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Z. Säugetierkunde **62** (1997) 12–22
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Spatial organization and habitat utilization of badgers *Meles meles*: effects of food patch dispersion in the boreal forest of central Norway

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Receipt of Ms. 08. 12. 1995
Acceptance of Ms. 17. 09. 1996

Abstract

Habitat utilization, home range size and territory size in relation to food availability for badgers (*Meles meles* L.) were studied for eight months in coniferous forest influenced by agricultural activity in central Norway. The diet in both spring and autumn was dominated by earthworms; berries formed only an insignificant part of it in autumn. Earthworms in soil samples were unevenly distributed among different biotopes, with the highest earthworm biomass found in deciduous forest. Earthworm biomass was higher under cowpats on pasture, which increased the predictability of potential badger food. There was no difference in the composition of the home ranges between spring and autumn, but different biotopes within them were utilized. Deciduous forest was much used in both seasons, and the use of pastures increased in autumn. The dispersion of patches of deciduous forest within the group territories accounted for much of the observed variation in territory size.

Introduction

The dispersion and abundance of resources affects spatial and social organization in many birds and mammals (e. g. Davies 1991). The resource dispersion hypothesis (RDH) predicts that spatial organization will be determined by the dispersion of resource patches and that group size will be determined by the richness of these patches when animals occupy the smallest economically defendable area (Macdonald 1983 a; Kruuk and Macdonald 1985).

The European badger (*Meles meles* L.) has received much attention in connection with theories on the evolution of group living in carnivores, but we do not fully understand the advantages that influence this solitary forager to select group living in many populations. Attempts to explain the spatial and social organization of badgers have centred around food dispersion (e. g. Kruuk and Parish 1982; Macdonald 1983 a; Kruuk and Macdonald 1985; Woodroffe and Macdonald 1993). Spatial organization has been classified as territorial, with territories of a minimum size (Kruuk and Macdonald 1985), and the RDH permits one to predict that for a given food patch richness, territories will be larger where patches are more dispersed (Macdonald 1983 a).

Within the wide geographical distribution area of the badger in the Palaearctic (Neal 1986) there is a great variation in spatial and social organization among different badger populations, from groups to a solitary lifestyle (Woodroffe and Macdonald 1993). Many populations form stable social groups with 3–29 individuals (Cheeseman et al. 1987; Silva et al. 1994) of mixed age and sex where the members share a territory and occupy communal setts, but forage alone (Kruuk 1978). These groups are formed mainly by retention

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of individuals in their natal territory (Silva et al. 1994). Within the group territory, individual badgers can have different ranges (Kruuk 1989), and home ranges vary in size from 14 ha (Gloucestershire, England: Cheeseman et al. 1981) to 983 ha (Doñana, Spain: Rodrigues et al. 1996).

With regard to food, badgers are characterised as opportunists (reviewed in Roper 1994). Studies have shown that different food can dominate in the diet of badgers, e. g. cereals (Shepherdson et al. 1990), fruits and insects (Pigozzi 1991), fruits (Rodríguez and Delibes 1992) and rabbits (Martín et al. 1995). In common with many other studies on the diet of badgers in northern Europe (e. g. Kruuk and Parish 1981; Lüps et al. 1987; Neal 1988), investigations in Scandinavia have shown that earthworms are the most important prey (Skoog 1970; Lindström 1989). But, food consumption and the utilization of different types of food can be expected to change during the year as they become available (Kruuk and Parish 1981; Pigozzi 1991). Earthworms are rich in protein, essential amino acids, and fat (Macdonald 1983 b). They are likely to be particularly important in spring and early summer when badgers need to replenish resources used during their winter sleep and reproducing females have their lactation period. Berries, rich in carbohydrate, can be important to build up fat reserves when they become available during the autumn (Lindström 1989).

In this study, we analyse the diet, food availability, habitat utilization, home range size, and territory size of badgers in part of the boreal forest of central Norway, one of the northernmost reproducing badger populations in Scandinavia (Bevanger and Lindström 1995), to evaluate their spatial organization.

