Home range of the badger (*Meles meles*) in a heterogeneous landscape in Denmark

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Abstract: Spatial organisation of badgers (*Meles meles* L. 1758) in a heterogeneous landscape in Denmark was studied during 1997-1999. The landscape was dominated by intensively managed agricultural and forest areas, traversed by streams surrounded with bogs and meadows. Seven habitat types were characterised according to land use and vegetation. Home range size estimated by radio-telemetry varied between 2.96 km^2 and 3.94 km^2 (100% minimum convex polygons). Individuals from a social group had similar home ranges (95% overlap), whereas home ranges of individuals from neighbouring social groups had little overlap (1-2%). Travelling distances up to 6.9 km per night were observed. Males had larger activity centres than females. Individual habitat selection differed considerably. Most badgers avoided agricultural areas and villages, but no habitat types were preferred or avoided by all individuals. Large home range sizes and long nocturnal travelling distances compared to other temperate regions in Europe indicate that heterogeneous Danish landscapes provide few stable food patches for badgers. We suggest that the natural seasonal and spatial variability of food resources is amplified in areas dominated by managed forests and large-scale arable lands resulting in low population densities of badgers in Denmark.

Keywords: badger, *Meles meles*, home range, space use, habitat use.

Introduction

Badgers (*Meles meles*) live in social groups occupying a common sett and territory (Kruuk 1989). Several studies have illustrated the badgers' ability to accommodate their spatial organisation to environmental conditions, habitat variability and human landuse throughout the geographic range (e.g. Cheeseman et al. 1981, Kruuk & Parish 1987, Nolet & Killingley 1987, Brøseth et al. 1997, Feore & Montgomery 1999, Revilla & Palomares 2002). The flexible spatial organization and ecology results in considerable variations in badger densities (0.12-38 individuals per km^2), social group sizes (2 to >20), and territoriality (0.2-25.5 km^2) (Johnson et al. 2002, Kowalczky et al. 2003).

The resource dispersion hypothesis (RDH) is currently the most widely acknowledged explanation for the social group living of badgers (Kruuk & Macdonald 1985, Kruuk 1989). The RDH proposes a set of conditions that permit group formation. The RDH hypothesizes that a patchy, unpredictable but abundant dispersion of food resources determines territory sizes of social groups and that richness of the food patches determines social group size. The social organisation reverts to the general spacing pattern of solitary individuals when the population is under food stress or the population is based on non-patchily distributed food resources (Kruuk & Parish 1987, Revilla & Palomares 2002).

Badgers are usually associated with mosaic landscapes comprising deciduous forests and permanent pastures in northwestern Europe (Neal & Cheeseman 1996). Particularly in the British Isles badgers may occupy small territories and attain high densities, whereas territories are larger and densities are considerably lower in

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forest dwelling populations in Eastern Europe and scrublands in Spain (Johnson et al. 2002, Revilla & Palomares 2002, Kowalczky et al. 2003). In highly managed landscapes habitat deterioration may restrict badgers to small patches fragmented by large matrixes of sub-optimal agricultural areas reducing abundance and survival of badger populations (Virgós 2001).

The objectives for the present study were to examine home range size and habitat use of badgers in a characteristic, managed heterogeneous landscape in Denmark. No detailed studies on spatial organisation of badgers in Denmark have been published. The study was part of a larger investigation on the ecology of badgers in Denmark (Pertoldi et al. 2000, Pertoldi et al. 2001, Madsen et al. 2002, Pertoldi et al. 2003, Pertoldi et al., in press, Prang et al., in prep.).

Materials and methods

Study Area

The study was performed in eastern Jutland in Denmark (56°27´N, 09°47´E) (figure 1). Mean annual temperature was 8.2°C and mean annual precipitation was 783 mm in the study period (Danmarks Meteorologisk Institut 2004). The mean daily temperature varied between –1.3°C in January and 16.6°C in August. The study area is a mosaic landscape comprising intensively managed agricultural lands and forest areas traversed by streams surrounded by large bogs and meadows. Land cover data were based on a national mapping (Areal Information System, Nielsen et al. 2000). To analyse habitat selection the landscape was categorised in seven biotopes

