

## Latrine marking patterns of badgers (*Meles meles*) with respect to population density and range size

CHRISTINA D. BUESCHING,<sup>1</sup> CHRIS NEWMAN,<sup>1</sup> KATRINA SERVICE,<sup>1</sup>  
DAVID W. MACDONALD,<sup>1,†</sup> AND PHILIP RIORDAN<sup>2</sup>

<sup>1</sup>Wildlife Conservation Research Unit, Department of Zoology, The Reenanati-Kaplan Centre,  
University of Oxford, Tubney House, Tubney OX13 5QL UK

<sup>2</sup>Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS UK

**Citation:** Buesching, C. D., C. Newman, K. Service, D. W. Macdonald, and P. Riordan. 2016. Latrine marking patterns of badgers (*Meles meles*) with respect to population density and range size. *Ecosphere* 7(5):e01328. 10.1002/ecs2.1328

**Abstract.** European badgers (*Meles meles*) use shared defecation sites, termed latrines, to demarcate group ranges. While some latrines are small, comprising few pits with few fresh scats spread over a small area, others are large, comprising many pits with many fresh droppings and extending over a large area. Although many studies have investigated badger latrine usage patterns, and speculated on latrine function, this variation in relative latrine size remains unexplained. Using nearest neighbor analyses, we analyzed the latrine positioning, use, and inter-latrine distances from four study areas with different population densities. We found that latrines were spaced regularly throughout the range, and border marking was prioritized, increasing the chances of traversing badgers intercepting a latrine. While the numbers of latrines increased with group range size, the number of fresh feces per latrine decreased, suggesting that fresh feces may be a limiting resource in the maintenance of latrines, and that maintaining latrine spacing pattern is more important than the actual number of fresh feces in each latrine. We thus posited that, where territories are small and groups large, the capacity to produce feces exceeds the minimum need for perimeter marking, resulting in fecal redundancy and large latrines. In contrast, in larger territories, especially when occupied by smaller groups, badgers may experience fecal constraint, thus maintaining smaller latrines. We concluded that latrine maintenance and fecal scent-marking activity in badgers involves a trade-off between group size and group range area, leading to different degrees of fecal constraint, while energetic costs of signaling are minimized.

**Key words:** border defense; density dependence; England; European badger; fecal constraint; feces marking; group range; latrine use; *Meles meles*; olfactory communication; scent-marking; territoriality.

**Received** 1 April 2015; revised 16 September 2015; accepted 21 September 2015. Corresponding Editor: R. R. Parmenter.

**Copyright:** © 2016 Buesching et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** david.macdonald@zoo.ox.ac.uk

### INTRODUCTION

Scent-marking is a conspicuous element of the behavior of many carnivores (e.g., Brown and Macdonald 1985, Macdonald 1985, Gorman and Trowbridge 1989) where most exploit feces and urine, as well as the secretions of specialized glands (Johnson 1973, Gosling and Roberts

2001), as olfactory signals. In contrast to glandular secretions, which are often costly to produce (Alberts 1992, Gosling et al. 2000), feces and urine are obligatory metabolic by-products of any heterotrophic diet. They are readily available and “free” substances for scent-marking (Gosling 1981, 1985, Macdonald 1985) that can also be adapted to convey information about the

marking individual (e.g., Kimura 2001). While urine marking is typically difficult to study insofar as marks, once deposited are, in the majority, not visible (Peters and Mech 1975, Macdonald 1985), visual detection of feces (droppings/scat) can reveal how individuals or groups, utilize their environment (e.g., Gompper et al. 2006, Zhou et al. 2013). In addition, the amount of feces produced by an individual is fundamentally proportional to food consumption (Kendall et al. 1992, Cavallini 1994, Kohn and Wayne 1997, Putman 2008), and fecal volume can thus be used to estimate of the number of individuals in an area (European badgers *Meles meles*: e.g., Tuytens et al. 2001, deer: e.g., Buesching et al. 2014, gazelles: Wronski et al. 2012).

While many solitary carnivores deposit single feces strategically to convey olfactory information to conspecifics, some group-living carnivores use communal latrines (reviewed by Buesching and Jordan in press). These are typically used by several, or all, group members, and generally appear to mark the interface between adjacent group ranges (Gittleman 1989). This difference in fecal marking behavior can be attributed, at least partly, to the fact that only group-living species can produce sufficient droppings to maintain border latrines (Macdonald 1980, Sillero-Zubiri and Macdonald 1998). Understanding latrine marking patterns is thus important to understanding social carnivore societies and intergroup dynamics (for examples see Buesching and Jordan in press).

