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TERRITORIAL MARKING WITH FAECES IN BADGERS (MELES MELES): A COMPARISON OF BOUNDARY AND HINTERLAND LATRINE USE

by

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(With 5 Figures)

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Summary

Badgers (*Meles meles*) defecate, urinate and scent mark at latrines which seem to have a territorial function. The main aim of the present study was to compare defecation patterns at boundary and hinterland latrines, in order to test the hypothesis that these two types of latrine have a similar function. We investigated latrine use by means of a year-round survey of all the latrines in 7 badger territories, by bait-marking of 15 territories, and by monitoring latrine use in 6 radio-collared badgers belonging to three social groups.

The spatial distribution of latrines within a territory was bimodal, with the greatest densities of latrines close to the outside, and close to the centre, of the territory respectively. Boundary latrines were larger and more consistently used than hinterland latrines, but these differences could be accounted for by the fact that boundary latrines are visited by the members of more than one social group. Defecation at latrines was subject to seasonal variation, with a major peak in latrine use in spring and a minor peak in autumn. The spring peak was largely attributable to an increase in the use of hinterland latrines, the autumn peak to an increase in the use of boundary latrines. Males visited boundary latrines considerably more often than did females, but both sexes visited hinterland latrines equally often. Overmarking occurred equally often at both types of latrine and involved animals from the same as well as from different groups, but there was a significant tendency for more between-group than within-group overmarking. Overmarking occurred mainly on fresh, as opposed to old, faeces deposits.

The sex and seasonal differences in use of boundary latrines suggest that these function at least partly as a form of mate-guarding, to deter neighbouring males from entering a territory for mating purposes. It is less clear why females mark at hinterland latrines. One possibility, consistent with the observed spatial distribution of hinterland latrines, is that they function to defend the main burrow system, which is used for breeding; another is that

¹⁾ The year-round latrine survey was carried out by L.C. and the automatic monitoring of latrine use by S.C. All investigators participated in bait-marking. T.R. and J.B. were supported by grants from the S.E.R.C. and the Association for the Study of Animal Behaviour, S.C. and J.O. by S.E.R.C. studentships, and L.C. by a German Academic Exchange Scholarship. We thank Robinson Farms Ltd for allowing us to work on their land. Drs P. Lürs and A. TURNER kindly commented on the manuscript.

they carry information about social status. Overmarking probably serves to obliterate the marks of competitors, which are members of neighbouring social groups in the case of boundary latrines, but may be members of the same social group in the case of hinterland latrines. We conclude that previous ideas about the function of territoriality in badgers, and about the information conveyed by latrines, are oversimplified.

Introduction

Many mammals, including diverse species of carnivores, use faeces to mark their territories (see reviews by BROWN, 1979; MACDONALD, 1980, 1985; GORMAN & TROWBRIDGE, 1989). In such species, faeces is usually deposited, either alone or together with urine and the secretions of specialised glands, at particular locations known as latrines.

The hypothesis that latrines assist in demarcating a territory rests partly on the observation that in some species, latrines occur mainly on territory boundaries (*e.g.* wolves: PETERS & MECH, 1975; golden jackals: MACDONALD, 1979). Intuitively, this pattern of spatial distribution of latrines seems reasonable since boundary marks would give the earliest possible warning to a potential intruder (GORMAN, 1990). On the other hand, other species site their latrines mainly in the centre or hinterland of the territory (*e.g.* otters: KRUUK & HEWSON, 1978; ferrets: CLAPPERTON, 1989). In an attempt to explain why hinterland marking is sometimes seen, GORMAN (1990) suggests that it is necessitated in cases where the territory is large in comparison to the number of defenders, thus making regular visits to the boundary uneconomical. In support of this view, he presents comparative evidence from four species of African carnivore (aardwolf, spotted hyena, striped hyena and brown hyena) showing that hinterland marking occurs when the length of the territory boundary, divided by the size of the territory-holding group, is relatively large. In addition, GORMAN reports that spotted hyenas engage in boundary marking in the Ngorongoro Crater, where they live in large groups (30 to 80 animals) and defend small territories (30 km²), but in hinterland marking in the Kalahari Desert, where they live in small groups (3 to 15 animals) and defend large territories (1000 km²). As well as being consistent with the idea that hinterland marking is associated with small groups defending large territories, this observation shows that the two scent-marking strategies are not necessarily species-specific alternatives: they can function as facultative responses to prevailing ecological conditions within a single species.

While GORMAN's hypothesis is plausible, it has so far only been applied to cases in which a single species or population of animals engages either in boundary or in hinterland marking. Thus a question remains as to why, in some species, both types of marking occur at the same time (see review by MACDONALD, 1980). The European badger (*Meles meles*) is one such example: a single social group typically utilises latrines both around the boundary and in the hinterland of its territory (e.g. KRUUK, 1978; ROPER *et al.*, 1986; DAVIES, 1987). One possible explanation of this, following the logic of GORMAN's hypothesis, is that badger territories are so small that a single social group can afford to mark both the boundary and the hinterland, thus maximising the chance of an intruder being confronted with a latrine regardless of where it chooses to enter the territory. This is plausible, since badgers are medium-sized, relatively mobile animals, their territories are not usually more than 1 km² in area and mean group size is 5 to 6 adults (see review by CRESSWELL *et al.*, 1990). On the other hand, a recent report suggests that boundary latrines are visited mainly by adult male badgers whereas hinterland latrines are visited by both sexes (BROWN *et al.*, 1992). Thus the two classes of latrine may have different sex-specific functions. For example, boundary latrines may function mainly for inter-group communication between males and hinterland latrines for intra-group communication between individuals of both sexes. Or, the two types of latrine might function to defend different resources on which the two sexes rely to different extents, such as mating partners for males (ROPER *et al.*, 1986) and food resources (MACDONALD, 1983; KRUUK, 1989) or breeding burrows ("main setts") for both sexes (ROPER, in press).