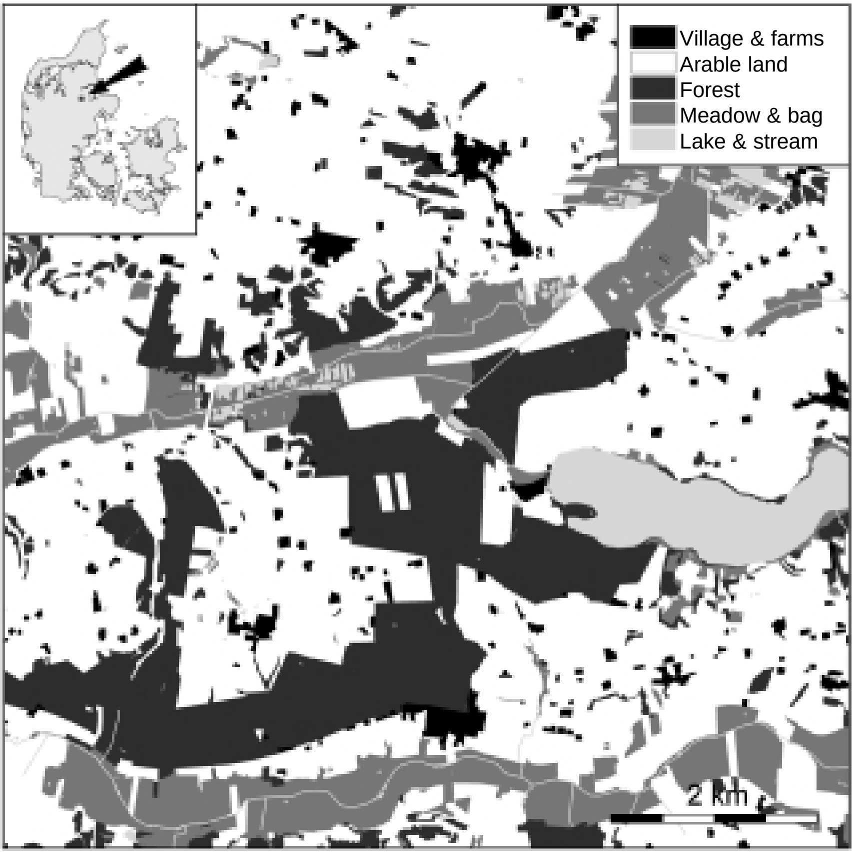


Figure 1. The study area in eastern Jutland in Denmark. The habitat types deciduous forest, coniferous forest and scrubs have been combined for clarity.

according to land use and vegetation: agricultural, coniferous forests, deciduous forests, scrubs, meadows, bogs, and villages and farm buildings. Coniferous forests were dominated by dense stands of Norway spruce (*Picea abies*) with no herb vegetation on the forest floor. Deciduous forests comprised mainly mono-aged beech (*Fagus sylvatica*) stands and minor stands of oak (*Quercus* sp.) and ash (*Fraxinus excelsior*). Old deciduous forests had herb vegetation and undergrowth. Vegetation in scrubs consisted of grassland with trees and bushes. Willow (*Salix* sp.), alder (*Alnus glutinosa*), and birch (*Beluta* sp.) dominated the vegetation in the bogs. Meadows were characterised by rich mixed herb vegetation.

Study animals and radio telemetry

Badgers were caught in box traps placed near eight main setts. Trapping was performed in September 1997 and in spring and summer 1998 and 1999. The captured badgers were immobilised with an intramuscular injection of medetomidine (0.12 mg/kg) and ketamine (6 mg/kg) and marked subcutaneous with a microchip. Age was estimated from body weight and tooth wear. Reproductive status of females was recorded. A total of 22 badgers was caught (including twelve cubs). Eight adult and two subadult badgers were fitted with radio-collars (Televilt, Ramsberg, Sweden) (table 1). The badgers were located by triangulation using a handheld antenna. Discontinuous radio-tracking (Harris et al. 1990) was conducted from September 1997 to December 1999. The majority of radio-tracking was conducted during 8-hour sessions over four consecutive nights during spring (March-May) and summer (June-August) in 1998 and 1999. It was attempted to locate each individual badger once an hour throughout the tracking sessions. Total distances travelled by individual badgers were estimated when more than three radio-locations were obtained during an activity period and diurnal resting sites were known.