In the European badger, latrine use has been studied since the 1970s (Kruuk 1978, for review see Roper 2010). Badgers are macro-osmatic nocturnal mustelids, which, in high-density populations, form social groups (Johnson et al. 2001), where in some populations group ranges appear demarcated by a system of shared defecation sites (Kruuk 1978, 1989, Delahay et al. 2000, Stewart et al. 2002, Macdonald et al. 2004, Kilshaw et al. 2009). These latrines consist of one or more (in extreme cases up to several hundred) shallow pits (Tuytens et al. 2001), in which feces are deposited alongside urine and glandular secretions (Kruuk 1978, Pigozzi 1990, Stewart et al. 2001, Roper et al. 2003). Multiple droppings are usually found in the same pit (Stewart et al. 2001).

Two types of latrines can be distinguished: *border* (or boundary) *latrines*, which are shared

between members of neighboring groups, and thus appear to demarcate group range peripheries, and *hinterland latrines*, which are situated in the interior of the range, and are generally used only by members of the same social group (Roper et al. 1993, Stewart et al. 2002, Bodin et al. 2006).

Many studies have investigated different aspects of badger latrine usage patterns, and speculated on latrine function, typically predicated upon the concept of range exclusivity/territorial defense (see Kilshaw et al. 2009, Roper 2010). A commonality between studies, however, is the observation that some latrines are small (in the sense that they comprise only a few pits, spread over a relatively small area and contain only few fresh scats), whereas others are large, comprising many pits, with many fresh droppings and extending over a large area (e.g., Tuytens et al. 2001). Two sociological parameters are relevant here: the number of animals in each group available to generate the feces and the size of their territory through which the feces are distributed. According to the Resource Dispersion Hypothesis (RDH), these two parameters are determined, separately and respectively, by the richness of food patches and by their dispersion (Macdonald 1983, Johnson et al. 2001, Macdonald and Johnson 2015).

Thus, if group size remains stable, we can predict that either the number of border latrines, and/or the amount of fresh feces deposited at border latrines, and/or the volume of feces per defecation should be a decreasing function of range size. Where territories are small, and groups large (i.e., at high population density), it is even possible that the capacity to produce feces exceeds the minimum need, perhaps resulting in fecal redundancy, whereas in larger territories, especially when occupied by smaller groups (i.e., at low population density), badgers may experience fecal constraint (Macdonald 1980). With increasing territory size, badgers could thus, hypothetically, vary their defecation patterns in five different ways: (1) They could decrease the number of latrines per unit area; (2) They could decrease the frequency of fecal marking at each latrine, which would result in lower numbers of fresh feces at each latrine; (3) They could increase inter-latrine spacing distances; (4) They could prioritize marking at border latrines over marking hinterland latrines; and (5) badgers could, in theory, attempt

to manipulate the total number of scats available for latrine marking by dividing fecal matter into a larger number of smaller “mini-scats”. This last option, however, seems unlikely, as gut peristalsis is under autonomic control (Lubowski et al. 1987, Olsson and Holmgren 2011), and we found no evidence for this tactic, neither in this study nor elsewhere, nor has its occurrence been described in any other terrestrial carnivore species.

In this study, we review bait-marking data collected from four study areas with different population densities (Tuytens et al. 1999), where we have conducted previous research (Wytham Woods, Oxfordshire: Stewart et al. 2002, Johnson et al. 2001, Kilshaw et al. 2009, North Nibley, Gloucestershire: Tuytens et al. 2001, Macdonald et al. 2006, E1, South Gloucestershire and E2, Wiltshire: Macdonald et al. 2006, Riordan et al. 2011, details see Table 1), to test, which of the above strategies badgers might implement under conditions of fecal restraint.

## MATERIALS AND METHODS

Data from four different badger populations in the South West of England were used (for details see Table 1).