The present study had four separate, but related, aims. First, we intended to compare the properties of boundary and hinterland latrines on the grounds that if the two classes of latrine have a single function, as is suggested by GORMAN (1990), then they should share the same properties. To do this we carried out a year-round survey of latrines in a sample of badger territories, recording various measures of latrine use. Secondly, we looked at the spatial distribution of latrines within each territory, in the hope that this might offer some clues as to their function. We predicted that if hinterland marking is simply boundary marking which is extended in towards the centre of the territory, then the density of hinterland latrines should be highest towards the outside of the territory.

If, on the other hand, hinterland marking functions specifically to defend the sett (ROPER, in press) then the density of hinterland latrines should be greatest close to the sett. Thirdly, we used bait-marking to investigate the occurrence of overmarking (*i.e.* the deposition of faeces on top of a pre-existing deposit, rather than in a new location) at the two types of latrine. We predicted that if overmarking is a mechanism of inter-group communication then it should occur mainly at boundary latrines and should involve members of neighbouring social groups. If, on the other hand, it is concerned with intra-group communication then it should occur mainly at hinterland latrines and involve only members of the resident social group. Finally, by automatically monitoring visits of radio-collared badgers to boundary and hinterland latrines we sought to substantiate BROWN *et al.*'s (1992) report that the pattern of latrine use is sex-specific.

Material and methods

Study area and animals.

The study was conducted in an area of private farmland in the South Downs (a range of chalk hills) near Lewes, in the south-east of England. Vegetation consisted of 35% permanent pasture, mostly on the hillsides, and 63% arable crops, mostly on the hill tops and valley bottoms. The pasture was grazed by sheep and cattle, while the arable crops consisted mainly of wheat (*Triticum aestivum*), rape (*Brassica rapifera*), maize (*Zea mais*) and linseed (*Linum usitatissimum*). There were also scattered farm buildings and small patches of scrub and woodland (for further details see ROPER *et al.*, 1986).

The study area contained 15 social groups of badgers in an area of 6.2 km², giving an estimated population density of 13.5 adults/km² (SCHMID, 1992). The results reported here, which form part of a longer-term study of this population of badgers, mainly concern 7 neighbouring social groups whose territories lay roughly in the centre of the study area. The 7 focal groups were surrounded on all sides by neighbouring occupied territories.

Monthly latrine surveys.

In order to obtain information about the seasonal pattern of latrine use, the 7 focal territories were searched for latrines once per month during the period March 1991 to February 1992. Each monthly survey took 3-4 days.

A badger latrine consists of one or more shallow pits (about 12 cm diameter x 8 cm deep) in which faeces is deposited. The number of these "dung pits" that each latrine contained was counted; and, for each dung pit, the number of faeces deposits that it contained and the approximate age of each deposit ("fresh" = 1-2 days; "recent" = 3-6 days; "old" = 7 days) were recorded. The age of faeces deposits could be judged from their surface appearance and degree of dehydration, taking into account the prevailing weather conditions. The surveyor also scored the presence of anal secretion: a yellow, fatty substance, extruded from the anal glands, which is sometimes deposited at latrines, either with faeces or on its own (KRUUK, 1978; ROPER *et al.*, 1986; DAVIES *et al.*, 1988). For most of the analyses reported below, however, incidences of anal secretion were too few to allow meaningful comparisons to be made.

Because faeces deposits were not always found in the same places in every month of the year it was necessary to distinguish a "latrine site" (defined as a geographical location where dung was found in at least one month of the survey) from a "latrine" (a single dung deposit or group of deposits identified in a single survey). The 12 surveys revealed a total of 725 latrines at 230 latrine sites.

Bait marking.

Bait marking was carried out in April each year from 1988 to 1993, in order to determine which latrines were used by which social groups of badgers. Small amounts of bait, consisting of a mixture of peanuts, sugar syrup and brightly-coloured indigestible plastic chips, were placed at the main sett belonging to each of the 15 social groups in the study population, each day for 10 successive days. A different colour of plastic marker was used for each sett. During the following week the whole area was systematically searched for latrines and at each latrine that was found, faeces was inspected for the presence of plastic markers. By relating each latrine at which markers were found to the main sett from which the markers originated, it was possible to deduce which latrines contained faeces deposited by members of each social group (see Fig. 1a; for further details of the method see KRUUK, 1978; ROPER *et al.*, 1986).

