Spatial organization and territorial behaviour of the European badger *Meles meles*

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(With 8 figures in the text)

The paper describes habitat preferences, spacing, range sizes, group composition and territorial behaviour of the European badger in a study area in southern England. Animals were followed at night with the aid of radio-location and night-vision equipment, and colour-marked food was used to establish range-size.

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Introduction

In several studies of the larger Carnivora, it has become clear that there is a close relationship between the social organization of a species and the way in which it exploits its food supplies (Kruuk, 1972, 1975), a point made earlier for birds by Crook (1964), and confirmed since then for many other groups of animals (review in Wilson, 1975). In carnivores an important factor in this relationship is the extent to which an animal has to collaborate with conspecifics in order to catch its prey; several species have evolved co-operative methods of exploiting a particular ecological niche and there is evidence that this, in turn, has affected many aspects of their behavioural repertoire.

There are, however, a number of apparent anomalies, in which gregarious, group-living species appear to exploit a food supply for which no co-operation is necessary; indeed
individuals may even interfere with each other as in the coati, *Nasua narica* (Kaufman, 1962; Smythe, 1970) and some of the mongooses (e.g. *Mungos mungo*, Rood, 1975).

The question arises as to the biological function of their gregariousness. Probably, such species have evolved their social system under selection pressures different from those operating on the group structures of carnivores such as Canidae (Mech, 1970), Felidae (Schaller, 1972) or Hyaenidae (Kruuk, 1975) and it is important to establish what their group organization is and what kind of selective advantages are associated with it. One species which appears to have a gregarious social organization, without showing individual co-operation during foraging, is the European badger (*Meles meles* L.) whose behaviour and ecology is still very little known. In this paper, I will try to fill some of the gaps for this species by describing the factors which influence the distribution of badger setts and the range-size of their inhabitants in Wytham Woods, near Oxford, England. A preliminary description will also be given of badger group composition, and the importance of territorial behaviour in the spatial distribution will be discussed. A later paper (Kruuk, in prep.) will describe the badgers' foraging strategy in an attempt to understand the function of their spatial distribution.

The study area

The Wytham Woods study area is immediately outside the city of Oxford, and is bounded by the river Thames to the north-west, the Seacourt Stream to the north-east, the Oxford bypass road to the east and the Oxford–Eynsham road to the south (Fig. 1). Excluding built-up areas, this amounts to a total of approximately 1080 hectares, of which 36% is woodland (391 ha) and the rest farmland, divided approximately equally between arable land and pasture. The boundaries are crossed infrequently by badgers.

The woodlands are described by Elton (1966), the history of planting and exploitation is documented by Grayson & Jones (1955) and the geology by Arkell (Mss). For this study, the following information is relevant. The area is situated on and around a two-topped hill, which forms the eastern extremity of the Cotswolds range, with altitudes ranging from 60 to 165 m above sea level. The soil of the lower parts surrounding Wytham Hill is heavy Oxford clay, while the hill itself consists of a stony, Jurassic coral rag. Between these two formations is a narrow belt of coarse calcareous grit sand which girdles the hill tops.

The woodland vegetation is dominated by oak (*Quercus robur*), beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*) and hazel (*Corylus avellana*); dominant species in the understorey are dog's mercury (*Mercurialis perennis*), various brambles (*Rubus* spp.), stinging nettles (*Urtica dioica*) and bluebells (*Endymion nonscriptus*). Between the mature woodlands are dense plantations, mostly planted in the early 1960's, of coniferous trees mixed with beech, oak and ash, with little undergrowth. Occasional single mature pine (*Pinus sylvestris*), spruce (*Picea abies*) and larch (*Larix decidua*) are found scattered through the deciduous woodlands. The area is intersected by many rough cartrcks and footpaths, providing easy access.

The study was carried out from March 1972 till March 1975, during which period there was a certain amount of change in the farmland from pasture into arable and vice versa; but in general the fields remained under the same regime. Fields were separated from each other by barbed-wire fences. The pastures were grazed by cattle, and the arable land was mostly under wheat and oats.
Methods

Badger setts and latrines were found by intensive searching of every part of the study area, making use of the knowledge of previous workers, and following every badger path. The animals were observed near their setts from a platform in a tree and on those setts where more intensive observations were carried out, a 12 V red light was suspended above the holes.

![Diagram](https://via.placeholder.com/150)

**Fig. 1.** Distribution of badger main setts (black) and outliers (open circles) in Wytham Woods. Stippled: woodland areas. White: agricultural land. Hatched: Belt of calcareous grit sand.