Home range estimates and habitat use

Spatial analyses were performed in an ArcView GIS environment (Environmental System Research Institute Inc., Redlands, California, USA). Home ranges were calculated using the Arc View extension programme Animal Movement (Hooge & Eichenlaub 1997). Home ranges were estimated as 100% minimum convex polygons (MCP) (Mohr 1947). The MCP home range estimate facilitates comparison with bait-marking studies and it has no assumption about the statistical distribution of observations (Harris et al. 1990). The MCP index is strongly affected by sample size and requires large sample sizes to reach an asymptote (Ford & Myers 1981). In the present study more than 50 radio-locations were

Table 1. Sample periods of radio-collared badgers. M = males, F = females. M2 lost its collar in 1998, but was trapped again in the following spring.

ID	Age	Date of capture	Radio-tracking period	Cause of termination
M1	Adult	September 1997	3 months	Transmitter lost
M2	Adult	March 1998	3 months	Transmitter lost
		February 1999	3 months	Transmitter lost
M3	Adult	March 1998	3 months	Transmitter lost
M4	Adult	March 1998	18 months	
M5	Adult	March 1998	2 months	Transmitter lost
M6	Adult	March 1998	17 months	Traffic killed
F1	Subadult	April 1998	19 months	Traffic killed
M7	Adult	February 1999	3 months	Transmitter lost
F2	Subadult	April 1999	7 days	Transmitter failure
F3	Adult	June 1999	6 months	

required to obtain asymptotic MCP home range sizes. Overlap between home ranges was calculated as percentage overlap between individuals' MCP. Activity centres were derived as fixed kernel home range estimates (Seaman & Powell 1996). The study area was defined as the minimum convex polygon encompassing all radio-locations and a surrounding 3 km buffer zone. Availabilities of the different habitat types described above were determined as the proportions of the habitats in the study area and in the MCP home ranges of individual badgers. Likewise, for each badger the proportion of radio-locations within each habitat type was calculated. Two methods were used to analyse the habitat utilisation on the same data: the compositional analysis (Aebischer et al. 1993) and the method described by Neu et al. (1974). The two methods have different scope of analysis and different shortcomings affecting the validity of the analysis, often at the statistical level. The problems are discussed below.

Results

A total of 1044 radio-locations were collected. Home range sizes and habitat use were estimated from 577 radio-locations of active badgers. Radio-locations of M4 from the second year were excluded from home range size and habitat use analyses as frequent trappings of M4 (occasionally twice a night) confounded their validity. Based on trapping record and observations the maximum size of social groups was four and two cubs.

Individual home ranges varied between 2.96 km^2 and 3.94 km^2 (table 2). Individuals from the same social group (M6 and F1) had a 95% overlap of the home ranges (figure 2). M1 also belonged to this social group. All locations of M1 were within the home ranges of M6 and F1. Insufficient numbers of radio-locations were obtained to estimate M5's and M7's individual range. They were trapped at the same main sett and had 85% overlap of ranges. The home range of their social group was estimated to 4.23 km^2 by combining the radio-locations of M5 and M7.

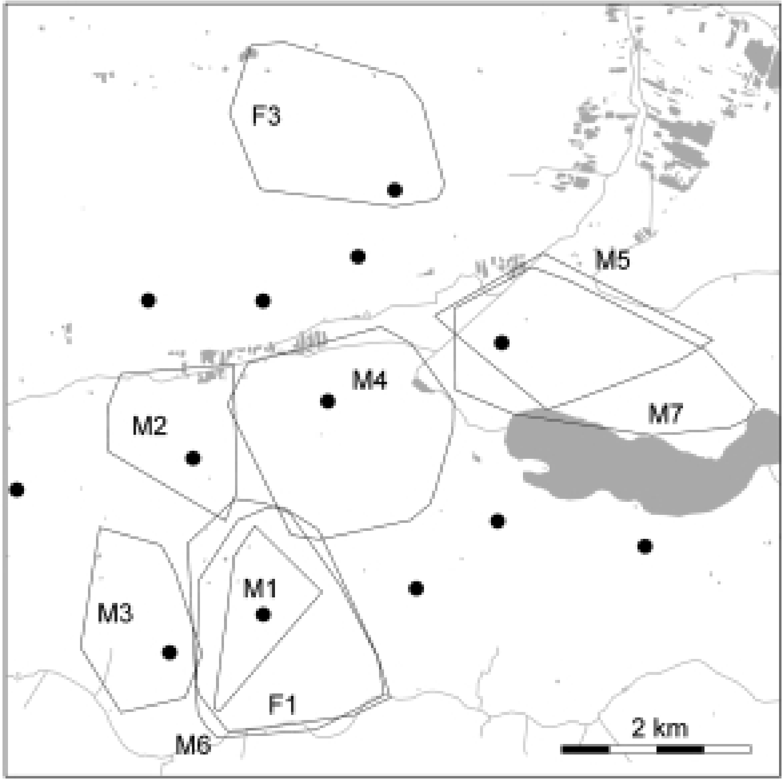
Home range overlap between neighbouring social groups was 1-2%. Home ranges of social groups were stable between years. A bait-marking study performed in the year prior to the radio-tracking (Madsen 1999) identified territory boundaries similar to home ranges of M6 and F1 as determined by radio-tracking. An adult female trapped at their main sett was radio-tracked in 1992 (Taastrøm 1993). Its home range overlapped with 97% of the present range of the social group. Combining results from radio-tracking and bait-marking studies the home ranges of M2's and M3's social groups were respectively 2.39 km^2 and 2.29 km^2.