### *Bait marking*

At all sites, bait marking was used to determine latrine usage patterns, following the methodology described by Kruuk (1978), and refined by Delahay et al. (2000) and Kilshaw et al. (2009), allowing direct comparison between populations. Each main sett was fed a uniquely colored indigestible plastic marker, mixed in with a peanut-syrup bait matrix, for 12 consecutive days. Feeding of bait commenced at the same time of year at all sites (i.e., last

week of February / first week of March; before spring green up). Subsequently, the area around these setts was surveyed systematically for latrine locations (recorded as a six-figure grid reference), and size (i.e., the number of pits at each latrine containing fresh feces). A latrine was defined as one or more pits containing at least one feces, color-marked or otherwise (Delahay et al. 2000).

### *Delineation of badger social group ranges*

Minimum convex polygons (MCPs; Johnson et al. 2001) were generated based on the outermost color-marked returns for each sett, providing an estimate of the group range size. Where possible, MCPs were modified by field evidence (e.g., boundary runs, as described in Delahay et al. 2000, Johnson et al. 2001).

Where insufficient (< 6) returns were found per social group (i.e., sett baited), group ranges were excluded from the respective analyses (for numbers of MCPs included for each study site see Table 1), as were all latrines not containing color-marked feces.

### *Classification of latrines*

Following the method of Delahay et al. (2000), latrines situated within 30 m of the MCP-delineated boundary were classified as Border latrines, whereas latrines inside this peripheral zone were classified as Hinterland latrines. Badgers are also known to use underground latrines in their setts (Roper 2010), but no data were available on these. Tables of latrine characteristics, exported from the GIS, were analyzed using SPSS for Windows version 18.0 (2009; SPSS, Chicago, Illinois, USA), and for all analyses a *P*-value of  $\leq 0.05$  was considered significant.

Table 1. Description of study sites (BM = Bait Marking).

Site	Location	For details see:	Size	BM years	Number of groups	Approx. density
E1	S. Gloucestershire	Riordan et al. (2011)	40 km <sup>2</sup>	2002 2003	38 32	5 adults/km <sup>2</sup> 5 adults/km <sup>2</sup>
E2	Wiltshire	Riordan et al. (2011)	20 km <sup>2</sup>	2002 2003	12 14	5 adults/km <sup>2</sup> 8 adults/km <sup>2</sup>
NN	Gloucestershire	Tuytens et al. (2000)	13.4 km <sup>2</sup>	1995	15	9 adults/km <sup>2</sup>
WW	Oxfordshire	Macdonald and Newman (2002), Macdonald et al. (2004, 2009)	6 km <sup>2</sup>	2003	23	32 adults/km <sup>2</sup>

### Nearest-neighbor analyses: patterns in latrine location/ placement

To test whether latrines were distributed randomly throughout each group range or whether latrine distribution followed a regular pattern, we used the GIS mapping package ArcView 3.0. Nearest Neighbor Analysis (NNA; Krebs 1999:620), following Kruuk (1978) and Gosling (1981, 1985); see also Stewart et al. 2001, Johnson et al. 2001). NNA measures the distance of each data point (in this case, each latrine) to its nearest neighbor, and then compares the observed pattern with the pattern expected from a sample of points following complete spatial randomness. A value of  $R = 0$  indicates a clumped pattern;  $R = 1$  indicates a random pattern; while  $1 < R \leq 2.15$  (i.e., the maximum value) indicates a regular pattern. To test, if these NNA values could be an artifact of MCP generation, a corresponding number of MCPs of equivalent areas were generated randomly for the E1 (2002) data subset, and the resulting latrine pattern was also analyzed using NNA.

### Numbers of latrines and group range area

To investigate whether the numbers of latrines used by each group were related to the groups' range sizes, we plotted the total number of latrines in each group range against the range area (derived from the MCPs; including all border and hinterland latrines with feces containing

bait, along with other apparently contemporaneous feces from the respective social group).

We again used the ESRI software application Random Point Generator v1.3 to generate 20 randomly positioned MCPs for the E1 (2005; ArcView GIS, author: Jeff Jenness) data subset reflecting site-specific group range sizes established by the survey data, and then test whether this relationship could be an artifact of the MCP-based analysis. The derived regression was used to predict the number of latrines in simulated group ranges, and results were compared to the actual data obtained from bait-marking.