A number of badgers from different setts were fitted with radio-transmitters, which allowed me to follow the animals at night and to establish in which holes they were spending the day. The animals were caught with stopped snares placed in their run-ways, checked at midnight and at daybreak. After capture, the badgers were covered with a sack and immobilized with ether. They were then weighed, assigned an age-category according to tooth-wear, and the radio-harness was fitted. It was usual to take the animal to the nearest badger hole to let it recover in the entrance.

The transmitter and its aerial were embedded in acrylic, and fitted to the back of the badger, with a soft leather harness consisting of straps around the neck, the chest and between the forelegs. Radios had different frequencies (102 Mc band), and different pulse rates (40–70/min).
receiver, manufactured by Davtron Inc., Minneapolis, was carried by the observer together with a directional dipole aerial. Embedded in the plastic with the transmitter was a "beta-light", ca. 2-5 cm diameter, manufactured by Saunders Roe Ltd., U.K., and emitting a soft, greenish light comparable to the light of a few glow-worms together. These lights greatly helped observation of badgers at close range, once the animal had been tracked down with the directional radio system.

For actual observation of the badger's behaviour after it had been found, 7 x 50 binoculars or infra-red night glasses—a combination of an infra-red search light, 3-stage electronic image intensifier and infra-red converter and binoculars, manufactured by the Old Delft Optical Industries, Delft, Holland, were used. This device could be carried by a walking observer together with the radio-receiver and allowed detailed observation of badgers in complete darkness at 2-150 m (though animals could still be distinguished as badgers up to 250 m). Notes were made on a small dictaphone which were later transcribed into various categories of field notes and on to maps. During these nocturnal observations, great care had to be taken to remain unnoticed by the badgers, by behaving unobtrusively, wearing non-rustling clothes and keeping down- or cross-wind of the animals. The badgers with radio-transmitters were followed for a total of 290 hours; frequently the movements of two or more animals could be followed simultaneously.

As a second means of establishing the animals' ranges, the badgers were fed on their setts with small quantities of peanuts, made sticky with treacle, left near the entrances and replaced daily. Mixed with the peanuts were circular pieces of thin coloured polythene, 6 mm across, or strips 3-5 mm wide and 2-3 cm long. Different setts were provided with different colours or shapes of markers. All known badger latrines (see below) were checked twice weekly for the presence of colour markers. This experiment was carried out over three weeks in May–June 1974 at four setts, in the main study area within Wytham (Marley Wood), and over six weeks in February–March 1975 at 20 setts all over Wytham Wood.

Results

Location and distribution of setts

Badgers almost invariably spend the day underground in their sett. This sett might have a single entrance or many. In this study two different types of sett were distinguished:

Main setts had three to 21 entrances (mean 10.5), which were usually connected underground, and joined above ground with clear paths. In Wytham, there were 14 main setts

<table>
<thead>
<tr>
<th>Table I</th>
<th>The habitats of badger setts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area in ha</td>
<td>%</td>
</tr>
<tr>
<td>Woodlands, on calc. grit sand</td>
<td>86</td>
</tr>
<tr>
<td>Woodlands, on other soils</td>
<td>305</td>
</tr>
<tr>
<td>Agricultural land, on calc. grit sand</td>
<td>62</td>
</tr>
<tr>
<td>Agricultural land, on other soils</td>
<td>624</td>
</tr>
<tr>
<td>1077</td>
<td>100.0</td>
</tr>
</tbody>
</table>

Statistical significance (except for those combinations where insufficient data are available), binomial tests, all setts together: Setts in woodland/agricultural land ($P = 0.36$), $z = 7.54$, $P < 0.001$. Setts in calc. grit sand/other soils ($P = 0.16$), $z = 16.40$, $P < 0.001$. Setts in woodland, grit sand/woodland, other soils ($P = 0.22$) $z = 12.66$, $P < 0.001$. Setts in grit sand, woodland/ grit sand, agricultural land ($P = 0.58$) $z = 5.03$, $P < 0.001$. 
in continuous use. Sometimes they had an *annexe*, usually less than 50 m, though once 150 m away, with a well-worn path to the main sett, fewer entrances, and usually also in continuous occupation.

*Outliers* had one, occasionally two entrances, without a clear connection with a main sett and were used intermittently; in Wytham I found 56.

It is generally recognized that badger setts are more frequently situated under woody vegetation than in the open (Neal, 1948, 1972; Neal & Harrison, 1975; Southern, 1964; Paget & Middleton, 1974), although no quantitative evidence is available. This general statement holds true in Wytham (Table I); 90% of all the setts occurred in the 36% of Wytham covered by woodland, a significant preference.