Mean total distance travelled by individual badgers was 3.42 ± 1.44 km (range 1.67-6.90

Table 2. Home range sizes (km2) estimated as 100% minimum convex polygons (MCP) and fixed kernel isolines. Kernel estimates are 95% (K95), 90% (K90), 75% (K75), and 50% (K50) isolines. The analyses of M4 were based exclusively on the radio-locations from 1998. *Home range estimates only indicative figures as numbers of radio-locations were insufficient.

ID	Active radio-locations	MCP	K95	K90	K75	K50
M1	23	1.04*				
M2	48	1.62*				
M3	29	1.77*				
M4	74	3.94	5.03	4.02	2.32	0.59
M5	31	2.55*				
M6	109	3.84	5.00	4.33	2.34	0.54
F1	139	3.54	4.02	3.11	1.47	0.43
M7	29	3.69*				
F2	3	–				
F3	95	2.96	1.61	0.95	0.23	0.11

Figure 2. Home ranges (100% minimum convex polygons) of badgers and dispersion of active main setts. Figure frame as in figure 1. Grey areas indicate lakes and streams.



km) (n=30). No difference was detected between nocturnal travelling distances of males and females (t=1.08, df=28, N.S.). Activity periods up to 8 hours per night were observed. The area covered by males on single nights (MCP) tended to be larger than areas covered by females (males: n=12, mean 0.95 ± 0.73 km^2, range 0.14-2.08 km; females: n=18, mean 0.56 ± 0.46 km^2, range 0.09-1.93 km^2; t=1.78, df=28, P=0.09). Males covered larger areas per night than females during the summer season (June-August) (males: n=7, mean 1.15 ± 0.66 km^2, range 0.14-1.89 km^2; females: n=15, mean 0.60 ± 0.48 km^2, range 0.09-1.93 km^2; t=2.23, df=20, P<0.05). Up to 65% of the total individual home range (MCP) was covered during a single night. Estimated from fixed kernel isolines males had larger activity centres than females (table 2).

The compositional analysis revealed that the radio-tagged badger population used the available area randomly (table 3), i.e. no habitat type was preferred or avoided by all individuals (study area: λ=0.0751, N.S.; MCP area: λ= 0.0675, N.S.).

Analysis as described by Neu et al. (1974) showed that the habitat use of badgers was significantly different from habitat availability (χ^2=453.97, df=54, P<0.001). Large variability of individual habitat selection caused the high χ^2-value and no habitat type could be characterised as key habitat for all individuals. However, most individuals avoided agricultural areas and villages, and preferred deciduous forests. Habitat use within individual home ranges varied. Habitat availability within M6's and F1's individual home ranges was similar (χ^2=0.61, df= 6, N.S.) but while F1 used habitats as available in its home range (χ^2=4.76, df=6, N.S.), M6 tended to avoid agricultural areas (χ^2=23.18, df=6, P< 0.001). M4 used habitats as available within its home range (χ^2=10.90, df=6, N.S.). F3 had very high percentage of agricultural lands in its home

Table 3. Percentage of habitat availability and habitat use by badgers in a heterogeneous landscape in Denmark.

Habitat type	Habitat availability	Overall habitat use	
		Mean ± S.D.	Min.-max.
Agricultural	66.65	46.51 ± 15.94	27.59-72.41
Coniferous	8.02	13.80 ± 10.15	0.00-31.03
Meadows	6.70	4.73 ± 4.17	0.00-12.90
Bogs	6.24	7.49 ± 5.31	0.00-13.79
Deciduous	6.10	20.84 ± 11.40	0.00-37.93
Urban	4.75	2.06 ± 3.29	0.00-8.70
Scrubs	1.54	4.57 ± 3.55	0.00-8.70

range (86%) and showed a strong preference for deciduous forest (χ^2=153.47, df=5, *P*<0.001).