## RESULTS AND INTERPRETATION

### Number of latrines correlated with group range area

Group range area, and the number of latrines therein, correlated significantly across all study sites and years (Pearson's correlation: E1<sub>2002</sub>:  $r = 0.60$ ,  $n = 38$ ,  $P < 0.01$ ; E1<sub>2003</sub>:  $r = 0.79$ ,  $n = 32$ ,  $P < 0.01$ ; E2<sub>2002</sub>:  $r = 0.59$ ,  $n = 12$ ,  $P = 0.01$ ; E2<sub>2003</sub>:  $r = 0.55$ ,  $n = 14$ ,  $P = 0.04$ ; NN:  $r = 0.70$ ,  $n = 15$ ,  $P < 0.005$ ; WW:  $r = 0.84$ ,  $n = 13$ ,  $P < 0.005$ ) with larger ranges encompassing more latrines (Fig. 1).

In contrast, there was no significant correlation between the number of latrines encompassed by the random MCP simulation and range area, based on E1<sub>2002</sub> data ( $r = 0.31$ ,  $n = 20$ ,  $P = 0.18$ ; Fig. 2).

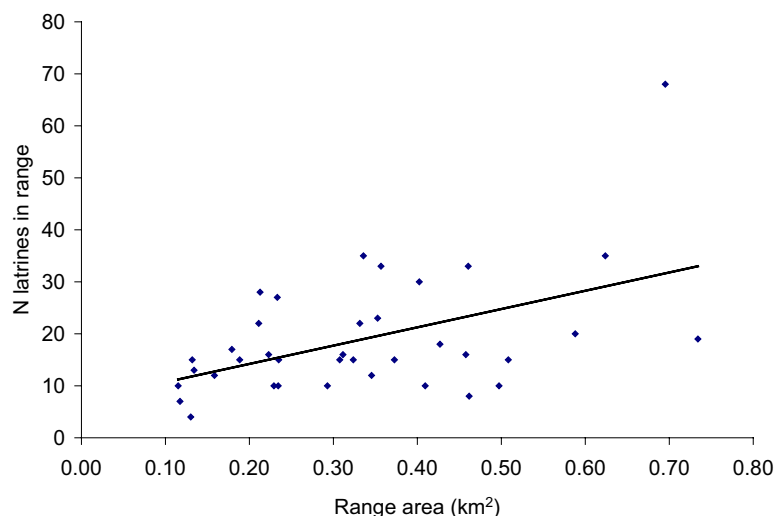


Fig. 1. The relationship between number of latrines and area of social group range as estimated by MCP for the E1 study site in 2002. Number of latrines / group range area:  $r = 0.60$ ,  $P < 0.001$ ; Number of dung pits / group range area:  $r = 0.46$ ,  $P < 0.01$ .

Linear regression models predicting the number of latrines per group range exposed a similar positive association between latrine numbers and range sizes across all four study areas and all years (Fig. 3). In WW, where the population

density was between three- and six-times higher than in the other three areas, the linear relationship between number of latrines and group range size exhibited the steepest slope. E1 and E2, followed very similar, intermediate slopes, while NN showed the shallowest slope. The simulated MCPs, in contrast, showed an even shallower slope. This correlation of latrine numbers with group range area indicates that latrine spacing might be important: badgers appear to attempt to prevent inter-latrine distance increasing above a certain maximum.

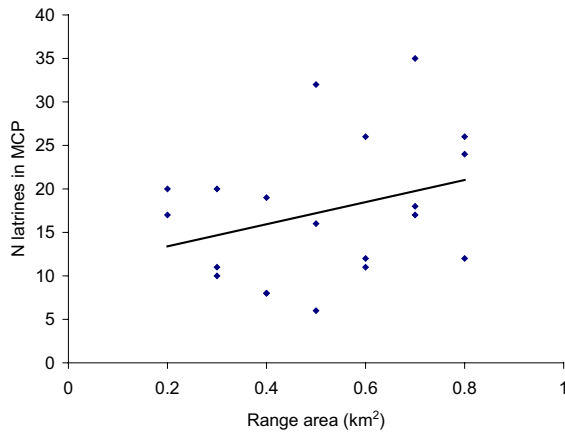


Fig. 2. The relationship between number of latrines for a set of randomly positioned MCPs at the E1 study site in 2002. Number of latrines / group range area:  $r = 0.31, P = 0.18$ .