In addition, the geology of an area influences the badgers' choice of living sites (Southern, 1964; Dunwell & Killingley, 1969). In Wytham, the narrow belt of calcareous grit sand occupies only 14% of the study area (Fig. 1), whilst it contained 89% of all the setts, including all the main setts; again a significant preference (Table I). The two preferences are independent of each other, i.e. woodlands are preferred within the calcareous grit sand zone, and grit sand is selected within the woodlands (Table I).

It is likely that the selection of woodland is a preference for cover round the sett rather than any other aspect of the woody vegetation (as indicated by the location of one main sett under a house in open agricultural land). The selection of calcareous grit sand could be a result of a preference for steep hill sides, as many slopes in Wytham were associated with that particular geological formation. However, several main setts and outliers were on relatively flat ground, and steep slopes were found also above and below the belt of grit sand. It is likely, therefore, that the badgers' preference is based on a choice of soil type. The grit sand was clearly much easier to dig than any other soil in Wytham. From the location of many springs immediately below the grit sand belt, it appeared that this layer was well drained.

Thus, there is clear evidence for a habitat preference in the distribution of badger setts in Wytham. It is likely, however, that the distribution of setts is influenced by other factors as well: even when taking habitat preferences into account, the distribution of main setts appears to be distinctly non-random (Fig. 1). In order to test this, the distribution of observed nearest-neighbour distances between main setts was compared with the distribution of nearest-neighbour distances between points that were randomly spaced but which showed the same habitat preference compared with the observed setts. The co-ordinates of the random points were obtained from a random numbers table; 14 points were plotted on a map of the calcareous grit zone, 13 of these in woodland, one in agricultural land and this was repeated three times (Fig. 2). It showed that the observed distribution of main setts was significantly different from random, and was clearly truncated at about 300 m. There was no departure from random in the distribution of outliers.

It is concluded that badger setts in Wytham were closely associated with wooded vegetation on a narrow zone of calcareous grit-sand. Main setts were non-randomly spaced, at least 300 m apart; this indicates the presence of a social spacing-out mechanism, as it is unlikely to be caused by some non-randomly distributed environmental variable.

**Ranges of individual badgers: clans**

Twenty-three animals were caught and provided with a radio-transmitter. Of these, only 12 could be followed long enough to establish the size of their ranges—the others managed
to remove their harness soon after capture, or their radios failed, and one was killed on the road. The movements of these 12 badgers were recorded over periods ranging from $3\frac{1}{2}$ to seven months; one badger was followed for four months one year and $3\frac{1}{2}$ months the next year. A map was drawn up for each individual of all its observed movements, and a minimum-size convex polygon drawn around the points at which it was observed (Fig. 3).

Two females and two males which, together with other badgers, appeared to belong to the same main sett (Jew's Harp) occupied ranges of 50 and 51 ha (females) and 52 and 58 ha (males). These ranges overlapped almost entirely with each other (Fig. 4) and it was decided that the range of the Jew's Harp sett was the area enclosed by a convex polygon drawn around the extreme points of the four individual ranges combined (70 ha). Two males from a neighbouring main sett (Platform) also had ranges which overlapped almost entirely with a combined area of 21 ha bordering on, but not overlapping with, the range of the Jew's Harp sett. The range of these two males bordered on the other side with the range of badgers from the next main sett (Marley). The relation between the ranges of animals from Marley and the next main sett along (Botley) was more complicated. Two of...
FIG. 3. Range of female no. 4, from the Jews Harp sett, observed by radio-tracking. Woodland areas are stippled. Black dots indicate setts, arrows indicate observed movements; areas where she foraged for prolonged periods (½–3 hours) are hatched. April–October 1974.

FIG. 4
the females from Marley had almost identical ranges (combined 47 ha), bordering on and exclusive of ranges of the badgers mentioned before; two females of the Botley main sett showed the same pattern (59 ha), bordering on the range of the Marley females. However, two males appeared to belong to both Marley and Botley setts, spending the day in either of them and having nocturnal ranges completely incorporating the ranges of the females of both setts (combined male and female range 107 ha).

These observations have been summarized in Fig. 5 which excludes the observations on badgers with radio transmitters which were watched over shorter periods. Of this category (nine badgers), four belonged to the setts mentioned above and the little we saw of their ranges fell within the ranges of those setts. Five badgers belonged to neighbouring setts and the few observations are consistent with those above; there was no overlap of ranges except for one male badger which appeared to belong to two different main setts.

I concluded, therefore, that in all observed cases animals of the same sex from one main
sett have the same ranges, but that sometimes ranges of males and females differ—males may "belong" to different main setts, and their ranges may overlap with those of the females of those main setts. I will call the ranges of these males the "clan ranges"; thus within the clan ranges, females may have ranges exclusive of those of females from other main setts. Thus, a clan is defined here as a group of badgers jointly inhabiting an area; females may use part of that area only.