Discussion

Spatial organisation of badger populations across Europe correlates with environmental variables as determined by annual differences between maximum and minimum temperatures (Johnson et al. 2002). Furthermore, territory size is determined by the spatial dispersion and availability of earthworms, the principal food for badgers in most European populations (Kruuk 1989, Neal & Cheeseman 1996, Kowalczky et al. 2003). Home ranges of badgers in Denmark were larger than observed in other populations in the temperate region of Europe (Cheeseman et al. 1981, Kruuk & Parish 1987, Nolet & Killingley 1987, Herrmann et al. 1997). Home range sizes in Denmark were comparable to more harsh environments dominated by poor conifer forests in Norway, unimproved grasslands in Ireland, and scrublands in Spain (table 4) (Brøseth et al. 1997, Feore & Montgomery 1999, Revilla & Palomares 2002).

Travelling distances of badgers in Denmark were longer than reported in high-density populations in England (Neal & Cheeseman1996) but comparable to travelling distances measured in low-density populations in Spain (Revilla & Palomares 2002). Length of travelling distances and foraging trips increases with reduced availability of food resources (Kruuk 1989). Adult males travel longer distances, spend more time along territory boundaries and visit boundary latrines more than subadult males and females (Roper et al. 1993, Neal & Cheeseman 1996, Revilla & Palomares 2002). In the present study we did not detect such differences between males and females probably because of small sample size. However, males had larger activity centres and covered larger areas during a single activity period compared to females. Parental care may have influenced the size of activity centres and habitat utilisation of the females. F1 was a non-

Table 4. Data on density and territory size in badger populations in Europe (means or min.-max.).

Country	Territory size (km^2)	Density (ind./km^2)	Reference
England, Gloucestershire (mean)	0.22	28.53	Cheeseman et al. 1981
England, Wytham Woods (mean)	0.60	17.35	Johnson et al. 2002
Germany	0.60-1.10	1.9-2.9	Herrmann et al. 1997
Ireland, Castleward	0.50	11.90	Feore & Montgomery 1999
Ireland, Katesbridge	1.27	1.60	Feore & Montgomery 1999
Ireland, Glenwhirry	3.45	0.86	Feore & Montgomery 1999
Norway	5.4	–	Brøseth et al. 1997
Poland, Białowieza	12.8	0.15-0.21	Kowalczyk et al. 2003
Scotland, Aviemore	1.21	2.2	Kruuk & Parish 1987
Spain, Doñana NP	4.12	0.2-1.0	Revilla & Palomares 2002
The Netherlands	0.78	3.8-6.0	Nolet & Killingley 1987

breeding female when it was trapped. It was observed at a sett with a cub and may have functioned as a helper in the first year of the study. Its diurnal resting pattern during the second year and observations of cubs suggests that F1 had cubs (van Teeffelen et al. 2001). F3 was emaciated and had recently lactated when it was trapped in June. Four cubs were later trapped at the same sett.

The study area was centred in a forest area and trappings were conducted at setts in the forest area. Although densities of setts in areas dominated by agricultural lands are probably lower than in forest, the home ranges located in areas dominated by agricultural lands were not larger than home ranges with substantial forest areas. The absence of common habitat preferences for all individuals suggests that the badgers exploited food resources occurring in all the different habitats.

Earthworms (*Lumbricus* sp.) are the principle food item for badgers, but cereals and small mammals have a higher importance in Denmark (Madsen et al. 2002) than recorded in other food studies of badger populations in the temperate region of Europe (Kruuk 1989, Neal & Cheeseman 1996). Permanent pastures and deciduous forests are important for badgers as these habitats may house large populations of earthworms (Hofer 1988, Brøseth et al. 1997). A small study indicated that earthworm biomasses were low in our study area (401 kg/ha in pastures, 21 kg/ha in deciduous woodlands) (Madsen 1999). Earthworm biomasses in pastures and deciduous woodlands in high-density badger areas in England (Wytham Woods) were estimated to 971 kg/ha and 837 kg/ha, respectively (Hofer 1988). Only a few small patches were managed as permanent pastures in the study area. Most grass fields were intensively managed monocultures for ensilage production included in crop rotation schemes. As earthworms are long-living species, these grass fields may hold relatively small biomasses of earthworm. Furthermore, these grass fields may have minor importance to badgers as feeding patches as periods with low grass, which makes earthworms accessible for badgers, are short (Kruuk 1989). A small proportion of the meadows in the study area were grazed by cows (*Bos taurus*) or sheep (*Ovis aries*) but since meadows were often flooded during winter, they were an unfavourable habitat for earthworms.

