

Badger abundance and activity in relation to fragmentation of foraging biotopes

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Eurasian badgers (*Meles meles*) living in the southern boreal forest of Sweden prefer to forage in patches of agricultural land (AL). In two adjacent areas with different proportion AL, capture-recapture studies from spring 1989 and 1991, and track-board surveys from spring 1991 and autumn 1993, showed that both population density and the frequency of track-board visits were higher in the richer area. In 1993, one even richer and one poorer area were included in the track-board survey to increase the variance in proportion and patchiness of AL. Also in the richest area of these, the proportion of track-board visits was high. However, this was also the case in the poorest area. More track-boards were visited in or close to agricultural patches than expected from random. Among the areas, this preference increased with decreasing proportion of AL available, except in the poorest area where no preference could be detected. We argue that the observed pattern was a result of: 1) decreasing population density, 2) increasing activity and larger individual home ranges, and 3) a change in biotope preference, as the degree of biotope fragmentation increased and the possibility of efficient utilisation of the preferred patches decreased.

1. Introduction

The Eurasian badger (*Meles meles* L.) is widely distributed, occurring from the Mediterranean in the south, to the boreal zone of Fennoscandia and Russia in the north (Neal 1986). The centre of its distribution lies within the nemoral zone, where it feeds mainly on invertebrates, especially earthworms. Diet composition and food preferences are known to reflect differences in

the availability and abundance of prey among regions, landscapes, home ranges, seasons and years (e.g. Skoog 1970, Kruuk & Parish 1981, Mouches 1981, Shepherdson et al. 1990, Lambert 1990, Pigozzi 1991, Hofmann & Stubbe 1993).

During the last century, badgers have expanded their range in Scandinavia far into the boreal zone (Bevanger & Lindström this volume). In previous studies (Seiler & Lindström,

unpublished), we found that badgers, living in the southern boreal zone, highly preferred to forage in patches of active or abandoned agricultural land. Average home range size was negatively, and group size positively related to the amount of such biotope in the landscape. In addition, these studies found that badgers fed primarily on small food items, easily gathered, such as earthworms and other invertebrates, small vertebrates, and berries. Due to human cultivation and/or to soil conditions, active and abandoned agricultural land is relatively rich in badger food, especially earthworms (Stöp-Bowitz 1969). However, along a gradient from southeast to northwest in the boreal zone of Sweden, such biotope occurs in increasingly more scattered and smaller patches, embedded within a matrix of boreal coniferous forest on poor, raw-humus soils. To the badger, this implies an overall lower availability of foraging biotope and an increase in distance among the remaining biotope patches. We may thus assume a concomitant lowered population density of badgers in northwestern landscapes.

In this paper, we report capture-recapture estimates of population density, and track-board indices to badger abundance and activity along a fragmentation gradient from landscapes with continuous agricultural land to almost pure coniferous forest.

2. Study areas

The study was performed in south-central Sweden (Fig. 1), in the transition zone between the boreo-nemoral and boreal vegetation zones; the "Limes Norrlandicus" (Fransson 1965). Within a distance of less than 60 km, the transition zone includes a rise in average altitude from about 50 m A.S.L. in the south, to about 300 m in the north. This produces a gradient in the duration of snow cover from 80 days in the south, to 160 days in the north (Ångström 1974). Associated with the rise in average altitude, and glacial and marine history, soil conditions also differ, from richer soils in the south, generally used for agricultural purposes, to relatively poor podsol and raw-humus soils in the boreal forest (Lundkvist 1953). Agricultural land occurs only scarcely and patchily throughout the boreal zone, and was often abandoned and afforested with conifers during the 1950's and 1960's. Despite afforestation, soil conditions in former agricultural patches, and thus the abundance of earthworms and other badger prey, are still superior to those in pure coniferous forest areas (Seiler & Lindström,