Material and methods

Study area

The study was carried out in the municipality of Malvik (63° 18′–63° 27′ N, 10° 35′–10° 57′ E), in the county of Sør-Trøndelag, in 1993. The area is in the middle boreal region and comprises 60 km^2 of coniferous forest affected by agricultural activity, restricted by a river in the north, a lake in the south and hills of high altitude in the east and west (Fig. 1). Heifers and sheep roam freely beyond the fenced-in

Fig. 1. The study area (60 km^2) at Malvik, Sør-Trøndelag county, Norway. Black areas: deciduous forest and agricultural land, grey areas: coniferous forest and fen, white areas: water

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farmland from the beginning of June to mid-September. The area is chiefly situated 200–500 m above sea level, but extends above the climatic tree line near its eastern edge; large parts are hilly with rocky slopes. The mean annual temperature is 1.5 °C (January–5.8 °C and July 9.8 °C), the mean annual precipitation is 1260 mm (min. May and max. September), and there are on average 163 days with snow cover (the depth peaking in February–March).

Maps (1 : 5 000) from the Norwegian Mapping Authority and field surveys were used to construct a habitat map over the study area, based on vegetation communities and soil fertility (Tab. 1) (Fremstad and Elven 1987). We vector-digitized the habitat map as a thematic polygon map (Burrough 1986), using a geographical information system (GIS), where polygons divided the habitat into biologically meaningful subunits (biotopes) suitable for analysis in the context of patch theory (Haslett 1990). The software used for creation of the habitat map was PC ArcInfo 3.4 d+ (ESRI 1990). Calculation of total area, mean polygon size and number of polygons for different biotopes were done by importing ArcInfo PAT-files into the software of SPSS for windows, release 6.0 (SPSS Inc. 1993).

Table 1. Biotopes classified in the area studied at Malvik, in the boreal forest of central Norway

Biotope	% of area	Characteristica
Poor coniferous forest	62.2	Coniferous forest on poor soil and rocks. Mainly spruce (*Picea abies*) and some pine (*Pinus sylvestris*). *Vaccinium* spp. common in the field layer.
Rich coniferous forest	17.3	Coniferous forest (spruce) on rich soil. Field layer with some low and tall herbs. >50% of area covered by conifers.
Deciduous forest	1.3	Deciduous and mixed deciduous forest on rich soil. Mainly white birch (*Betula pubescens*) with some aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and alder (*Alnus incana*). <50% of area covered by conifers. Field layer rich in low and tall herbs.
Fen	10.1	Moist area rich in mosses. Poorly developed tree and shrub layer.
Arable land	3.6	Grassland harvested twice a year. Renewed every 3–5 years by ploughing. Monoculture.
Pasture	1.0	Former arable grassland now harvested by cows (*Bos taurus*) and sheep (*Ovis aries*) from late-June to late-September.
Water	4.5	Small lakes and ponds

Diet identification

Badger faeces were collected from latrines near setts (n = 18) in two periods. Spring samples (n = 35) were taken until mid-July, before the expected diet shift to berries occurs (Skoog 1970). Bilberries (*Vaccínium myrtíllus* L.) were available to the badgers from July 20, cowberries (*V. vitis-idaéa* L.) somewhat later. In mid-July, every known latrine was visited and defecations were removed to avoid confusion between seasons. Autumn samples (n = 30) were taken until mid-October. Only fresh faeces were collected, and an attempt was made to take each sample from only one defecation. Prior to detailed laboratory analysis, they were stored in plastic bags at –18 °C as soon as possible after sampling, to stop the decomposition of earthworm gizzard rings.

Faecal analysis was mainly carried out according to the procedure developed by Kruuk and Parish (1981). Each faecal sample was washed through a mesh sieve (1.25 mm) using 500 ml of water, and three samples (1.5 ml) from each were examined under a 40× binocular microscope for the presence of

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earthworm chaetae. The food remains retained in the sieve after additional washing were put into a white tray with water, identified and counted. The line of best fit between the chaetae score (x) and the number of gizzard rings (y) in samples where the latter had not started to decompose was $y = 4.05\,x + 4.00$ ($r = 0.73$, $P < 0.001$, $n = 30$). This line was used to estimate the number of earthworms in samples where counting gizzard rings was impossible or uncertain. The number of gizzard rings give the absolute number of earthworms eaten. To obtain the best weight estimate of earthworms eaten by badgers in the study area, we estimated a mean earthworm weight from earthworm remains found in the stomachs of two dead badgers, victims of road accidents, found less than 3 km from the study area (2.54 g, n = 75).