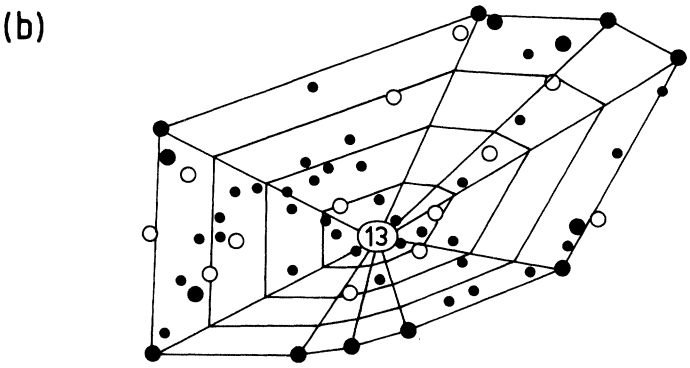
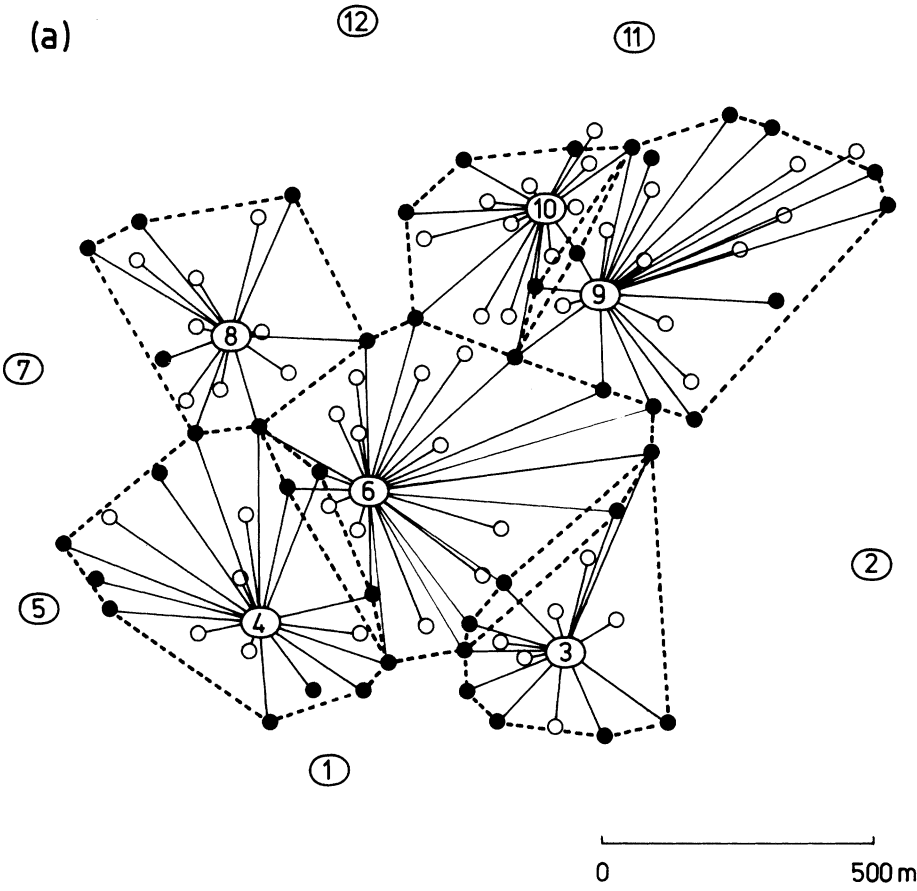
As well as recording the presence of bait markers we also recorded the same data as in the monthly latrine surveys (see above). Care was taken, prior to the first bait-marking operation, to standardise the methodology and to obtain consistency of recording between the different individuals who assisted in data collection.

Classification of latrines.

A major aim of the study was to compare boundary latrines with hinterland latrines. However, different indicators of territory boundaries do not always agree, so an element of subjectivity enters into any attempt to say precisely where territory boundaries lie (CHRISTIAN, 1993). Accordingly, there is no accurate objective way of classifying boundary and hinterland latrines.

To avoid this problem, we classified latrines on the basis of data obtained from bait-marking (see above). Latrines were classified as "shared" if they contained markers originating at the main setts of two neighbouring social groups of badgers; as "unshared" if they contained markers originating from a single main sett; and as "unmarked" if no bait markers were found in them. Since shared latrines are, by definition, places at which the latrine system of one social group meets that of a neighbouring group (Fig. 1a), it seems reasonable to assume that they demarcate territory boundaries. This assumption is substantiated by the fact that shared latrines were on average further away from the corresponding main sett, in all 15 territories, than were unshared latrines (Wilcoxon test, $T = 0$, $N = 15$, $p < 0.001$). They were also further away from the nearest main sett than were unmarked latrines (Wilcoxon test, $T = 0$, $N = 15$, $p < 0.001$). In addition, shared latrines were often linked by clear badger paths running circumferentially around the territory; and radio-collared animals have been seen to travel along these paths from one latrine to another, in a manner suggestive of boundary patrolling (CHRISTIAN, 1993). Furthermore, when minimum-area convex polygons were drawn around the outermost shared latrines for each social group, the sides of these polygons were largely contiguous and non-overlapping, as would be expected if they demarcated territory boundaries (see Fig. 1a).

