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Activity patterns of the invasive raccoon dog (*Nyctereutes procyonoides*) in North East Germany

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Abstract. To study annual and circadian activity proportion and activity allocation during the pup rearing period we analysed VHF telemetry-based data from the invasive, socially monogamous raccoon dog in North Eastern Germany. Proportions of active fixes for 26 adults indicate a mean annual activity level of 58.3 %. There was no difference between males and females in mean annual activity or in the mean activity in each of the different seasons. A mean winter-activity level of 47.0 % ± 32.4 active fixes indicates that raccoon dogs did not hibernate; however, they became less active as the temperature decreases in winter. There were clear differences in the proportion of active fixes observed in the biological seasons, with the highest activity level (70.3 %) during the pup rearing period. Circadian activity rhythm, sampled on a daily basis, indicates that raccoon dogs were mainly crepuscular and nocturnal with a mean activity level of 86.8 %. The mean diurnal activity level across the seasons was 32.4 %, ranging from 15.0 % in winter to 56.6 % during the pup rearing period. Allocation of active fixes for 24-h continuous observations during the first six weeks after parturition showed that males were mostly inactive, resting with the pups in the den, while females foraged to satisfy their increased energy requirements. This point to a clear division of labour between parents, during the pup rearing period.

Key words: monogamy, circadian activity, breeding behaviour, winter dormancy

Introduction

Invasive species often show great flexibility in adaptation to environmental and climatic conditions and in behaviour (Ehrlich 1989, Sidorovich 1993, Kauhala 1996, Sakai et al. 2001). The raccoon dog was introduced as a fur species to the western Soviet Union in the 1930s-1950s. Today it is widespread in Northern and Eastern Europe, is still spreading in Central Europe (Drygala et al. 2010), and was recently listed by the DAISE project amongst the top 100 most damaging invasive species in Europe (Daise 2013). Previous studies indicate that the raccoon dog is socially monogamous with indistinctly developed territoriality, bi-parental breeding system and a high share of paternal care (Ikeda 1983, Yamamoto 1987, Kauhala et al. 1993, Kauhala et al. 1998, Drygala et al. 2008c). Male parental care is unusual in mammals, occurring in 5-10 % of species (Kleiman & Malcolm 1981, Woodroffe & Vincent 1994) and has been repeatedly suggested as a factor that may favour the evolution or maintenance of social monogamy (Kleiman 1977, Wittenberger & Tilson 1980, Clutton-Brock 1989). Because a few studies have shed light on the adaptive nature of male care in mammals (Clutton-Brock 1991) our aim was to analyse in more detail variation of activity behaviour of the raccoon dog using VHF telemetry-based data. Space use patterns of the invasive canid indicate a clear division of labour between the parents during the period in which the pups are nursed: males guard the litter in the den or in the close vicinity, while the females forage to satisfy their increased energy requirements (Kauhala et al. 1998, Drygala et al. 2008c). Thus, we asked whether this specific behaviour is reflected in differences of activity patterns, between male and female raccoon dogs during the pup rearing period. It has been suggested that the distribution area of the raccoon dog is mainly determined by climate (i.e. day length and ambient temperature). The longer the growing season, the better the raccoon dog does, at least in northern areas (Helle & Kauhala 1991). Due to a general lack of data on activity behaviour of the species in Central Europe, another objective was to investigate whether and in what way seasonal factors such as hibernation, day length and ambient temperature can affect activity pattern.

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We hypothesised that the percentage distribution of the proportion of active *versus* inactive fixes differed between biological seasons and between paired mates. Moreover, the temperate climate in central Europe was assumed to be a predictor of frequent winter activity. This is the first study ever into the activity patterns of the raccoon dog in Central Europe.

Material and Methods

Study area

Our study area of roughly 250 km² was located in Mecklenburg Western-Pomerania approximately 55 km west of the German-Polish border (53°36′ N, 13°14′ E; 5-145 m a.s.l.). The climate is temperate – 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. Temperature peaks ranged from –21 °C in January to +33 °C July. The total annual precipitation averaged 431 mm and mean annual relative humidity was 75 % (German Weather Service/Neubrandenburg 2003). 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). It is also characterised, however, by a vast, homogeneous, agricultural landscape in which cereal crops, especially maize (*Zea mays*), are cultivated. Although the human population is sparse (49 inhabitants/km², Uecker-Randow District Residents' Registration Office, 2008), the area is dissected by a number of dirt roads, facilitating radio tracking. The land in the region is mainly used for cattle grazing (32.9 % of the area) and crop growing (28.4 % of the area). Forests (27.5 % of the area) 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*) (Drygala et al. 2008a). The area is inhabited by a diverse community of predators, including five medium-sized carnivores: the raccoon dog, raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), otter (*Lutra lutra*) and badger (*Meles meles*). Possible predators of raccoon dogs, especially of juveniles, are white-tailed eagles (*Haliaeetus albicilla*), domestic dogs (*Canis familiaris*), red foxes and badgers.