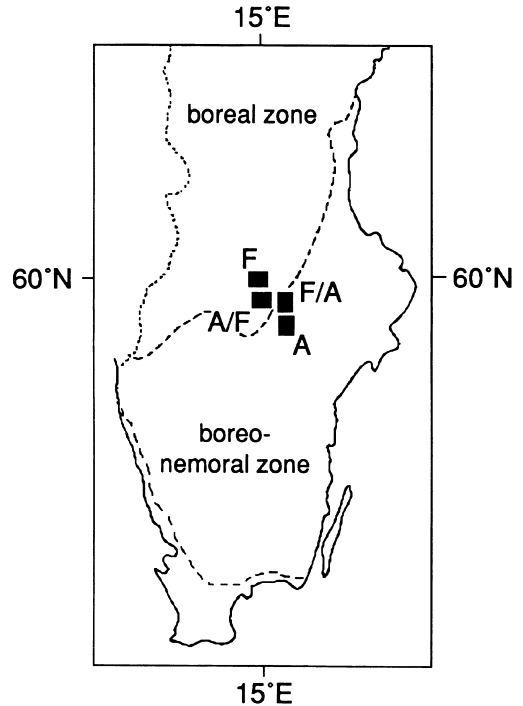


Fig. 1. Location of the study areas in south-central Sweden. F = the northern, forested area, F/A = the intermediate area around Grimsö, A/F = the area around Ramsberg, and A = the southernmost area dominated by agricultural biotope (58%). The borderline "Limes Norrlandicus" is indicated by the geomorphological border (broken line) (Fransson 1965).

unpublished). Therefore, in the following we have simplified landscape structures by classing biotopes as either *agriculture* (active as well as abandoned) or *coniferous forest* (including clearcuts, plantations and bogs).

The first part of the investigation, i.e. the trapping study and the track-board survey of 1991, were conducted in the Grimsö Wildlife Research Area (F/A) and a nearby area near the village of Ramsberg (A/F), 10 km northwest of Grimsö (Fig. 2). Both areas mainly comprise boreal coniferous forest on sandy and rocky soils, interspersed with bogs and lakes. In the Ramsberg area, about 22% is agricultural biotope, mainly pastures and some cultivated fields, whereas in the Grimsö area, only 11% of the area consists of mostly abandoned agricultural patches. A detailed description of the Grimsö area is given in Angelstam et al. (1982).

In September 1993, we repeated the track-board survey including two new areas, in order to increase the variation in the proportion and patchiness of agricultural land. The northernmost area (F), 20 km north of Ramsberg, consists