When unshared and unmarked latrines were compared with respect to distance from the nearest main sett, using mean values across each class of latrine for each of the 15 territories, no significant difference was found (Wilcoxon test, $T = 26$, $N = 15$, $p > 0.05$). Furthermore, almost all unshared latrines occurred within the territory boundaries defined by shared latrines (Fig. 1a). Unshared and unmarked latrines therefore constitute a single



population of hinterland defecation sites. Accordingly, we lumped unshared and unmarked latrines into a single category of "other" latrines, where it was appropriate to do so for purposes of analysis.

The assumption that only shared latrines constitute boundary markers is conservative, in the sense that some unshared or unmarked latrines occurred close to the outside of territories and so may well have been, in reality, boundary latrines (Fig. 1b). Thus, our use of bait-marking results to define boundary and hinterland latrines would tend to reduce any differences between the two classes of latrine that we might find.

Spatial distribution of latrines.

To quantify the spatial distribution of latrines, each of the 15 bait-marked territories was divided into four concentric bands, centred on the main sett belonging to the territory in question (Fig. 1b). This was done by defining each territory boundary as a minimum-area polygon linking the outermost shared latrines. Radii were then drawn from the main sett to each corner of the polygon, and points were marked on each radius a quarter, half and three-quarters of the way along it. These points were then joined to make four concentric polygonal bands. The number of latrines in each band was counted, the area of the band calculated, and the density of latrines per band expressed as number of latrines per hectare.

Monitoring of latrine use by radio-collared badgers.

Visits to latrines were automatically monitored in six adult radio-collared badgers (4 males, 2 females) during a 12-month period (for details of trapping procedure and fitting of radio collars, see CHRISTIAN, 1993). The apparatus consisted of a wooden box containing four separate radio receivers (Mariner type M52), each of which was tuned to a single animal and linked to a 35-cm monopole antenna fitted to the outside of the box. The box was placed at a latrine and receiver gains were adjusted so that a receiver was activated if the radio-transmitter to which it was tuned came within 8 m of the box. Whenever possible the box was camouflaged by placing it under cover of vegetation; and, so as to allow animals to habituate to the box, no data were recorded until it had been stationed at a latrine for at least 3 days. Data (the times at which a receiver was activated and de-activated) were recorded separately for each receiver on an electronic "Squirrel" data logger (Grant Instruments Ltd.) and unloaded into a portable computer.

Fifteen latrines chosen from the territory of a single social group were monitored on a total of 285 nights. Nine of these latrines were classified as "unshared" on the basis of bait-marking (see above); the remaining six were "shared" with neighbouring social groups. Four of the radio-collared animals (2 males, 2 females) belonged to the resident group and their presence was recorded at both unshared and shared latrines; the remaining two animals (2 males) were from neighbouring groups and so were only recorded at shared latrines.

Fig. 1.(a) Part of the study area showing results of bait-marking. Numbered ovals denote main setts; filled circles denote shared latrines; open circles denote unshared latrines. A line connects each latrine where bait markers were found to the sett where the markers originated. Broken lines show territory boundaries drawn as minimum-area convex polygons around the outermost shared latrines belonging to each social group. (b) A single territory showing how the area circumscribed by shared latrines was divided into four concentric bands. Small filled circles denote unmarked latrines; other conventions as in Fig. 1a

Results

Spatial distribution of latrines.

When the density of latrines was calculated in each of four concentric polygonal bands in each of the 15 bait-marked territories (Fig. 1b), the greatest density of latrines was found to occur in the outermost region (band 4, see Fig. 2). This confirms that badgers employ a boundary-marking strategy. Across the other three bands, however, latrine density was inversely related to distance from the main sett. Thus, an incoming intruder which had already passed the territory boundary would be progressively more likely to meet a latrine the closer it came to the main sett. The overall trend in latrine distribution was highly significant (Friedman test, $\chi_r^2 = 19.24$, $df = 3$, $p < 0.001$).

Comparison of shared and other latrines.

The monthly latrine survey involved a total of 174 shared latrines at 26 sites and 551 other latrines at 204 sites, in the 7 territories. Whereas

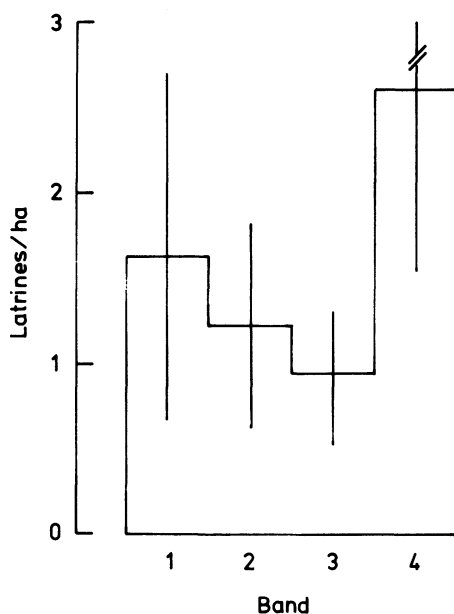


Fig. 2. Density of latrines (mean and SD, $N=15$ territories) in each of four concentric bands centred on the main sett and spanning the whole territory. Band 1 is closest to the main sett; band 4 is immediately inside the territory boundary.