Telemetry

Raccoon dogs were captured live using wire-box traps and fish bait between June 1999 and December 2003. They are easy to handle, do not require immobilization and the study complied in full with ethical standards. VHF telemetry-based activity data (n = 10679 fixes) were collected for 26 radio collared adults (13 males, 13 females). The number of fixes obtained ranged from 49 to 1781 per animal, with a mean of 411 ± 522 SD. Adults were distinguished from young animals (< 1 year) on the basis of body weight, coat and according to studies on the red fox, by the attrition of teeth. Especially the three peaks on the incisors show a distinct attrition after one year of age (Harris 1978, Suchentrunk 1984, Kaphegyi 2005). Transmitters (Wagener, Cologne) weighed 180 g and lasted about two years, but efforts were made to replace the collars before they stopped working. We located the animals using a handheld H antenna (HB9CV) or a three-element Yagi antenna and TRX-1000s receivers (Wildlife Materials, USA) as often as possible at different times of the day and night (point method).

As recommended by Garrott et al. (1986), we used multiple triangulations with at least three fixes per localisation to eliminate reflected signal errors. The mean distance between observer and animal was usually < 1 km. To improve the accuracy of the fixes we also made visual observations as often as possible, using binoculars and night vision (distance < 300 m), of radio collared animals in fields of short grass. We determined whether the animal was active or inactive solely on the basis of the amplitude fluctuation and bearing shift of the signal (Andelt 1985), listening for a period of at least two minutes. When animals are inactive the signal is almost constant. When they are active, the signal varies due to the movement of the antenna in relation to the receiving antenna (Skirnisson 1986, Kowalczyk & Zalewski 2011).

To study activity patterns during the pup rearing period we radio-tracked three raccoon dog pairs once a week continuously for 24 hours (n = 36) for the first six weeks after the pups were born. Contact with the tracked pair was maintained consistently and we managed to locate both the male and the female every 15 minutes (in a total of 3456 locations).

Data analysis

To take into account seasonal changes in the daylight span, 24 hours were divided into night and day, with night defined as the time from 30 minutes after sunset until 30 minutes before sunrise (Doncaster & MacDonald 1997). We are well aware that day length changes seasonally and is thus not independent in a statistical sense. Activity patterns were calculated for each month.

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Seasonal divisions should ideally reflect real aspects of the animal's ecology (Harris et al. 1990). Accordingly, we divided activity data into the following four seasons: oestrus 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) (Drygala et al. 2008b). To estimate the circadian activity rhythm, the mean values of activity data were calculated for every hour. To analyse the correlation between activity and temperature we used location data collected from 7 p.m. to 5 a.m. in November and December. 755 activity fixes of adults were assigned to temperature intervals of 1 °C. Temperature intervals for which we had less than 10 fixes were excluded from the analysis. To analyse the correlation between activity and day length, the annual activity data were assigned to 12 months.

Statistical analysis

Statistical analysis was performed using SPSS 21.0.1. The normality of sample distributions between animals was tested using the one-sample Kolmogorov-Smirnov test. The significance of differences in % activity between the sexes, different time periods and day and night was tested using Pearson's χ^2-statistic. When dealing with uniformly distributed activity data (24-hour radio tracking sessions), we used the t-test to test the significance of differences between the sexes and between day and night. All values are presented as mean ± SD.