To show the significance of different food items in the total diet we used frequency of occurrence and weight percentage of consumed fresh biomass, because these two measurements together are thought to give the best estimation of overall diet (Korschgen 1980). To reveal differences in diet between seasons we used the G-test to test for differences in the frequency of occurrence and the Mann Whitney U-test corrected for ties for the biomass consumed.

Earthworm availability

Earthworm availability was estimated by hand sorting (Edwards and Lofty 1977) in randomly selected polygons, six in each biotope, from the digitized map. In each polygon, a position was randomly selected and a rectangle (10×20 m) trending north-south was marked out. Using an iron frame, sample quadrats (20×20×15 cm) were removed for hand sorting at every 10 m, i. e. six samples per polygon. These soil samples were searched by hand in a white expanded polyester box, and all potential badger food was retained. The biomass in the soil samples was determined in the laboratory, and the mean fresh weight (g/m^2) was calculated for every biotope.

To find out whether faeces from domestic animals increased the biomass and the chance of earthworms being present, 18 soil samples that had a cowpat within the iron frame were taken from pasture land. The method was otherwise like that used for hand sorted, random soil samples. We used the Kruskall Wallis test to test for overall differences between biotopes and the Mann Whitney U-test corrected for ties to locate differences. Differences between samples taken under cowpats on pasture and random samples in the same biotope were tested by the Mann Whitney U-test corrected for ties.

Radio tracking

Between March and August 1993, 11 badgers (5 males and 6 females) were trapped at setts, in cage traps or leg-hold traps. The badgers were immobilized by an intramuscular injection of 2.5 ml of ketamine hydrochloride (cf. Cheeseman and Mallinson 1980) and taken to a veterinary surgeon who implanted a transmitter (Telonics: IMP/400/L, 142 MHz) in the abdominal cavity as described by Fowler and Racey (1988). The animals were sexed, weighed, marked with an individual number tattooed on the upper inside of the left hind leg, and a tooth (I^{3V}) was taken for age determination (Ahnlund 1976). Following the surgery, the badgers were given an intramuscular injection of an antibiotic (600 mg benzyl penicillin procain.) and returned to the sett where they were released.

The badgers were located by triangulation on irregular occasions from a car and on foot, using a hand-held, Yagi-type antenna connected to a VHF receiver (Televilt) and a compass (Silva Ranger: Type 15), or by direct observations (10.2%). Bearings were taken from at least two points, the time interval between them being less than five min. and the angle between them being as close to 90° as possible. Animals were located on average 2 times (range 1–5) during their activity period at night for on average 37 nights (range 9–58). Discontinuous locations were preferred because of their applicability in range and habitat utilization analysis (Harris et al. 1990).

Radio-tracking data were collected during two seasons: spring, mid-April to the beginning of July (8 animals), and autumn, the beginning of August to the beginning of October (9 animals). The division into two tracking periods was made because of the expected interseasonal shift in diet, with a consequent change in behaviour. On average, 50 fixes (range 21–65) were made on each animal each season. We calculated individual 95% minimum convex polygons as home range estimators separately for spring and autumn using Ranges IV (Kenward 1990). Territories were estimated by calculating 95% minimum convex polygons from fixes of animals in the same social group (more than 80% overlap in home range and at least three common setts, or for one animal: less than 20% overlap and no common setts). We used telemetry fixes to estimate territories because no boarder markings with latrines were

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found, as known from high density populations (cf. Kruuk 1989). The home range- and territory areas were copied as an ASCII text file from Ranges IV to ArcInfo where biotope composition and food patch dispersion could be calculated from the habitat map.

Habitat utilization was compared with availability, excluding water, using compositional analysis to reveal any habitat selectivity (Aebischer et al. 1993 a). Home ranges were compared with the study area, and fixes with home ranges. The proportion of fixes in different biotopes was found by creating a point coverage from an ASCII text file with the localizations and overlaying this with the digitized habitat map in ArcInfo. Overall deviation from random utilization was tested with χ^2 as the test statistic, the t-test being used to find where utilization deviated from random, and a ranking in the order of use was created (Aebischer et al. 1993 a). A MANOVA-test was used to test for differences in habitat use between seasons (Aebischer et al. 1993 b).