shared latrines were about equally likely to contain anything from 1 to 15 dung pits and had a mean size of 4.4 pits/latrine, other latrines usually contained only 1 to 3 pits and had a mean size of 2.6 pits/latrine (see Fig. 3a). Similarly, shared latrines contained, on average, 8.7 faeces deposits/latrine whereas other latrines contained only 4.2 deposits (Fig. 3b). In both cases the frequency distributions shown in Fig. 3 differed significantly ($\chi^2 = 83.7$, $df = 7$, $p < 0.01$; $\chi^2 = 113.1$, $df = 12$, $p < 0.01$). In addition, shared latrines contained significantly more deposits of anal secretion (mean = 0.7 deposits/latrine) than did other latrines (mean = 0.3 deposits/latrine) ($\chi^2 = 26.1$, $df = 3$, $p < 0.01$). For all three measures, the difference between shared and other latrines was also significant when mean scores in each of the 7 territories were compared (Wilcoxon tests, $T=0$, $N=7$, $p=0.02$). To summarise, shared latrines contained about twice as many dung pits, dung deposits and anal secretion deposits as did other latrines.

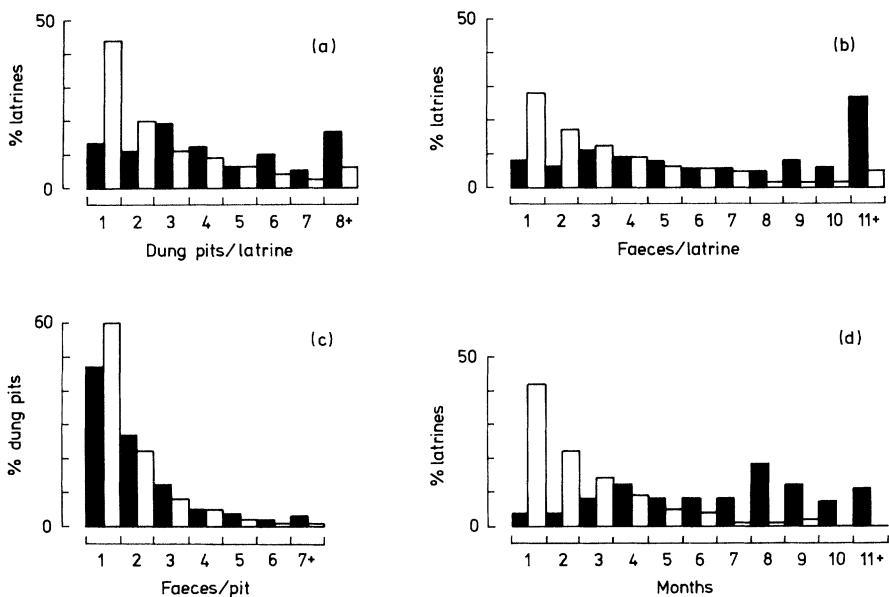


Fig. 3. Results from the monthly latrine survey. (a) Percentage of latrines having a given number of dung pits. (b) Percentage of latrines containing a given number of faeces deposits. (c) Percentage of dung pits containing a given number of faeces deposits. (d) Percentage of latrines that were in use during a given number of months. Black bars: shared latrines. White bars: other latrines.

To compare shared and other latrines with respect to overmarking, we calculated the number of faeces deposits per pit in each class of latrine. On average, shared latrines contained 2.0 deposits/pit whereas other latrines contained 1.6 deposits/pit. Although most pits in both types of latrine contained only one or two deposits (Fig. 3c), the difference between the frequency distributions was significant ($\chi^2 = 48.2$, $df = 6$, $p < 0.001$). In addition, there was a significant difference when mean number of deposits/pit per territory was compared for each latrine type across territories (Wilcoxon test, $T=0$, $N=7$, $p=0.02$). However, when the mean number of dung deposits/pit was compared for shared and other latrines of equal size, no significant difference was found (Sign test, $x = 4$, $N = 14$, $p = 0.13$). We conclude that when the overall difference in size of shared and other latrines is taken into account, overmarking with faeces occurs equally often at both types of latrine.

The extent to which shared and other latrine sites were regularly used was examined by comparing the number of months, out of the total of 12, during which fresh or recent faeces was found at the latrine sites in question. Whereas the modal number of months in which shared latrine sites were found to contain faeces was 8, and the mean number was 6.7, the corresponding figures for other latrine sites were 1 and 2.7 respectively (Fig. 3d). These differences in the frequency distributions of latrine use were significant ($\chi^2 = 51.6$, $df = 1$, $p < 0.01$; data were combined over histogram bins in order to increase the expected values to more than 5 per cell). Thus, shared latrines were in use during about twice as many months of the year as were other latrines (Wilcoxon test, $T=0$, $N=7$, $p=0.02$).