Results

Proportion of active fixes

Raccoon dogs (n = 26) were mainly nocturnal, with a clear difference (χ^2 = 1861.5, df = 1, $p < 0.001$) in activity patterns observed between night and day (Fig. 1). Number of location between animals were not normally distributed (Kolmogorov-Smirnov – Z = 22.5, Dmax ± 0.22, $p < 0.001$). The individuals investigated had a mean annual activity level of 58.3 % ± 9.9 SD ranging from 70.3 % ± 19.2 during the pup rearing period in spring and early summer to 47.0 % ± 32.4 in winter. There were clear differences (χ^2 = 18.0, df = 3, $p < 0.001$) in the activity patterns observed in the various biological seasons. From May to June, when raccoon dogs need to care for their litter, both females (52 % ± 1.3 day activity) and males (58.1 % ± 5.2 day activity) appeared to be diurnal. The lowest diurnal activity was observed in winter for both females (9.1 % ± 5.5) and males (13.4 % ± 5.9), and raccoon dogs were 7.6 % less active than statistically expected (885 recorded versus 958 expected active fixes) between November and February. There were no differences between males and females in mean annual allocation of active fixes (χ^2 = 0.008, df = 1, $p > 0.9$) or in mean activity in each of the different seasons (Mar-Apr: χ^2 = 1.7, df = 1, $p > 0.2$; May-Jul: χ^2 = 0.3, df = 1, $p > 0.5$; Aug-Oct: χ^2 = 1.0, df = 1, $p > 0.3$; Nov-Feb: χ^2 = 2.0, df = 1, $p > 0.1$).

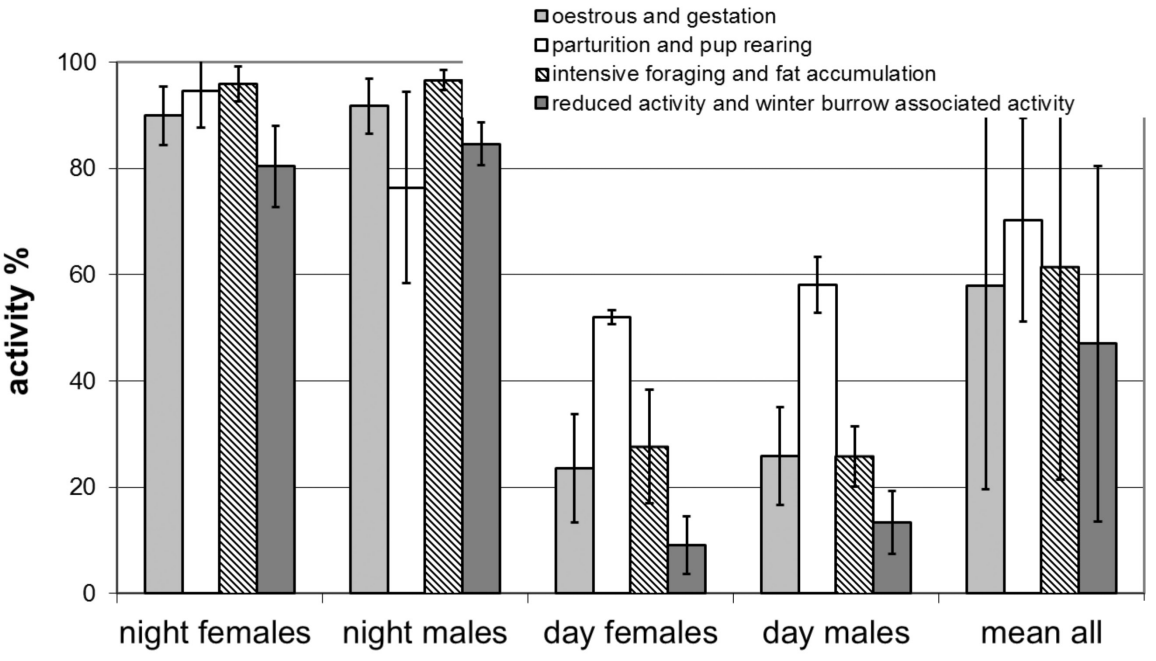


Fig. 1. Seasonal activity pattern of male (n = 13) and female (n = 13) raccoon dogs.

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Circadian activity rhythm

Raccoon dogs (n = 26) were more active during the night hours than during day hours in all seasons, with a mean nocturnal activity level of 86.8 % ± 7.0 ranging from 80.5 % ± 3.8 SD during the pup rearing period to 96.6 % ± 4.3 in autumn. The mean diurnal activity level across the seasons was 32.4 % ± 17.4, ranging from 15.0 % ± 15.1 in winter to 56.6 % ± 9.8 during the pup rearing period (Fig. 2).