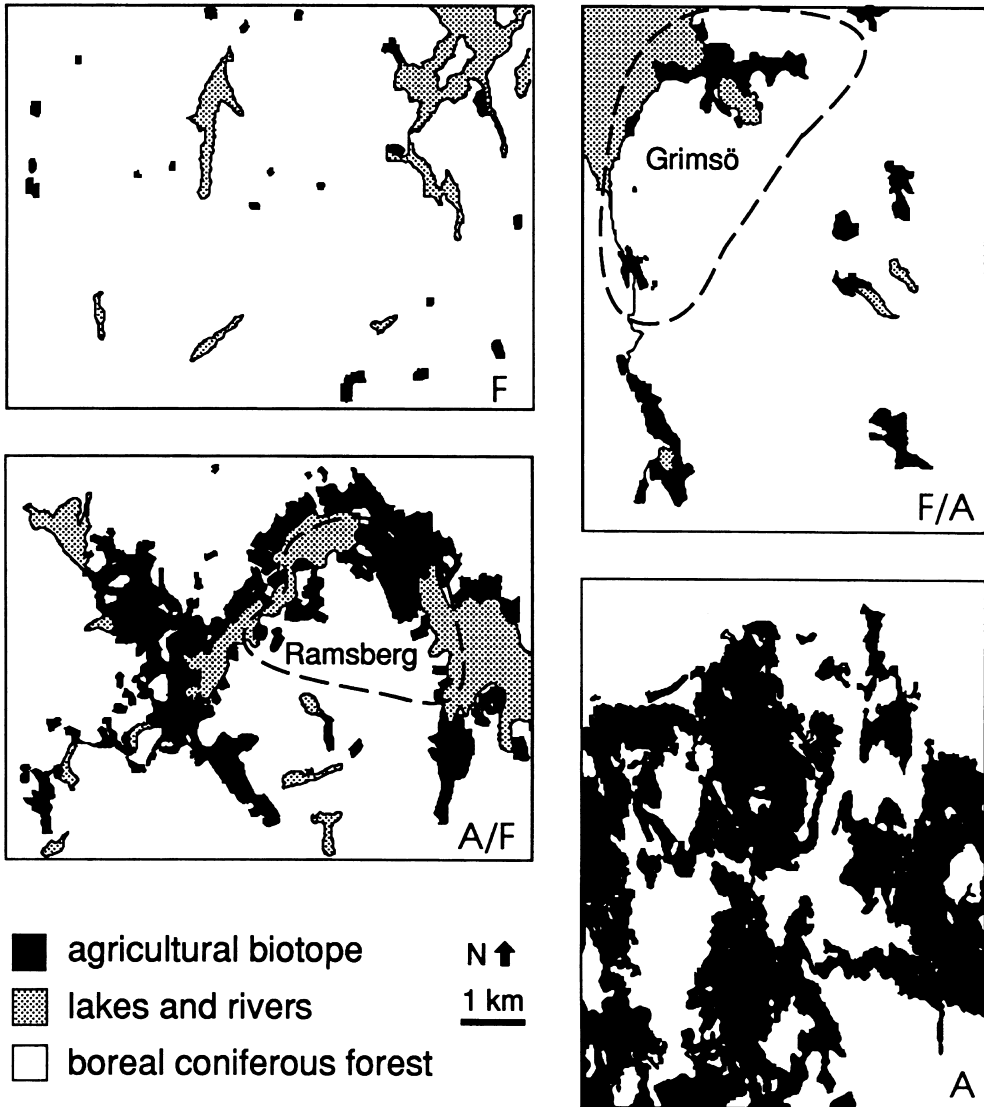


Fig. 2. Biotope distribution in the four study areas. Trapping and the first trackboard survey in spring 1991 were done in parts of F/A (Grimsö) and A/F (Ramsberg) only (encircled by dotted lines). Each square encompasses about 50 km².

of intensively managed, almost pure boreal coniferous forest (Fig. 2). Only 4% of this area has been used as pastures or farmland in the past, but all agricultural patches are abandoned and most of them are afforested. A few houses are still inhabited, but the majority is used as temporary retreats for hunters and tourists. The southernmost area (A), 30 km south of Grimsö, is dominated by highly productive agricultural land (about 58%), such as cultivated fields, pastures and meadows, interspersed with stands of mixed forest. Several small settlements and farms occur throughout

this area, as it is typical for the agricultural landscape in south-central Sweden.

Thus, these four study areas lie along a gradient, where the badgers' preferred foraging biotope, i.e. agricultural biotope, becomes fragmented into small and isolated patches embedded in a matrix of less productive coniferous forest and bogs. Only during late summer and autumn, when *Vaccinium* berries are ripening, does also the coniferous forest provide much food for the badger (Seiler 1992).

3. Materials and methods

Badgers were trapped in tunnel-traps during four weeks in March–April 1989 in parts of the F/A area (Grimsö), and in April 1991 in parts of the A/F area (Ramsberg) (Fig. 2). Badgers were marked individually with a belly tattoo and equipped with ear-tags and radio-transmitters. The traps were distributed with about 2.5 traps per km². The outer limits of the trapping areas were defined as one average home range radius outside each periphery trap (507 m in Grimsö, and 380 m in Ramsberg, unpublished data).