Finally, we examined month-to-month variation in use of latrine sites. Data on the total number of faeces deposits found at all latrine sites per month showed clear seasonal variation, with a major peak in faeces deposition in spring (March and April) and a minor peak in autumn (September and October) (Friedman test, $\chi_r^2 = 22.7$, $df=11$, $p < 0.02$; see Fig. 4a). A similar pattern was found when only data from unshared latrines were analysed, except that the autumn peak was less evident (Friedman test, $\chi_r^2=19.9$, $df=11$, $p < 0.05$; Fig. 4b). By contrast, faeces deposition at shared latrines showed a markedly different pattern, with signs of a peak in autumn but no peak in spring (Fig. 4c). In this case, however, there was no overall significant seasonal trend (Friedman test,

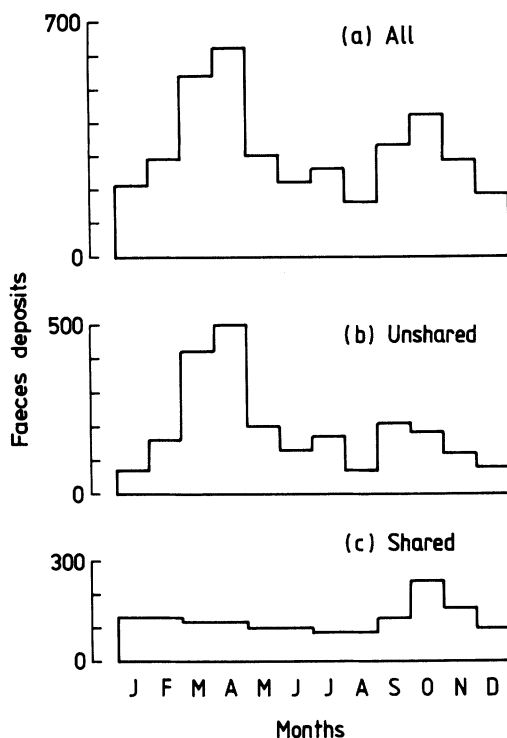


Fig. 4. Results from the monthly latrine survey showing seasonal variation in the total number of faeces deposits found in (a) all latrines, (b) unshared latrines and (c) shared latrines.

$\chi_r^2=12.8$, $df=11$). There was no significant correlation between the patterns of faeces deposition in shared and unshared latrines (Spearman test, $r_s = 0.39$, $N = 12$, $p>0.05$).

In order to see whether the differences shown in Fig. 4 were attributable to differences in the number of latrines in use in any one month, we carried out a similar analysis on the number of latrines containing fresh or recent faeces. Data from all latrines (Fig. 5a), and from unshared latrines only (Fig. 5b), showed a large peak in spring and little variation throughout the rest of the year (Friedman tests, $\chi_r^2=20.6$ and 23.1 respectively, $df=11$, $p<0.05$). In shared latrines (Fig. 5c) there was little evidence of any seasonal variation (Friedman test, $\chi_r^2=7.0$, $df=11$). No significant correlation was found when shared and other latrines were compared (Spearman test, $r_s = 0.47$, $N = 12$, $p>0.05$). To summarise, shared latrines

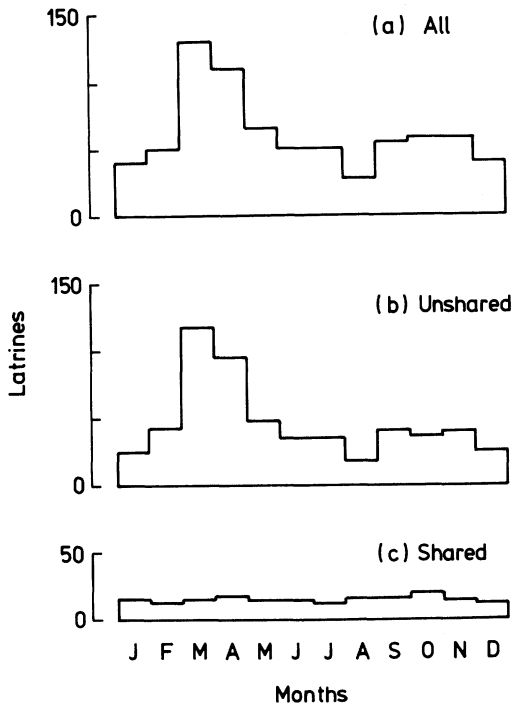


Fig. 5. Results from the monthly latrine survey showing seasonal variation in the number of latrines containing at least one fresh or recent dung deposit. (a) All latrines; (b) Unshared latrines; (c) Shared latrines.

were equally likely to be in use in all months of the year, but tended to contain more faeces deposits in autumn. Other latrines, by contrast, were both more frequently used and larger in the spring.

Other results concerning overmarking.

A subsidiary aim of the project was to compare the incidence of overmarking within and between groups. To do this we used data from bait-marking in order to compare the frequency with which faeces deposits containing the same colour of bait marker, or different colours of marker, were found in the same or different dung pits within any one latrine. We used data only from shared latrines ($N = 53$ latrines at 32 sites). Overmarking involved both markers of the same colour and of different colours, but was significantly more likely, by comparison with random deposition, to involve markers of different colours (Table 1). In other

TABLE 1. Number of instances in which bait-markers originating from a single social group, or from neighbouring groups, were found in a single dung pit or in different pits at the same latrine

Origin of bait markers	Same pit	Different pits
Same group	50 (62)	307 (295)
Different groups	87 (75)	348 (360)

"Same pit" represents instances of overmarking. Expected values, assuming overmarking occurs at random with respect to group ownership, are shown in brackets. $\chi^2 = 4.7$, $df=1$, $p<0.05$.

words, overmarking was somewhat more frequent between animals from different social groups, but did also occur within a single social group. In addition, we used data from the monthly latrine survey in order to determine whether, when overmarking occurred, a new faeces deposit tended to be laid on top of a fresh, recent or old one. We included data only from latrines in which overmarking with fresh dung was recorded and in which there was a choice of fresh, recent and old dung on which a new deposit could be placed ($N = 114$ latrines at 94 sites). There was a significant tendency for new faeces to be placed on top of fresh faeces, though overmarking did sometimes occur on top of recent or old faeces (Table 2).