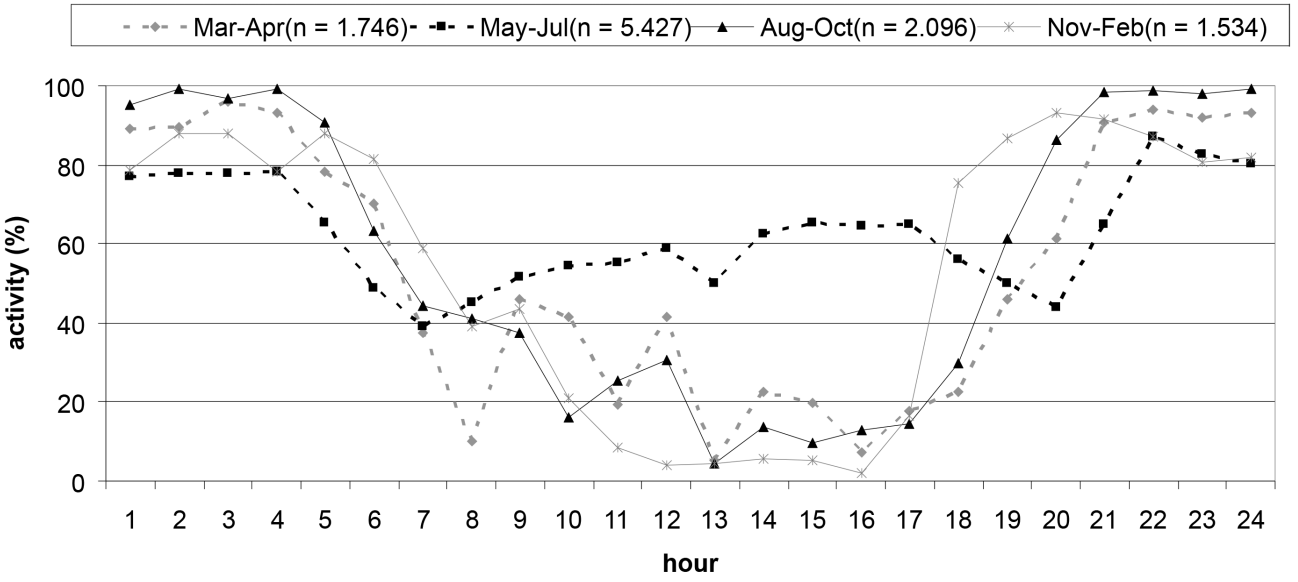


Fig. 2. Circadian rhythm in the different seasons (n = fixes).

Impact of temperature and day length on activity pattern

A positive correlation ($R^2 = 0.62$, n = 742 inactive fixes, $p < 0.05$) between proportion of inactive fixes and ambient temperature shows that raccoon dogs become less active as the temperature decreases in winter. At above 0 °C only 8.1 ± 4.7 % of the temperature intervals (n = 8) indicate inactivity, whereas at below 0 °C, 33.9 ± 13.0 % of the localization sets (n = 7) indicate inactivity (Fig. 3).

There was a positive correlation ($R^2 = 0.84$, n = 7216 active fixes, $p < 0.05$) between day length and proportion of diurnal active fixes. In summer (May-June), when the mean day length was 17.3 h, 55.6 % ± 11.3 fixes indicated activity. In contrast, during the winter months (November-February), when the mean day length was 9.2 h, we detected a level of just 11.3 ± 4.4 % daytime activity (Fig. 4).

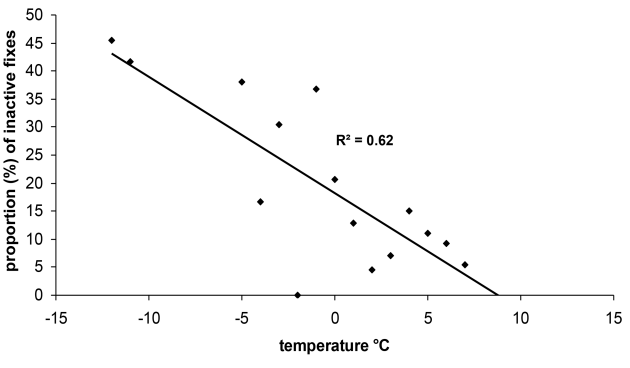


Fig. 3. Proportion (%) of inactive fixes in relation to ambient temperature for 12 male and 10 female raccoon dogs (742 fixes), recorded in winter (Nov-Feb) during the night (19-5h, peak of activity). Each dot represents dataset of > 10 fixes for one particular 1 °C temperature interval.