Food marking experiments

Plotting the movements of animals with radio transmitters was laborious, and although several other kinds of information were collected during the nocturnal observations, the rate of information gain on range size was slow. This was largely due to the badger's habit of foraging for a long period of time in a relatively small area (Kruuk, in prep.). Moreover, it was clear that the boundaries of badger ranges were often associated with certain landscape features, a phenomenon that was obscured by the polygonal range outlines in Fig. 5. It was decided therefore to use additional evidence, partly to supplement the data on ranges determined by radio-tracking, and partly to estimate badger ranges in the rest of the wood using a less laborious method.

**Table I**
Range-sizes of badgers, in hectares, as determined by radio-tracking, compared with areas surrounded by colour-marked latrines and by paths

<table>
<thead>
<tr>
<th>Area</th>
<th>Range as determined by radio-tracking</th>
<th>Part of radio-range outside latrine-range</th>
<th>Part of latrine-range outside radio-range</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>latrines &amp; paths</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jews Harp</td>
<td>70.1</td>
<td>67 (= 9.6%)</td>
<td>5.7 (= 8.3%)</td>
</tr>
<tr>
<td>Platform</td>
<td>20.6</td>
<td>10 (= 4.9%)</td>
<td>6.7 (= 25.5%)</td>
</tr>
<tr>
<td>Marley/Botley</td>
<td>107.2</td>
<td>0 (= 0%)</td>
<td>40.2 (= 27.3%)</td>
</tr>
<tr>
<td>Total</td>
<td>197.9</td>
<td>7.7 (= 3.9%)</td>
<td>52.6 (= 21.7%)</td>
</tr>
</tbody>
</table>

When badgers were in the border area of their range, they were using paths which appeared to constitute the actual boundary of the range—they did not, or rarely, go beyond those paths. Associated with the paths, a relatively large number of badger latrines were found in the border area. To use these characteristics for describing the ranges of badgers from the different setts, badgers were fed with marked food on those setts of which the ranges were known through radio tracking, and this was repeated the next year on all main setts in Wytham Wood. The recoveries of colour markers from latrines in both these experiments (Fig. 6) showed that there was a reasonably good correspondence between the ranges of badgers found with the two methods (Table II); this established the food-marking method as a reliable method to assess ranges of badgers elsewhere. Discrepancies between the two methods were mainly where there were few badger latrines, which was true especially in those areas where a badger range was not bordered by another badger range.

There were further complications in the interpretation of Fig. 6; for instance, on one occasion a colour marker was found in badger faeces in the centre of another range well away from the sett's usual range; this was called an incidental visit. The relation between the most westerly sett and its neighbour to the east was uncertain; it might be another case of some of the inhabitants occupying the ranges of both setts. Finally, a difficulty arose
when latrines were situated around the edge of large fields, creating an apparent no-man’s land in areas which were definitely used by badgers and in which also other signs, such as a badger path, were lacking. In such cases, the boundary was assumed to be in the middle of the field.

![Diagram](image)

**Fig. 6.** Recoveries in latrines of food markers presented on the setts. Sett numbers refer to Table III. Black dots are latrines; further legends as in Fig. 1.

Using the information from radio ranges, from the food marking recoveries and from the mapping of badger boundary paths, the Wytham Woods were divided up in 13 exclusive ranges (Fig. 7). The mean range size was 87 ha but this was not a very useful estimate, since the ranges on the outside of the area had rather vague outer boundaries. Moreover, there were important differences between spatial organizations of groups of badgers inhabiting the ranges, which made lumping meaningless (see below). The ranges of four badger groups were completely surrounded by others; their sizes were 26, 56, 57 and 69 ha respectively. The smallest of those ranges (“Platform Sett”) was inhabited by males only (see below) which left only three ranges which we might, perhaps, consider to be “typical” in size (mean 61 ha).
Clan composition

There have been a number of previous attempts at estimating the badger population in Wytham (Hancocks, pers. comm.) by watching setts at dusk and counting the number of emerging animals. There are a number of objections to this method; it is often not possible to watch all entrances simultaneously, some badgers emerge very late, and from observations on badgers with radios, I found it difficult to estimate what proportions of clan members were in a sett on a particular day. Nevertheless, it is possible to obtain a rough estimate of the number of badgers per sett, by watching during several evenings and making use of recognizable individuals (Table III). Although these estimates are of limited use and reliability, they serve to illustrate the order of magnitude of the population and of the different badger clans. It is suggested that up to 12 animals may live together in a clan.