To evaluate spatial organization as predicted by the RDH, we analysed territory size in relation to food patch dispersion. A patch was defined as an area at least 20 m from the nearest area of same biotope, and over 0.05 ha in size. These seem to be distinguishable by badgers when foraging (Mellgren and Roper 1986). To measure food patch dispersion, we calculated the overall mean distance from the perimeter of each earthworm-rich patch (deciduous forest) to the perimeter of all other patches of deciduous forest within the territory, using ArcView (ESRI 1992). Regression analysis was used to test how patch dispersion affected the variation in size of the territories. With six badgers followed for both seasons, spring data were randomly selected from three of the animals and autumn data from the other three to use for habitat utilization analysis, together with data from all the badgers followed through one season. This was done to avoid dependence in the data between seasons. When spring and autumn data were analysed separately, every animal was used.

Results

The diet in the study area was dominated by earthworms both in spring (75.7%) and autumn (53.9%) (Tab. 2). There was no difference in the frequency of earthworms in the diet between seasons ($G = 1.04$, $P = 0.31$), but they constituted more of the fresh biomass consumed in spring than in autumn ($z = 3.44$, $P < 0.001$). There was no difference in the berries in the diet between seasons, neither for frequency ($G = 2.95$, $P = 0.09$), nor biomass ($z = 1.82$, $P = 0.07$). Frogs were the only food item showing any sign of seasonal diet shift; they were both taken more often in the autumn ($G = 19.93$, $P < 0.001$) and constituted a larger amount of the autumn diet ($z = 3.98$, $P < 0.001$).

Table 2. Diet of badgers in a boreal forest area in central Norway, expressed as frequency of occurrence (Freq) and percent of consumed fresh biomass in the total diet (% Bio)

Food item	Spring (n = 35)		Autumn (n = 30)	
	Freq	% Bio	Freq	% Bio
Earthworms	1.00	75.7	0.97	53.9
Amphibians (*Rana temporaria*)	0.20	4.5	0.60	25.0
Small rodents	0.29	7.7	0.20	5.7
Birds	0.23	3.4	0.17	3.0
Beetles	0.77	2.4	0.70	1.4
Other insects	0.66	1.5	0.83	3.7
Gastropoda	0.23	0.3	0.20	0.3
Berries	0.06	0.1	0.20	3.6
Carrion and domestic waste	0.20	4.3	0.13	3.2
Other or unidentified	0.14	0.1	0.03	0.2

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There were significant differences between biotopes in both total biomass potential badger food ($H = 120.4$, $df = 5$, $P < 0.001$) and earthworm biomass ($H = 124.8$, $df = 5$, $P < 0.001$), based on the soil samples (Tab. 3). Deciduous forest contained a greater earthworm biomass than all the other biotopes (z's all > 1.96, P's all < 0.05). Samples taken in pasture, and which had cowpats within the sample square, had higher earthworm biomass ($z = 2.25$, $P < 0.05$) and biomass of other potential badger food ($z = 5.98$, $P < 0.001$) compared with samples taken randomly in the same biotope.

The home ranges varied much in size, from 101 to 1489 ha. Male badgers had larger home ranges than females in spring ($z = 2.22$, $P < 0.05$), but no difference was found in autumn. Male ranges decreased while female ranges increased. from spring to autumn (Tab. 4).

Table 3. Total biomass and earthworm biomass found in hand-sorted soil samples taken in a boreal forest area in Malvik, central Norway

	Total biomass $g/m^2 \pm SE$	% earthworms of total biomass	n
Deciduous forest	100.2 ± 11.7	99.7	36
Pasture	65.8 ± 6.9	97.0	36
Rich coniferous forest	56.9 ± 9.1	99.6	36
Arable land	27.3 ± 5.6	98.2	36
Poor coniferous forest	2.1 ± 1.7	85.7	36
Fen	0.5 ± 0.2	20.0	36
Cowpat on pasture	168.9 ± 17.8	65.5	18