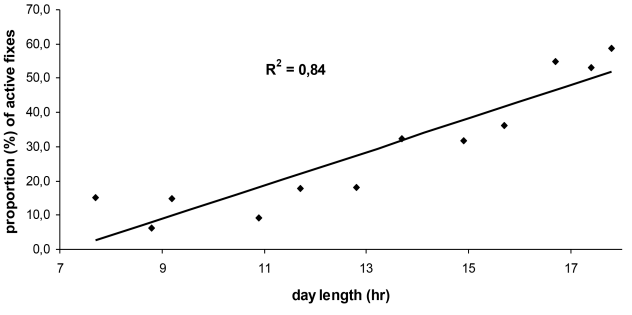


Fig. 4. Diurnal proportion (%) of active fixes (n = 7216) in relation to day length for 13 male and 13 female raccoon dogs. Each dot represents a dataset for one month (January to December).

Activity pattern during the rearing period

There was an obvious difference in the proportion of active fixes between the sexes during the first six weeks postpartum. Male (n = 3) raccoon dogs were more diurnal and less nocturnal than females (n = 3) and *vice versa* (Fig. 5). Females and males displayed mean

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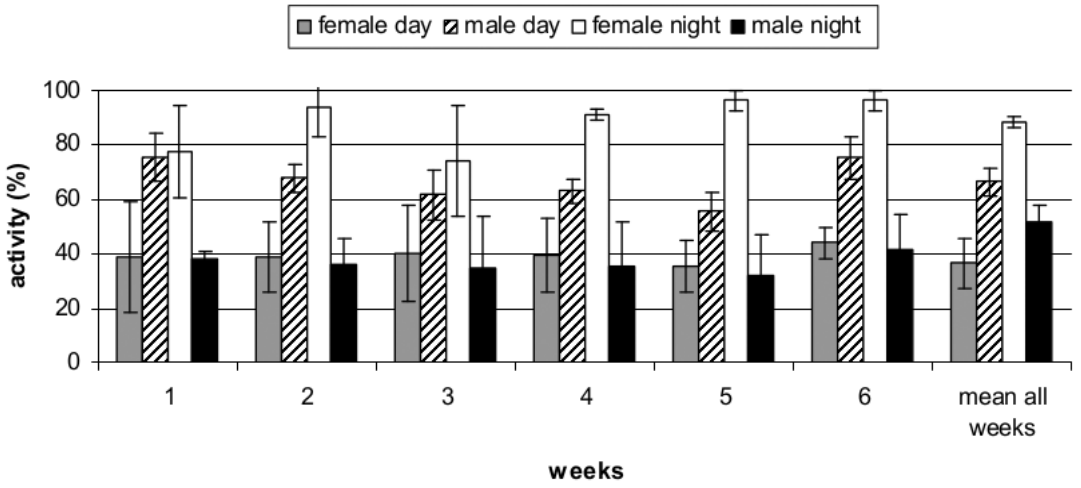


Fig. 5. Allocation of active fixes of adult female (n = 3) and male (n = 3) raccoon dogs in the first six weeks postpartum calculated during continuous 24 h radio-tracking sessions.

diurnal proportion of active fixes of 61.6 % ± 5.0 and 48.2 % ± 10.7 respectively. However, the differences between the sexes were not significant ($T = 1.96$, $df = 2.8$, $p > 0.1$) during the day. Nocturnal activity proportion for males (93.8 % ± 3.9 SD active fixes) and females (69.2 % ± 5.9 SD active fixes) did, however, differ significantly ($T = –6.0$, $df = 3.4$, $p = 0.006$).

Discussion

Monogamy is the most common form of social organization among dogs and foxes (Canidae, Kleiman 1977) and is often associated with living in pairs (Kleiman & Malcolm 1981). In the present study, paired mates displayed identical activity patterns and were mostly nocturnal throughout the year. This corresponds with the home range analysis, which showed paired mates roaming together in close vicinity with almost total overlap throughout the year (Kauhala & Holmala 2006, Drygala et al. 2008b).