The sex ratio of adult badgers caught in snares in Wytham was approximately equal (16 females, 15 males), which corresponds with observations elsewhere (Stubbe, 1965); I
assumed that males and females were equally likely to be caught in snares. But interesting differences appeared in the sex ratio of animals caught in different clan ranges (Table IV). Animals of the "Platform" range (which was unusually small and strangely shaped) were all males, whereas in the other ranges, females predominated. Joint ranges (where male ranges overlapped with those of females from two different main setts) had relatively more females than simple ranges, but this was not statistically significant. It is almost certain that there were no females in the "Platform" range at any time during the study, and I have called it a

The six males caught there were two very old individuals (judged from tooth wear), three young animals with virtually no tooth wear at all, and one middle-aged badger whose nose was missing, perhaps bitten off. They might have been excluded from normal clans, which would then have a larger number of females than males.

On none of the setts observed did we find more than one litter of cubs, and some setts had none.

**Behavioural interactions between badgers within the clan**

Individual badgers moved around solitarily inside a clan range; in hundreds of observations on badgers foraging, only cubs of less than six months old were seen to move in a group, with or without an adult female. On no occasion have I seen any direct competition between individuals for food.
Table IV
Sex-ratio of badgers in different clan-ranges
(Data from captured animals only)

<table>
<thead>
<tr>
<th></th>
<th>♂</th>
<th>♀</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simple clans</td>
<td>6</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>Joint sub-clans</td>
<td>3</td>
<td>11</td>
<td>14</td>
</tr>
<tr>
<td>Platform group</td>
<td>6</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>15</td>
<td>16</td>
<td>31</td>
</tr>
</tbody>
</table>

Fisher exact probability test:
Platform group versus others: \( P < 0.01 \)
Simple versus joint sub-clans: \( P > 0.05 \)

When badgers met within a range, they appeared to recognize each other, either as individuals or as fellow members of the same clan; if another badger did not originate from the same sett, aggression followed immediately. Several observations suggested that scent played an important role in such recognition, e.g. wind direction during encounters. Frequently, when badgers met on or near the sett, one individual pressed its anal region against the side or rump of another; presumably this left secretions from the anal and/or subcaudal glands on other individuals of the same clan. Domination of one badger over another was rarely seen. In a few instances, large boars tended to dominate the others, and adults could displace cubs. One indication of presumed dominance relationships came from observations where badgers with radio transmitters were sleeping. The large adult boars were always found in a main sett, whilst in the summer, a younger male and adult females spent many days in the small “outliers”, away from the main sett (Table V). One of these females was lactating.

Territorial behaviour

General

It has been stated (Neal, 1948) that badgers are non-territorial, i.e. that they do not defend a specific area against other badgers, except for the females defending the immediate area around a hole with small cubs. The spacing-out of main setts makes this improbable, at least in Wytham, and the defense of clan ranges against neighbours was confirmed by direct observation of aggression between neighbours on the range boundary.

Table V
The use of main sett and outliers by different clan members

<table>
<thead>
<tr>
<th></th>
<th>No. of days spent in</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Main sett</td>
</tr>
<tr>
<td>Adult ♂ (( n = 3 ))</td>
<td>35</td>
</tr>
<tr>
<td>1½–2 yr old ♂ (( n = 1 ))</td>
<td>6</td>
</tr>
<tr>
<td>Adult ♀ (( n = 3 ))</td>
<td>30</td>
</tr>
</tbody>
</table>

Adult ♂ versus adult ♀: \( \chi^2 = 24.0, df = 1, P < 0.001 \)
All ♂ versus adult ♀: \( \chi^2 = 14.0, df = 1, P < 0.001 \)
Adult ♂ versus young ♂: Fisher exact probability \( P < 0.001 \)
Adult ♀ versus young ♂: \( \chi^2 = 0.012, df = 1, P < 0.05 \)
Aggression and avoidance between clans

Five actual fights were observed; four of those were on the range boundary while one started near a sett which was 300 m from the boundary, and finished on the boundary. Only in this last case was the sex of both combatants known; they were males. In two of the other fights, males were involved but the opponents were not known, and in the remaining two fights I did not know the sex of any of the combatants. These last two clashes were in one of the few areas where a clan boundary was badly defined, a large pasture where four clan ranges met without obvious land marks. But two fights were on a well-defined border, one of these on a latrine. It was not always possible to observe details of aggression; however, it invariably involved bites and soft growling or “kekkering”. Once I saw prolonged mutual biting with the two badgers holding each other, rolling on the ground and over each other, while running and chasing were common during all of the interactions. The fight near the sett and one of the clashes on a well-defined border followed an intrusion from a neighbouring clan. The fights ended with the intruders repairing to their own range. As an example, I will describe one of the agonistic encounters in some detail.