Table 4. Badger home ranges in spring and autumn, from a boreal forest area in Malvik, central Norway. M = male and F = female, * no data

Badger no.	Age (years)	Home range size (ha)		
		Spring	Autumn	Change
F1	4	209	292	+83
F2	3	152	348	+196
F3	1	168	302	+134
M1	5	725	466	–259
M2	4	1 489	627	–862
M3	1	531	284	–247
F4	3	251	*	*
F5	2	224	*	*
M4	2	*	170	*
M5	0	*	101	*
F6	9	*	124	*

There was no significant difference in the biotope composition of the home ranges between seasons ($\Lambda = 0.690$, $P = 0.80$, $n = 11$). The home range selection made by badgers within the study area was clearly not a random one ($\chi^2 = 28.64$, $df = 5$, $P < 0.001$). They used biotopes in the following order: deciduous forest > pasture > arable land > rich coniferous forest > fen > poor coniferous forest. There was no detectable difference between the three top-ranking biotopes (t's all < 1.9, $df = 10$, P's all > 0.05), but there was a clear contrast between those and the lower ranking ones (t's all > 2.9, $df = 10$, P's all < 0.05).

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When fixes were compared with home ranges, a difference in biotope use within home ranges was found between spring and autumn ($\Lambda = 0.132$, $P = 0.03$, $n = 11$). The only biotope showing any significant seasonal effect was pasture ($F_{1,9} = 6.47$, $P = 0.032$). Biotope use was not random, either in spring (8 animals, $\chi^2 = 21.80$, $df = 5$, $P < 0.001$) or autumn (9 animals, $\chi^2 = 19.84$, $df = 5$, $P < 0.005$). In spring, the ranking of biotopes in order of use was: deciduous forest > rich coniferous forest > poor coniferous forest > arable land > pasture > fen. Deciduous forest was used significantly more than the other biotopes in spring (t's all ≥ 3.00, $df = 7$, P's all < 0.05). The ranking in biotope use in autumn was: pasture > deciduous forest > arable land > poor coniferous forest > rich coniferous forest > fen, with no significant difference between the three top-ranking biotopes (t's all < 1.6, $df = 8$, P's all > 0.10), but there was a clear contrast between those and the lower ranking ones (t's all ≥ 2.53, $df = 8$, P's all < 0.05).

The group territories varied from 203 to 910 ha (Fig. 2, Tab. 5), but showed no correlation with the area of deciduous forest ($r = 0.01$, $P = 0.50$, $n = 4$). Territories increased in size as the number of deciduous forest patches increased ($r = 0.99$, $P < 0.01$, $n = 4$) at the same time as mean size of deciduous forest patches decreased ($r = -0.95$, $P < 0.05$, $n = 4$). Dispersion of deciduous forest patches accounted for much of the observed variation in territory size ($r^2 = 0.90$, $P = 0.05$, $n = 4$, Fig. 3).