However, activity rhythm of raccoon dogs changed to diurnal during pup rearing, when a significant difference in the proportion of activity of the paired mates was evident. Males showed a high level of diurnal activity while guarding the pups. Females, in contrast, rested for most of the day, often in the close vicinity of the den. Also in Białowieża Forest (Poland) raccoon dog paired mates rested longer together during the non-breeding period, than in the pup rearing period (Kowalczyk & Zalewski 2011). Young raccoon dogs are assumed to be very vulnerable to nocturnal predators (i.e. red foxes, badgers) and to hypothermia (Helle & Kauhala 1993, Kowalczyk et al. 2009), since ambient temperatures in North East Germany can be below 0 °C in May in the first weeks postpartum. This is reflected in differences between the activity patterns of the sexes during the night. Males were mostly inactive, resting with the pups in the den, while females foraged to satisfy their increased energy requirements during the lactation period. These activity patterns point to a clear division of labour between the parents during the period in which the pups are nursed and which is confirmed by space use and time allocation analyses (Kauhala et al. 1998, Drygala et al. 2008c). Changes in activity pattern between paired mates seem to be the rule in socially monogamous canids. For example bat-eared fox (*Otocyon megalotis*) males spent significantly more time in the den vicinity than females between the birth and weaning of cubs and, with the exception of lactation, were involved in all aspects of pup care (Wright 2006).

We suggest that the beneficial nature of male care is related to the species' diet and we can make the assumption that within our research area, food was relatively abundant and food patches were densely distributed. Males were able to carry small and medium size food items to the den within a short amount of time. Thus, providing food to support the lactating female and a fast-developing litter is energetically profitable (Drygala et al. 2008c) and can make social monogamy the optimal mating strategy for males as well as females. Circadian activity patterns show that raccoon dogs are mainly nocturnal throughout the seasons but also consistently diurnal except in winter. A distinct positive correlation between day length and diurnal activity indicates that summer nights are too short for the animals to obtain sufficient food. Because the raccoon dog is more of a gatherer than a hunting predator (Kauhala et al. 1993) and relies on small food items (Drygala et al. 2000, Sutor et al. 2010), it adapts its activity accordingly. Diurnal activity as well as resting

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behaviour usually takes place in thick vegetation (Ward & Wuster-Hill 1989, Drygala et al. 2008a, Kowalczyk & Zalewski 2011) and is made possible, we assume, by the lack of large predators in our study area. Moreover, dependence on dens was only confirmed for the pup rearing period and during frosty winter periods. However, also during warmer periods of the year, raccoon dogs do use parts of badger dens in Poland (Kowalczyk et al. 2008). Nonetheless, the raccoon dog is a rather slow and clumsy animal which roams at a low mean speed (Saeki 2001). Its preference to forage and rest in dense vegetation during the day (Kowalczyk & Zalewski 2011) allows it to avoid other potential threats (e.g. domestic dogs, hunters).

As suggested by home range size estimates (Drygala et al. 2008b), raccoon dogs do not hibernate in Germany but do reduce their activity. In cold climates, raccoon dogs may hibernate during the winter (Kauhala & Saeki 2004). In Finland, hibernation usually lasts from November to March but when the winter is mild raccoon dogs may be active even in mid-winter. They usually sleep when the air temperature is < –10 °C, snow depth > 35 cm and day length < 7 h. However, winter dormancy may not be very deep; though animals stay in their dens during harsh weather, they often move about within them, falling into deep sleep only for short periods (Kauhala et al. 2007).

In Poland, where winters are fairly severe, raccoon dogs were lethargic from December to February or March, depending on the weather (Jędrzejewska & Jędrzejewski 1998). Dormancy started when the temperature dropped below –8 to –10 °C. During warmer periods of the winter, raccoon dogs sometimes left their burrows but never strayed further away than about 50 m. December and January were the only months during which no raccoon dog tracks were found in the regular feeding places of wild boar (Włodek & Krzywiński 1986).

In the temperate climate of North East Germany, where winters are milder and there is less snow, raccoon dogs are active throughout the winter. In our study area it is assumed that food is abundant year round and winter is not a critical period. Rodents, carrion (especially innards and the leftovers from game hunting) and vegetable matter (e.g. maize from bait stations for wild boar) are abundant in winter. Raccoon dogs start the winter in good condition too, weighing in at 8.2 kg ± 0.6 SD, n = 7 in autumn (October and November) (Drygala unpublished data). There was a weak correlation between temperature and activity and at temperatures below –5 °C raccoon dogs reduced their activity and sometimes stopped foraging for short periods. Their energy demands in winter are assumed to be low and they rely entirely on stored fat reserves. Raccoon dogs do not need to undergo winter dormancy, and just reduce their activity and home range size in Central Europe (Drygala et al. 2008b). Consequently, the condition of raccoon dog females in March (the mating period) is good, regardless of the weather and food availability during the winter and they are able to invest heavily in reproduction (9 pups in averaged, Boge 2006).

This combination of favourable circumstances, efficient breeding system and flexible behaviour is very likely to have supported the expansion of the species in Central Europe and will most probably continue to do so in the future.

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