The number of badgers in the populations were estimated according to i) the “unbiased Petersen Method” using mark-and-recapture data (in Krebs 1989), and ii) according to a “zero-truncated Poisson test”, using the frequency of recaptures to estimate the number of non-captured individuals (in Krebs 1989). The latter method bases on the assumption that the number of captures per individual follows a Poisson distribution, and gives thus a slightly different result than the Petersen Method.

During 1991 and 1993, we conducted track-board surveys in both areas, in order to receive an additional index of population density. The track-board method used here is similar to what was described as “grease nests” (Angelstam 1986) and “dummy nests” (Andrén 1992), and comparable to the “scent-stations”, commonly used for estimation of carnivore abundances in the USA (e.g. Raphael & Barrett 1981, Roughton & Sweeny 1983, Smith et al. 1994). The wooden track-boards were 0.6×0.6 m in size, smeared with a layer of lubrication grease (~ 0.2 cm thick) and covered by a thin plastic film or fine sand, where the animals preying upon the bait, left footprints.

In March–April 1991, 50 track-boards were systematically distributed at an interval of 350 m in each of the trapping areas. We used perforated tins of catfood as bait, and checked the boards after one and three weeks for badger tracks. The track-board study was repeated in September 1993, using pelleted dogfood and fish as bait. This time, we distributed 100 boards in each area, with a distance of 700 m between adjacent boards, in order to cover a wider range (50 km²) and to reduce the density of boards to one per 50 ha. This size (50 ha) approximates the smallest home range observed in the areas during 1989 and 1991 (Seiler & Lindström, unpublished). The method was also applied in the two additional areas (F and A) in 1993. The track-boards were exposed for 3 weeks.

The probability that an individual badger encounters a particular track-board will likely depend on pattern of the animal’s habitat utilisation. Therefore, we calculated Ivlev’s index of biotope preference P according to Krebs (1989) as

$$P = (U-A)/(U+A),$$

using the ratio between the proportion of boards placed in a particular biotope (A) and the proportion of boards visited within it (U). This index is standardised between -1 and $+1$, with randomised utilisation at zero and a maximum preference at $+1$.

4. Results and discussion

4.1. Grimsö and Ramsberg (two adjacent areas, 11% and 22% agricultural land)

After more than 800 trap nights in both areas, the capture rate in Grimsö was 64% lower than in Ramsberg ($\chi^2 = 27.49$, $P = 0.0001$, Table 1). Using the “unbiased Petersen method”, we estimated about 20 badgers in the Ramsberg area during spring/early summer. A similar result was obtained by the “zero-truncated method” (Table 1). Thus, the population density in the Ramsberg area was about 3 badgers per 100 ha. In Grimsö, the two

Table 1. Results of the capture and recapture study in Grimsö during spring 1989 and in Ramsberg during spring 1991. For trapping areas, see Fig. 2. Badger population densities were estimated with confidence intervals according to A) the “unbiased Petersen method” from mark-and-recapture data, and B) the “zero-truncated Poisson test” using the frequency of recaptures (in Krebs 1989). For the Petersen method, animals captured during the first two weeks of the trapping period were considered as the marked cohort.

	Grimsö (F/A)	Ramsberg (A/F)
Trapping area (ha)	1512	686
Total trapnights	820	824
Nights with capture	26	78
Capt. per 100 trapnights	3.17	9.46
Population estimate A:		
Marked animals during I.	12	15
Total captures during II.	9	11
Recaptured during II.	6	8
Unbiased Petersen estimate		
of total numbers	17.6	20.3
Density /100 ha	1.16	2.96
95% conf. intervals	0.81–2.21	2.24–4.56
Population estimate B:		
Number of badgers captured		
1 times	8	5
2 ×	4	3
3 ×	2	2
4 ×	1	1
5 ×	0	2
(>10 times) excluded	0	(3)
0-class completion	6.3	1.84
Total numbers	21.30	19.84
Density /100 ha	1.41	2.89

methods yielded estimates of 1.2 and 1.4 badgers per 100 ha, respectively, which was significantly less than in Ramsberg (unpaired, one-tailed t-test, $t = 2.33$, $df = 18$, $P < 0.05$).