Sex differences in latrine use.

Automatic monitoring of latrine use in 6 radio-collared badgers showed that all four males visited shared latrines on a substantially higher proportion of nights than did either of the two females (Table 3). By contrast,

TABLE 2. Number of cases of overmarking in which fresh faeces was deposited on top of fresh, recent or old faeces

Fresh faeces deposited on top of:	Observed	Expected
Fresh faeces	136	73
Recent faeces	57	70
Old faeces	17	67

Expected values were calculated for each latrine separately, based on the number of fresh, recent or old faeces available for overmarking. $\chi^2 = 94.1$, $df=2$, $p<0.01$.

TABLE 3. Total number of visits made by radiocollared badgers to shared (N=9) and unshared (N=6) latrines during a 12-month period

	Shared latrines						Unshared latrines			
	1F1	1F2	1M1	1M2	3M1	4M1	1F1	1F2	1M1	1M2
Nights monitored:	99	140	140	97	61	43	145	125	145	145
Nights visits were recorded:	7	8	39	21	19	10	43	18	30	28
%	7.0	5.7	27.9	21.6	31.0	23.2	29.7	14.4	20.7	19.3

Badgers are identified according to sex and social group: for example, 1F2 refers to female number 2 from group 1. All latrines were located in or on the boundary of the group 1 territory.

there was no evidence of a sex difference in the frequency of visits to unshared latrines. For both comparisons, however, the number of animals monitored was too small to allow statistical testing. Overall, individuals of both sexes were about as likely to visit a given unshared latrine on a given night (mean probability of visiting = 0.21, range 0.14-0.30) as individual males were to visit a shared latrine (mean probability = 0.26, range 0.22-0.31).

Discussion

Comparison of shared boundary and hinterland latrines.

If boundary and hinterland latrines serve to convey the same territorial message, as GORMAN (1990) implies, then they should be used in the same way and exhibit the same basic properties. Our results confirm that badgers use a mixed strategy involving both boundary and hinterland marking, but show that latrines are most frequent around the territory boundary and then increase in density again towards the centre of the territory. This in itself suggests that the two classes of latrine have different functions, since if hinterland marking were merely an extension of boundary marking into the interior of the territory, we would expect the density of hinterland latrines to increase with distance from the territory centre.

As regards a comparison of latrine use, the results show that boundary (*i.e.* shared) latrines are about twice as large, twice as likely to contain anal secretion and twice as likely to be in use in any one month, as hinterland (*i.e.* unshared and unmarked) latrines. However, these differences can be

accounted for by the fact that shared latrines are, on average, visited by slightly more than twice as many animals, since most are used by the members of two neighbouring groups and a few by members of three groups. Similarly, we found no difference in the degree of overmarking between shared and other latrines when the difference in frequency of use was taken into account. These findings are consistent with GORMAN's (1990) hypothesis.

On the other hand, we found a striking difference in the seasonal pattern of use of the two types of latrine, which seems to be sex-related. Previous studies (ROPER *et al.*, 1986; DAVIES, 1987; PIGOZZI, 1990) have shown that badger latrines are used more heavily in spring (February to April) than in autumn (September to October). Our results confirmed this pattern of use when boundary and hinterland latrines were not distinguished (Figs. 2a and 3a). But when data from boundary and hinterland latrines were considered separately, the large spring peak in latrine use was found to result from an increase in activity at hinterland latrines, whereas the smaller autumn peak resulted from activity at boundary latrines. In addition, our results from automatic monitoring of latrine use confirm those of a previous study (BROWN *et al.*, 1992) in showing that hinterland latrines are used by both sexes whereas boundary latrines are visited mainly by males. Putting these facts together, we conclude that whereas the spring peak in scent-marking activity is attributable to both sexes, the autumn peak is attributable mainly to males. This conclusion is consistent with evidence that the frequency of bite-wounding in adult badgers shows the same pattern of seasonal variation, with a major peak in spring in both sexes and a smaller peak in autumn which is confined to males (DAVIES, 1987; CRESSWELL *et al.*, 1992). To summarise, both sexes become territorially most active in spring, when they scent mark at hinterland latrines and also engage in overt fighting; and males also show a minor secondary increase in territorial activity in autumn, when they fight and engage in boundary marking.