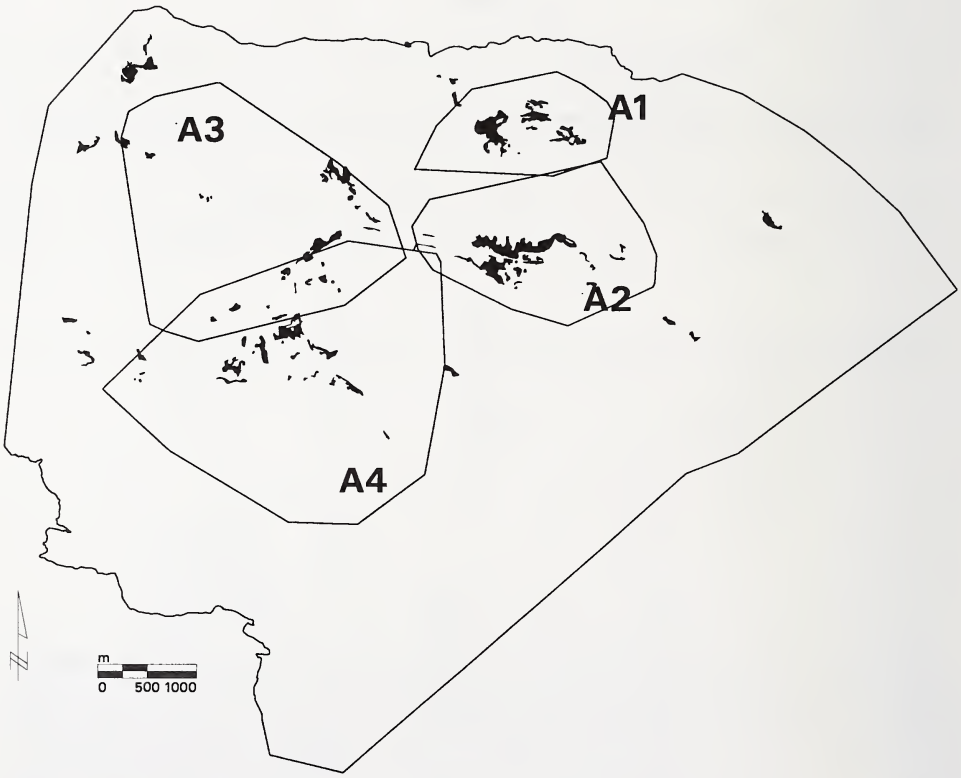

Fig. 2. Territories of four adjacent badger groups and dispersion of deciduous forest patches (black areas), in a boreal forest area of central Norway. (A1–A4 refers to territories in Tab. 5)

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Table 5. Territory size, amount of deciduous forest, number of deciduous forest patches and mean dispersion of deciduous forest patches within badger group territories in Malvik, central Norway

Territory	Number of badgers	Territory size (ha)	Amount of deciduous forest (ha)	Number of patches	Dispersion of patches (m)
A1	3	203	15.4	7	377
A2	3	368	22.1	15	688
A3	1	678	14.7	22	1 134
A4	3	910	18.8	33	1 137

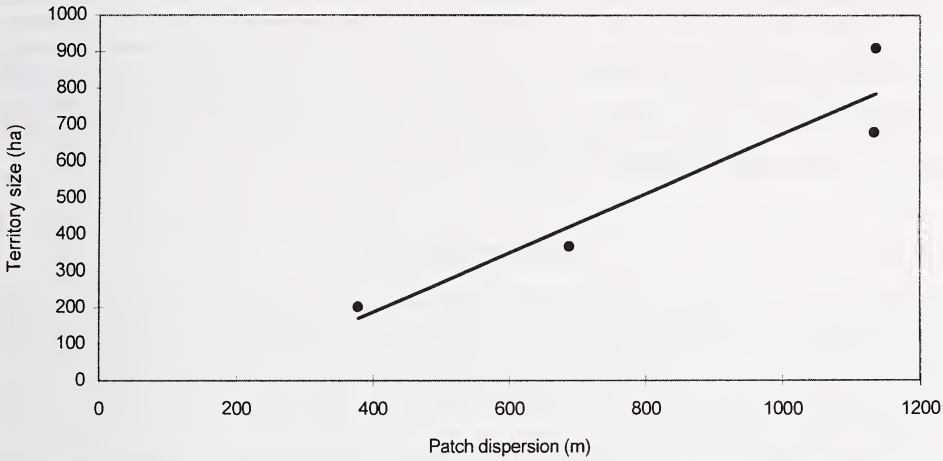

Fig. 3. Dispersion of deciduous forest patches accounted for 90% of the observed variation in territory size for badgers living in a boreal forest area in central Norway ($r^2 = 0.90$, $P = 0.05$)

Discussion

Dispersion of deciduous forest patches accounted for 90% of the observed variation in badgers territory size in the study area, even though the territories showed considerable variation in size and were huge compared to what is found in many other populations (reviewed in Woodroffe and Macdonald 1993). Earlier studies of badger populations living in more earthworm-rich habitats in the British Isles have shown that dispersion of important food patches can indicate the size of badger territories and that badgers adjust the confguration of their ranges in accordance with these earthworm-rich patches (Kruuk and Parish 1982; Silva et al. 1993), but such informations have been lacking from badgers living in a boreal habitat.

Recently, evidence has been put forward indicating that in some populations available sett sites can affect the spatial organization of badgers (Doncaster and Woodroffe 1993; Roper 1993). However, in the boreal forest of central Norway, where a territory on average contains twelve different setts (own unpubl. data), this seems less likely.