The difference in population density between the two areas was further supported by the results of the track-board surveys in 1991 and 1993. In spring 1991, 36% of all boards in Ramsberg were visited by badgers after already one week of exposure, compared to only 18% in Grimsö (Table 2). The difference increased further after three weeks of exposure (76% and 30%, respectively, $\chi^2 = 21.24$, $P = 0.0001$). In September 1993, however, the difference was not significant ($\chi^2 = 2.78$, $P = 0.095$), yet the survey revealed the same pattern as in 1991 (Table 2).

The observed difference in population density was in agreement with our unpublished radio tracking data mentioned above: Home ranges were significantly smaller and more overlapping, and group sizes were larger in the Ramsberg population compared to the Grimsö population.

4.2. Extended survey 1993 (four areas, 4–58% agricultural land)

To our surprise, there was no significant difference in the proportion of track-board visits between the agriculturally dominated landscape (A) in the south and the northernmost forested area (F) (χ^2 -test). Badger tracks were found on 22%

and 24%, respectively, of all boards, which was neither significantly different to the number of track-boards visited in the Ramsberg area (A/F).

There are at least three possible explanations for this divergence from our expectations:

- There were actually no differences in population density between the poorest and the richest area, i.e. the track-board survey correctly reflected the abundance of badgers.
- Other external factors overshadowed the effect of abundance. In particular, the absence or presence of alternative predators, which competed with badgers for the bait, might have been important.
- The frequency of visited track-boards measured the combined effects of individual activity and population density, and these two varied inversely with each other.

Alternative a) is contra-intuitive, and seems to be less likely considering the trapping data from Ramsberg and Grimsö, our previous radio tracking studies (see above), and literature on other badger populations (e.g. Kruuk 1986, Reason et al. 1993), all indicating a positive relationship between general productivity of the landscape and badger abundance. Hunting and human disturbances might indeed have reduced population density to some degree in the richest area. Still, the high number of badger tracks found in the forested landscape remains unexplained.

Andrén et al. (1985), Angelstam (1986), and

Table 2. Frequency of track-boards visited by badgers, for areas see Fig. 1 and 2. The boards were systematically distributed with an interval of 350 m in 1991 and 700 m in 1993, and checked for tracks after three weeks of exposure.

Area	no. of boards	% boards in agriculture	% visited by badgers	% visited by other predators
In April 1991				
F / A	50	28.0	30.0	–
A / F	50	52.0	76.0	–
In September 1993				
F / A	94	10.6	14.9	68.1
A / F	98	21.4	24.5	72.4
In the additional areas in Sept. 1993				
F	100	4.0	24.0	70.0
A	97	57.8	21.6	64.9

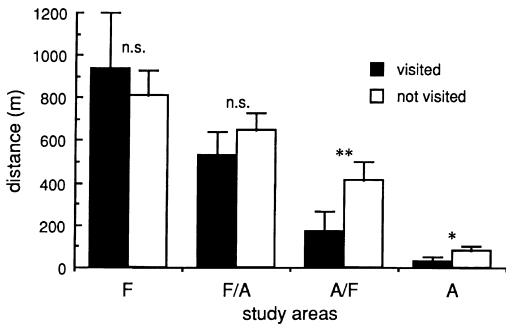


Fig. 3. Differences between the average distances of visited and not visited track-boards to the nearest patch of agricultural biotope. Means are given with 95% confidence intervals, and are tested in an unpaired two-tailed *t*-test. Asterisks denote levels of significance.