These results are relevant to arguments about the function of territoriality in badgers. Whereas some investigators have suggested that badger territories function to defend food resources (KRUUK, 1986, 1989; MACDONALD, 1983; PIGOZZI, 1990; WOODROFFE & MACDONALD, 1993), others have suggested that territoriality is a form of mate guarding, in which resident males defend females for mating purposes (ROPER *et al.*,

1986). The seasonal pattern of latrine use and of bite-wounding in adult males fits well with the latter hypothesis, since both histological (WANDERER & GRAF, 1982; CRESSWELL *et al.*, 1992; WHELAN & HAYDEN, in press) and behavioural (NEAL, 1977) data show that while badgers can mate in any month of the year, peaks in mating activity occur in spring and autumn. Furthermore, the idea that territoriality in badgers is a sexually selected activity, and therefore that it is concerned with mating behaviour, is consistent with evidence that (a) males show a higher overall level of bite-wounding than do females (DAVIES, 1987; CRESSWELL *et al.*, 1992); (b) there are sexually dimorphic features of the dentition and cranial morphology that are most easily interpreted in terms of male-male competition (LÜPS & ROPER, 1988; LÜPS, pers. comm.); (c) males have more often been observed to engage in territory boundary fights (KRUUK, 1978; SCHMID, 1992); and (d) sexually immature juveniles rarely defecate or urinate at latrines (BROWN *et al.*, 1992). However, a question remains as to why, if latrine use in males has the primary function of defending oestrus females, it should be concentrated at hinterland latrines in the spring and at boundary latrines in the autumn. One possibility is that females are most likely to be in the vicinity of the main sett in early spring, because they are only just emerging from a period of winter inactivity and because those that have just given birth will be caring for cubs (NEAL, 1977). In autumn, by contrast, badgers of both sexes range widely over the territory in the course of foraging behaviour (CHRISTIAN, 1993). But it should be noted that the switch in emphasis from hinterland to boundary latrines is not an all-or-none phenomenon: both types of latrine site remain active throughout the year.

There also remains the question of why females scent mark at latrines and, as the evidence from bite-wounding shows, sometimes engage in serious fighting. One possibility is that they are defending food resources against potential intruders from neighbouring groups (KRUUK, 1986, 1989; MACDONALD, 1983; PIGOZZI, 1990; WOODROFFE & MACDONALD, 1993); another is that they are defending the main sett which they need for purposes of rearing cubs (ROPER, 1992, in press). The facts that (a) females mark mainly at hinterland latrines, (b) this activity is greatest at about the time of breeding, and (c) the density of hinterland latrines increases with increasing proximity to the sett, are more consistent with the latter idea. In addition, the idea that territories function to defend

food resources is undermined by observations that badgers often make unchallenged excursions into neighbouring territories for feeding purposes (CHRISTIAN, 1993; ROPER & LÜPS, 1993). Another possibility, however, equally consistent with existing evidence, is that in females, latrine use and fighting are a response to intra-group competition for the opportunity to breed (CRESSWELL *et al.*, 1992). In this case, latrines could serve to communicate information about social status.

Overmarking with faeces.

Overmarking (*i.e.* the placing of a scent mark on top of a pre-existing mark) is common in mammals; but its occurrence is puzzling, since the best way in which to make a given amount of scent as conspicuous as possible is presumably to make a large number of spatially separate deposits (see reviews by MACDONALD, 1980; GORMAN & TROWBRIDGE, 1989). One possible explanation of overmarking is that it serves to renew scent which, having been deposited some time ago by the same animal or group, has lost its potency (MACDONALD, 1980). Alternatively, overmarking may be an attempt on the part of one territory-holding animal or group to obliterate the scent marks left by another (GOSLING, 1982). The first hypothesis predicts that overmarking should be a within-group phenomenon, and that when an animal overmarks it should do so on top of an aging mark. The second hypothesis, by contrast, predicts that overmarking should occur between members of different groups, and that it should involve the covering of a recently deposited mark.

Our results showed a strong tendency for faeces to be laid on top of fresh, rather than old, deposits (see PETERS & MECH, 1975, for a similar result involving urine marking in wolves). This is consistent with GOSLING's hypothesis. On the other hand, although we found a significant tendency for overmarking to be more common between rather than within social groups, the difference was slight; and we found no difference in frequency of overmarking between boundary and hinterland latrines. Thus, overmarking with faeces may be partly an attempt by members of one social group to obliterate deposits left by members of a neighbouring group, but this cannot be its only function. As with hinterland marking in general (see above), a possible, but at present purely speculative, explana-

tion of within-group overmarking is that it relates to the maintenance of inter-individual differences in social status.

Conclusions.

Previous accounts of territorial behaviour in badgers have tended to stress one or other potential function of territoriality and have assumed either that all group members cooperate in territorial defence to an equal extent (MACDONALD, 1983; KRUUK, 1989) or that defence is solely a male activity (ROPER *et al.*, 1986; DAVIES, 1987). The present results show that these views are oversimplified. In other carnivore species, latrines, as well as denoting that a territory is occupied, can convey information about individual identity, social status, reproductive condition and recent movement patterns (MACDONALD, 1980; GORMAN & TROWBRIDGE, 1989). It would not be surprising if the same applies to badger latrines. Furthermore, given that badgers do not just deposit faeces at latrines, but also urinate and lay down secretions from at least three separate types of scent gland (KRUUK, 1978; BROWN *et al.*, 1992), it seems unlikely that latrine use in either sex functions to convey a single, simple territorial message.

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