On 25 August 1974, at 01.50, male no. 7, a large radio-collared male from the Jew’s Harp clan, was walking on the boundary path between his clan range and that of the neighbouring Brogden’s clan, in open pasture land. He passed a slightly smaller badger of the Brogden’s clan which was foraging about 50 m from the boundary on its own side. Both appeared to notice each other (heads up briefly), but continued with their previous activities. About 100 m further, male no. 7 left the boundary path and walked slowly, whilst feeding on worms, into the field which was inside the Brogden’s range. In doing so, he moved upwind of the Brogden’s badger, and when male 7 had been foraging for 12 minutes in his neighbour’s range, this other badger suddenly ran up to him. Male 7 ran back to his own range, but was overtaken after a few metres and bitten in the rump. He escaped and ran across the boundary, pursued by his neighbour for about 30 m inside his own area. Then he suddenly turned and the other badger ran back, chased by male 7 about 50 m inside the Brogden’s range. The neighbour turned back and chased male 7 back into the Jew’s Harp range. During this chase, the two badgers almost ran into me on the boundary; both took fright and ran off to their respective setts. During this interaction, no sounds were uttered except for soft “kekkering” growls at the turning points of the zigzag, and at the point of physical contact.

On many occasions, badgers appear to avoid entering the neighbour’s range. Walking from somewhere inside their own range up to the exact boundary (paths or fence), they either turned back or followed the boundary for some distance. On two occasions, badgers following the boundary met another badger presumably belonging to the neighbouring clan, and the two animals merely avoided each other at 10–20 m by each walking into their own range.

Demarcation of borders

Badgers left several different kinds of evidence of their presence, which appear to be closely associated with the border of their ranges. These were paths, scent marks made by “squatting”, and latrines. All these signs were found near the setts as well.

Paths were usually associated with the sett but also occurred exactly on the border between ranges. They were mostly used by badgers and were presumably made by them;
they were especially conspicuous in areas where the border crossed large tracts of land (open fields, woodland) without the landmarks (fences, roads) that were usually associated with boundaries.

Squat-marking on the boundary paths was often done on hummocks, on which virtually every passing badger deposited a secretion of its sub-caudal gland, in a rather fast movement. Although these squats were performed wherever the badger happened to be, anywhere in its range, by males as well as females, they were particularly frequent on the boundary paths. On four occasions, badgers were seen to rub the sub-caudal region 30–40 cm up a tree or fence post on the boundary, whilst making a "handstand", a behaviour also described for other carnivores e.g. dwarf mongooses *Helogale parvula* (Rasa, 1973).

Latrines were aggregations of 1 to 60 defecations, deposited in small pits dug by the animals themselves. Each pit was 5 to 10 cm deep, though sometimes as much as 30 cm, and could contain several different defecations. The pits were short distances apart; an average latrine had pits scattered over an area of 2–4 square m. However, a few latrines had no pits at all, and some had all droppings in one large pit. Often there were pits without a defecation in it. Frequently, there were signs of vigorous scratching of the ground around the latrine. Latrine use appeared to be seasonal; it was most conspicuous early in spring (February to May) and to a lesser extent in October and November. In summer, ephemeral small latrines, single dung pits or single droppings might be found. Many latrines had been in use by badgers for several years—in the study area one existed for at least 12 years and probably longer. The droppings were not covered and could be well-formed or very fluid like a cow-pat. Often some brownish yellow, jelly-like substance was found on top of the droppings, or this might, indeed, be the only excretum in a pit; this was probably a product of the anal glands.

The time spent by a badger on a latrine varied from 20 to 90 seconds, and a number of different behaviour patterns were seen. They included squatting (i.e. pressing anal region on vegetation or hummocks many times per visit), vigorous scratching with forelegs and hindlegs, digging of pits with forelegs, defecation and/or urination in a pit. Probably all were associated with the depositing of glandular secretion, from anal, sub-caudal, digital glands and perhaps others as well. The behaviour was much more elaborate than required for faeces disposal, and it is likely that its function was related to the use of a territory. This is suggested first of all by the location of the latrines; they were closely associated with the border of clan ranges, occurring mostly within the 50 m strip on either side (Table VI, Fig. 8). Moreover, latrines occurred on those edges of the range where one badger clan bordered

### Table VI

<table>
<thead>
<tr>
<th></th>
<th>Total area (in ha.)</th>
<th>No. of latrines</th>
<th>Latrines per ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;50 m from sett</td>
<td>8.6</td>
<td>7</td>
<td>0.81</td>
</tr>
<tr>
<td>Elsewhere in range</td>
<td>136.5</td>
<td>13</td>
<td>0.09</td>
</tr>
<tr>
<td>&lt;50 m from border of range</td>
<td>62.3</td>
<td>45</td>
<td>0.72</td>
</tr>
<tr>
<td>Total</td>
<td>207.4</td>
<td>65</td>
<td>0.31</td>
</tr>
</tbody>
</table>