Andrén (1992) found a higher overall predation rate on ground nesting birds and a higher density of opportunistic predators in agricultural landscapes than in forested areas. This lends support to alternative b. However, in our data, there was no such increase in the overall number of visits. This might be due to the use of a different bait, i.e. pelleted dogfood instead of eggs. The proportion of boards visited by species other than badgers varied between 65% and 72% among the study areas (Table 2), and it was not unusual that there were tracks of different species together on one board. The most frequent alternative visitors were domestic cats and dogs in A (about 24%), foxes in A/F (10%) and F/A (15%), and small corvid birds in F (24%). Thus, the presence of competing predators had probably only a little effect on the frequency of badger visits. Abundance and activity of the badgers themselves (alternative c), was likely to be more important.

As shown by several previous investigators, visitation-rate to scent-stations is often related to mobility, behaviour, and especially to activity of the addressed species (see Roughton & Sweeny 1983, Raphael 1994, Smith et al. 1994). The probability that a badger will encounter a track-board placed in a particular biotope, will thus depend on pattern in its foraging behaviour and biotope selection. As opportunistic foragers, badgers are generally sensitive to local differences in food availability (e.g. Shepherdson et al. 1990). In our unpublished studies in the boreal zone, badgers were shown to prefer to forage in agri-

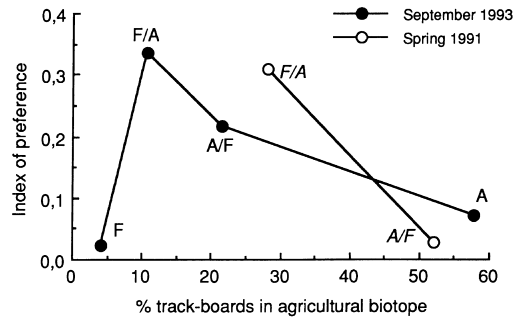


Fig. 4. Preference of agricultural biotope as calculated from the distribution of boards and badger visits, in relation to the proportion of agricultural biotope in each area (based on the distribution of boards). An index of preference is calculated according to Ivlev (1961, in Krebs 1989). The index is standardised between -1 and $+1$, with randomised utilisation at zero.

cultural land. They spent most of their active time within this biotope, where they moved more slowly and more convolutedly than in forests. Similar convoluted foraging movements were also described by Mellgren and Roper (1986), who made experiments with artificial prey distributions. Kruuk (1978) reported slow and convoluted movements for badgers foraging in pastures especially rich in earthworms.

Thus, the probability that a track-board will be encountered should be highest in patches of preferred foraging biotope, i.e. agricultural land, and decrease the farther the board is placed outside the patch boundary. This was true in the three richest areas and significant in A/F and A, where the average distance from the visited track-boards to agricultural biotope was shorter than for the not visited boards (one-tailed *t*-test: $t > 1.79$, $P < 0.019$, $df = 96$ and 95 , respectively, Fig. 3). Furthermore, in the two intermediate areas Ramsberg and Grimsö (A/F and F/A), badgers visited more track-boards placed in agricultural biotope than expected from the distribution of boards (for both years combined, in A/F: $\chi^2 = 6.44$, $P = 0.011$; in F/A: $\chi^2 = 9.60$, $P = 0.002$). Considering also area A, this preference for agricultural biotope increased with a decreasing proportion available (Fig. 4). Such a relationship should be expected if badgers had to spend a certain time each day in agricultural biotope to fulfil their food demands. It is also in accordance with

Charnov's (1976) marginal value theorem, predicting a longer stay-time in a productive foraging patch and thus a stronger preference, when the matrix is of an overall low profitability (Begon et al. 1990). Correspondingly, in previous radio tracking studies we observed a higher preference for agricultural land in individuals with less biotope accessible within their home ranges (Seiler & Lindström, unpublished). Yet in the poorest area, F, there was no such preference for agricultural biotope. Track-boards were visited many kilometres away from the nearest agricultural patch and the average distance was about 17% farther than compared to the not visited boards (Fig. 3).