The analysis of habitat utilisation by animals is a complex subject at the limit of the current methodology. The methods, which are commonly used or recommended, have their advantages and disadvantages, but no method is suitable for all studies (Neu et al. 1974, Alldredge & Ratti 1986, White & Garrot 1990, Aebischer et al. 1993). The compositional analysis focuses on habitat utilisation of the whole population with the number of animals as the sample size (Aebischer et al. 1993). This approach means that pooling data across animals is justifiable only if they do not differ, but all show the same preference/avoidance. This assumption is not fulfilled in the present study, as the animals showed individual variation in behaviour. In contrast to this the Neu-method uses Bonferroni confidence intervals, which make it possible to analyse the habitat utilisation of the individuals, where the tested variable are formed by the the radio-locations. However, the Neu-method uses the assumption that each individual observation has to be statistical independent. This assumption can be violated in several occasions in the present study. The positions of sequentially collected radio-locations from a tagged animal may be serially correlated and areas may be unavailable to an animal, as it may be constrained by the presence of other animals. The second assumption is probably not fulfilled in the present study as some of the individuals originate from the same sett. Furthermore, the activity of an animal is probably also affected by animals from neighbouring setts. We attempted to reduce this interaction by defining the minimum convex polygon as the area available to the animals.

The dispersion of habitat patches containing the important food resources determines territory sizes of badgers (Kruuk 1989). In accordance with the resource dispersion hypothesis, badgers may be characterised as a contractor species in high population density areas with relatively stable food resources (Kruuk & Macdonald 1985). We need a more comprehensive assessment of the spatial distribution of the food resources and social group size to make accurate classifications of habitat qualities and evaluate the RDH for badgers in Denmark. However, despite a small sample size and methodological limitations in the present study, the large home range sizes and long travelling distances per night suggest that the heterogeneous landscape in Denmark with intensively managed arable lands and managed forests provide relatively few food patches for badgers. We suggest that the larger seasonal and spatial variability of food resources in intensively managed landscapes results in larger home ranges and lower population densities of badgers in Denmark compared to other populations in temperate regions of Europe.

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Samenvatting

Homerange van de das (*Meles meles*) in een heterogeen landschap in Denemarken

Het ruimtelijk gedrag van de das (*Meles meles* L. 1758) werd onderzocht in een heterogeen landschap in Denemarken in de periode 1997-1999. Het studiegebied werd gedomineerd door intensieve landbouw en productiebos, en doorsneden door watergangen, veengebied en graslanden. Ten behoeve van dit onderzoek werden in het landschap, naar beheer en begroeiing, zeven habitat-typen onderscheiden.

Posities van de dieren werden bepaald met behulp van radio-telemetrie. De groottes van de hiermee geschatte homeranges varieerden tussen 2,96 km^2 en 3,94 km^2 (100% minimum convex polygons).

Dieren van een sociale groep deelden hun homerange (gemiddeld 95% overlap tussen homeranges), terwijl homeranges van dieren uit naburige groepen weinig overlap hadden (gemiddeld 1-2%). Verplaatsingen tot 6,9 km per nacht werden waargenomen, waarbij mannelijke dieren

grotere activiteitscentra hadden dan vrouwen. Habitatvoorkeuren verschilden aanzienlijk tussen individuele dieren. De meeste dassen vermeden landbouwgebied en dorpen, maar geen enkel habitat-type werd gemeden of geprefereerd door alle individuen.

Vergeleken met studies in andere gebieden in Europa waren in dit studiegebied homeranges groter en nachtelijke trektochten langer. Dit lijkt erop te wijzen dat het heterogene Deense landschap de das weinig stabiele foerageerlocaties biedt. We stellen voor dat de natuurlijke variatie in ruimte en tijd van voedselbronnen groter is in gebieden met veel productiebossen en grootschalige landbouw, met als gevolg grote homeranges en een lage populatiedichtheid.

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