No. of latrines, border area versus other parts of range: 

\[ \chi^2 = 47.6, df = 1, P < 0.001 \]
Landmarks nearby latrines

Landmarks are located within 10 m (usually within 3 m). This distribution is compared with a hypothetical random distribution of latrines in the same area and their location near landmarks. Some latrines were located nearby several kinds of landmark. Latrines with/without landmarks, observed/random: $\chi^2 = 28.1$, df = 1, $P < 0.001$

<table>
<thead>
<tr>
<th>Type of landmark</th>
<th>Observed</th>
<th></th>
<th>Random</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of latrines</td>
<td>% (n = 111)</td>
<td>No. of latrines</td>
<td>% (n = 100)</td>
</tr>
<tr>
<td>Car track</td>
<td>44</td>
<td>39.6%</td>
<td>11</td>
<td>11%</td>
</tr>
<tr>
<td>Vegetation boundary (e.g. woodland edge)</td>
<td>38</td>
<td>34.2%</td>
<td>14</td>
<td>14%</td>
</tr>
<tr>
<td>Fence (usually barbed wire)</td>
<td>35</td>
<td>31.5%</td>
<td>15</td>
<td>15%</td>
</tr>
<tr>
<td>Conifer tree</td>
<td>10</td>
<td>9.0%</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Others (pylon; tree in field)</td>
<td>2</td>
<td>1.8%</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>None</td>
<td>35</td>
<td>31.5%</td>
<td>69</td>
<td>69%</td>
</tr>
</tbody>
</table>

Table VII

on another (45 latrines in 45.8 hectares), not on the range limits where there were no badgers beyond (no latrines on 16.3 hectares; $\chi^2 = 16.1$, df = 1, $P < 0.001$). Neal (1948) stated that latrines occur especially near badger setts, and although it is true that each sett had at least one latrine in the immediate vicinity, this was clearly not the most common site for a latrine. Seventy-eight per cent of the latrines ($n = 87$) near the boundary were situated near a conspicuous landmark (Table VII), whilst the latrines within 50 m from a sett were usually anywhere in the woods (33% near a landmark, $n = 24$; $\chi^2 = 15.5$, df = 1, $P < 0.001$). Furthermore, the latrines on the territorial boundaries were larger than those near the setts or elsewhere in the range (Table VIII). If the depositing of secretions of the digital glands is an important feature of the latrines, one might perhaps expect a relatively larger number of pits per latrine on the boundaries; however, no significant difference was found (expressed as the number of droppings per pit) between the different kinds of latrine (Table VIII). Boundary latrines showed more extensive signs of scratching than ones at setts, with sometimes large areas of damaged or uprooted vegetation, but this has not been quantified.

The above data were obtained between February and May; in the summer months many boundary latrines were not used.

A few pilot experiments to study the function of the latrines were carried out. On four occasions, fresh faeces were taken from a strange latrine and deposited on a sett and the response of the badgers was observed. This was done twice in October, twice in February;

Table VIII

<table>
<thead>
<tr>
<th>No. of defecations per latrine and per dung pit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean no. of defecations per latrine</td>
</tr>
<tr>
<td>--------------------------------------</td>
</tr>
<tr>
<td>(a) Latrines &lt;50 m from sett</td>
</tr>
<tr>
<td>(b) Latrines elsewhere in range</td>
</tr>
<tr>
<td>(c) Latrines &lt;50 m from border</td>
</tr>
</tbody>
</table>

Median tests on no. of defecations per latrine:

a/b: $\chi^2 = 0.46$, $P < 0.6$

a/c: $\chi^2 = 4.27$, $P < 0.05$

b/c: $\chi^2 = 5.05$, $P < 0.05$
on no occasion did badgers show any response to the droppings apart from a few sniffs. Several interpretations are possible—the effect of strange droppings may only show itself by affecting subsequent interactions with other strange badgers, in other words the tests were not sensitive enough; or the function of the droppings may be merely to advertise the presence of other, more specific information contained in the secretions of sub-caudal or digital glands; or the droppings have a specific effect only in the appropriate context, i.e. on a boundary latrine. Clearly more observations are needed.

The behaviour of badgers on their latrines indicated that these latrines were of considerable importance in territorial maintenance. Moreover, the fights between neighbouring badgers, the conspicuousness of latrines and associated paths in the border areas and the frequency of the occurrence of those features all suggested that this territorial defence was an important phenomena in the badger's land utilization.