On a landscape scale, i.e. between biotopes, the distribution of visited track-boards appeared to be dependent on local differences in food availability and the badger's site preferences. However, on a regional scale, i.e. between landscapes, the degree of biotope fragmentation and the overall productivity of the landscapes may become more affective on visitation-rates. As described above, the boreal landscape is a mosaic of small patches of agricultural biotope embedded in a relatively low productive matrix of coniferous forests and bogs. With increasing fragmentation of agricultural land (smaller patches and longer inter-patch distances), the costs of travelling between patches will increase and the time possible to spend in each patch will decrease. Thereby the profitability of such a foraging pattern will be reduced. Eventually, an individual will do better in intensifying utilisation of the forest matrix, than in further increasing the preference for the agricultural biotope patches. Hence, at very high degrees of biotope fragmentation, this coarse-grained (*sensu* Wiens 1976) pattern in habitat utilisation, i.e. strong biotope preferences, might shift towards a rather fine-grained pattern, i.e. less selective habitat utilisation. This switch may be accompanied by an increase of the badgers tendency to exploit casual food resources. In addition, when the overall food availability is critically low and badgers are hungry, they might be more interested in the exposed bait, than when food is abundant. Thus the probability of encountering and visiting a track-board in the forest matrix will be increased due to a changed foraging behaviour.

A similar change from coarse-grained to fine-

grained utilisation pattern can be observed during the course of the year: In spring, badgers feed selectively on earthworms, and range over relatively small areas with high proportion of agricultural biotopes. In late summer however, the productivity of the coniferous forest matrix increases, due to the ripening of berries (*Vaccinium* spp.) which are then consumed by badgers in large quantities (Seiler & Lindström, unpublished). However, as berries are less patchily distributed throughout the boreal landscape than earthworms, badgers forage over wider ranges, and thus show weaker overall biotope preferences than during spring (Seiler 1992).

To conclude, we suggest that the observed pattern of track-board visits were a result of two counteracting mechanisms: population density and individual foraging activity. This should not be considered a post-hoc explanation of the results obtained, rather a hypothesis to be tested in future studies.

Several researchers, and most recently Smith et al. (1994), have stressed the importance of the individuals' mobility and activity as a factor influencing the visitation-rate on track-boards (see also Roughton & Sweeny 1982). Smith et al. (1994) found no correlation between visitation-rate and the abundance of predators (raccoons; *Procyon lotor*) in an experimentally reduced population. However, the authors observed significant differences in the frequency of visits between seasons and years. This variation was explained with a seasonal variation in home range size, foraging activity and mating behaviour (Smith et al. 1994).

In our study, we suggest similar reasons for the observed results: In rich landscapes, with contiguous preferred biotope, badgers are numerous, live in small territories, and they may gather food in the surroundings of farms, in fields and pastures, as described in plenty of behavioural studies (e.g. Kruuk 1978, Kruuk & Parish 1991, Shepherdson et al. 1990). As the proportion of rich biotope decreases, badger population density decreases as well, and individuals become more dependent on the preferred foraging patches, i.e. they increase the relative utilisation of these patches (Seiler & Lindström, unpublished). Such behaviour would lower the overall frequency of track-board visits, but increase the proportion of visited boards in

agricultural biotope, as observed in the Grimsö area. Finally, increasingly small and sparse patches of agricultural land will no longer support more than only a few badger individuals throughout the landscape. A selective utilisation of the isolated biotope patches will become unprofitable and badgers may switch to a more dispersed utilisation of the landscape matrix instead. Hence, individual badgers will expand their foraging range and intensify the search for food, and by that encounter and visit more track-boards. The switch in habitat utilisation pattern may thus indicate, that food resources in the landscape are critically scarce, and that a threshold for biotope selectivity has been passed. Below that threshold, individual resource acquisition, resource partitioning and population parameters may be different to what is observed in most other landscapes where badgers are studied.

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