kauhala et al. 2010, Zoller 2010, Sutor & Schwarz 2012). With respect to the transmission of pathogens and parasites – some of them significant as zoonoses – this colonization process is also of importance, because the raccoon dog is a susceptible vector species (Holmala & Kauhala 2009, Schwarz et al. 2011, Sutor et al. 2013).

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