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**Discussion**

Badgers in Wytham were thus organized in groups of variable sizes, inhabiting ranges of usually 50–150 ha; these ranges were defended against other badgers and an elaborate scent-marking system was associated with the boundaries. Even within this one study area, there was variation in group size and structure and in range sizes; a clear difference existed between groups in which males and females had the same ranges, clearly distinct from those of the neighbours, and others in which the males' ranges overlapped with those of females from two different setts. There was one "bachelor-territory" in the study area, much smaller
than the others, inhabited only by males who also marked their boundaries with latrines.

It should be stressed, however, that this description refers only to the study area; it is clear from observation elsewhere by ourselves and other workers that the social organization differs in other areas, e.g. in Scotland. There, for instance, bachelors are probably roaming and non-territorial as in populations of lions (Schaller, 1972). It is possible that the kind of social organization as described here is typical for an area with a relatively high density of badgers. The variation in these social systems between different environments should give important clues as to the underlying mechanisms and this is at present under study. The biological significance of the badgers’ group-use of their ranges will be discussed elsewhere, together with the species’ foraging strategies (Kruuk, in prep.).

It is clear that the badgers’ territorial behaviour has an important influence on the dispersion of the population, and it probably causes the observed spacing-out between setts. It is not known, however, whether territorial behaviour may limit population density as it does in birds with one-pair territories (e.g. Krebs, 1970). The badger clans inhabiting the territories varied in size, and it is possible that group-size limitation is an important, perhaps the only, population limiting mechanism. In this context, it is significant that not all mature females produce cubs every year (Neal & Harrison, 1955); most clans in Wytham produced only one litter annually, irrespective of the number of females. This might be related to a dominance structure within clans, a phenomenon which is found also in other social carnivores, e.g. wolves (Mech, 1970; Zimen, 1976), and dingoes (L. Corbett, pers. comm.), and its mechanism is as yet unknown. Also the fate of cubs at maturity has not yet been investigated; this recruitment to, and expulsion from, the clans will be crucial issues in a population study.

The badgers’ territorial behaviour is important also in the management of their populations. If animals restrict the movements of conspecifics, it is likely that for instance the spread of contagious diseases is impeded by this, and when interfering with badger populations for the purpose of combating bovine tuberculosis (Muirhead, Gallagher & Burn, 1974) or rabies, this should be borne in mind. In a high-density population such as the one here described, the amount of movement of individuals between clans appears to be small and circumscribed; elimination of part of the population might well cause individual animals to range over much larger areas. Further research to test these ideas could be of considerable importance for our knowledge of the effects of carnivore control.

Summary

Aspects of the social organization and territorial behaviour of the European badger (*Meles meles*) were studied in Wytham Woods near Oxford, where the species occurs in a relatively high density.

The animals spent the day-time in holes, classified as main setts and outliers; the setts were significantly associated with a relatively small area of calcareous grit and in woody vegetation. Within this preferred area, main setts were non-randomly distributed, suggesting a spacing-out mechanism with a minimum distance of 300 m between main setts.

The size of badgers’ ranges was assessed by following animals which carried radio-transmitters. Badgers from the same main sett had identical ranges, bordering on ranges of badgers from neighbouring main setts with little overlap. In two main setts the females had exclusive ranges whilst the ranges of males completely encompassed both females ranges.
One sett was inhabited by males only ("bachelors"), and it had the smallest range (21 ha); the other setts' ranges varied between 47 ha and 70 ha with the males of the two joint ranges occupying 107 ha. A method is described for accurately assessing the badger ranges by feeding colour-markers at main setts and retrieving these from the latrines. The results of this are compared with results from radio-tracking.

Each main sett and range was occupied by a group of badgers ("clan"), consisting of more females than males. Adult males spent the day in main setts, whilst females and a young male often slept in the smaller "outliers", especially in summer. The badger ranges were defended, and some of the territorial behaviour is described. Boundaries were marked by latrines near landmarks.

It is a pleasure to acknowledge the help I received from Professor N. Tinbergen, the hospitality in his research group and the donation of part of his Nobel prize to the badger study (for the purchase of the "hot-eye" and other equipment); I am very grateful to him. A great deal of the field work I shared with Mr P. Mallinson; his assistance was as essential as it was effective and pleasant. I would like to thank also Messrs H. Sweetman and G. Cantor for their help and Mr M. Dolan for the construction of radio-equipment. I am very grateful to the late Mr G. Ashby for the design, his advice and his practical help with the radio-transmitters. Drs M. Gorman and I. J. Patterson read the manuscript; their criticisms were of great help.

REFERENCES