In the boreal forest studied, where large coniferous forest areas containing few earthworms surround the agricultural land and the deciduous forest that is rich in earthworms, badgers prefer to forage in biotopes with high earthworm biomass both in spring and autumn. We found no increased utilization of poor coniferous forest nor any large quantities of berries in the diet in autumn, as shown in earlier studies from the boreal forest at

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Grimsö, south-central Sweden (Seiler et al. 1995; E. Lindström pers. comm.). Although utilization of poor coniferous forest increased during the autumn at Grimsö, earthworm-rich biotopes were still most used (E. Lindström pers. comm.). One possible explanation of the observed differences between the two boreal areas might be that earthworms were so readily available and numerous during the year of our study that the badgers did not eat berries (Shepherdson et al. 1990).

However, although no increased utilization of poor coniferous forest was found, badgers increased their utilization of pasture in autumn. In Scotland Kruuk (1989) found that badgers used places with high accumulations of sheep faeces as foraging patches. Such accumulations of faeces from domestic animals concentrate the availability and increase the predictability of earthworms (Lee 1985), thus making pasture a profitable biotope for badgers to forage at this time of year.

In spring resident males make extra-territorial movements and it is not uncommon with extra-group matings (Evans et al. 1989). Such behaviour can explain why male badgers in the boreal forest of central Norway had larger home ranges than females in spring. In our study area, where large poor coniferous forest areas surround the more utilizated biotopes rich in earthworms, there are probably good possibilities for male badgers to roam over large areas, searching for receptive females.

Acknowledgements

We are grateful for the financial support given by the NINA institute program on landscape ecology, the County Governor's office for environmental affairs in Sør-Trøndelag and the University of Trondheim. We would like to thank John Atle Kålås and Jon E. Swenson for useful comments on earlier drafts of this manuscript, and the North European badger group for helpful collaboration over many years. We also thank Torgrim Sund from Asplan Viak and the Sør-Trøndelag County Agricultural and Forestry Office for help to prepare the digitized polygon map, and the veterinary surgeon, Ingolf Hansen, for implanting the radio transmitters. We are indebted to Richard Binns for improving the English, and Andreas Seiler for help with the Zusammenfassung.

Zusammenfassung

Räumliche Organisation und Habitatnutzung von Dachsen (Meles meles): Verteilung der Nahrungsbiotope im borealen Mittelnorwegen.

Der Einfluß von Nahrungsangebot auf die Habitatnutzung sowie auf Streifgebiets- und Reviergröße von Dachsen (*Meles meles* L.) wurde über einen Zeitraum von acht Monaten im borealen, landwirtschaftlich geprägten Mittelnorwegen studiert. Die Nahrung bestand sowohl im Frühling als auch im Herbst vorwiegend aus Regenwürmern. Beeren spielten nur eine untergeordnete Rolle während des Herbstes. Das Vorkommen von Regenwürmern war sehr fleckenhaft, die größte Biomasse fand sich in Laubwaldbiotopen. Hohe Regenwurmdichten fanden sich ebenfalls unter Kuhfladen in den Weidegebieten, wodurch die Biomasse und die Vorhersagbarkeit von potentieller Dachsnahrung erhöht wurde. Zwischen Frühling und Herbst fand sich kein Unterschied in der Biotopzusammensetzung der Streifgebiete, allerdings wurden die Biotope in unterschiedlicher Weise genutzt. Laubwaldbiotope wurden das ganze Jahr über stark genutzt, Weideflächen hingegen vorwiegend im Herbst. Die Verteilung von Laubwaldbiotopen in den Gruppenrevieren hatte deutlichen Effekt auf die Größe der Streifgebiete.

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Zeitschrift/Journal: Mammalian Biology (früher Zeitschrift für Säugetierkunde)

Jahr/Year: 1997

Band/Volume: 62

Autor(en)/Author(s): Broseth Hendrik, Bevanger Kjetil, Knutsen Bard

Artikel/Article: Spatial Organization and habitat utilization of badgers Meies meles: effects of food patch dispersion in the boreal forest of central Norway 12-22