*The number of fresh feces per latrine was lower with larger group range area*

Combining data for all sites and years, there was a significant negative correlation between the average number of pits containing fresh feces present per latrine and group range area (Pearson's correlation:  $r = -0.27, n = 128, P < 0.01$ ). The number of latrines increases as a function of group range area, implying that fresh feces might be a limiting resource in the maintenance of latrines, and that maintaining an optimum latrine

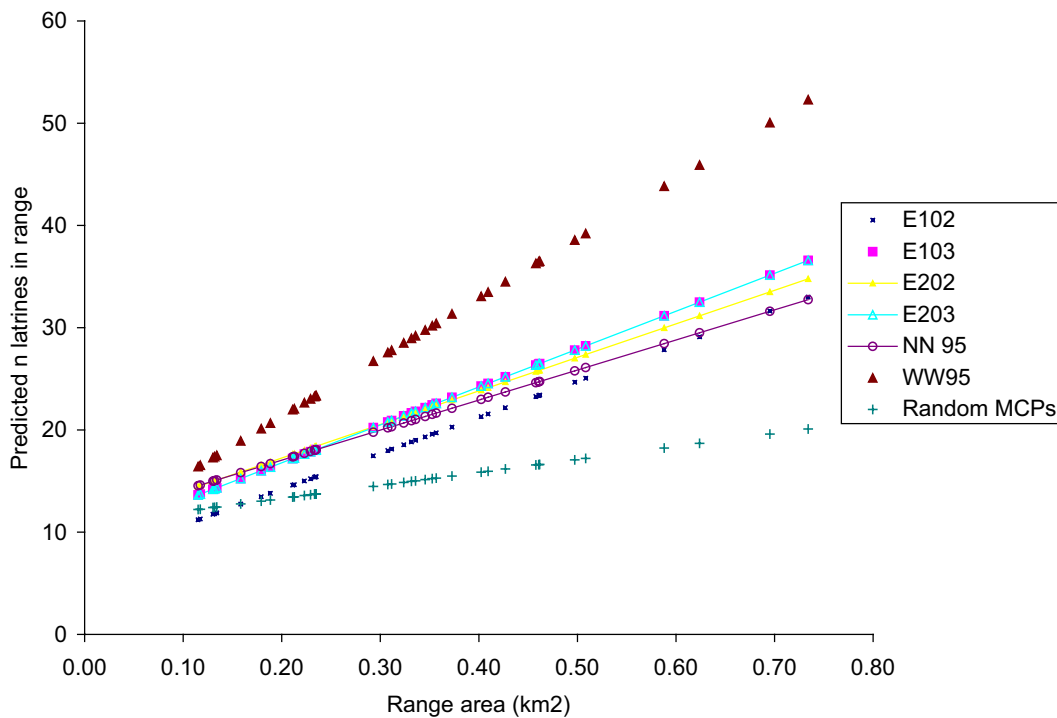


Fig. 3. The predicted number of latrines that would be found in group ranges of varying sizes at each of the study sites, based on the regression equation derived from bait-marking data for each study site/year.

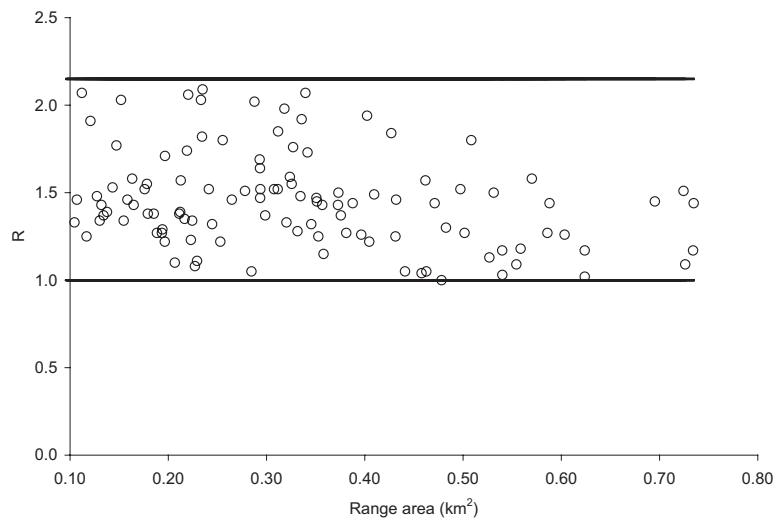


Fig. 4. R values resulting from nearest-neighbor analyses carried out for latrines within bait-marking-derived group ranges plotted against group range area (data from all group ranges are combined for each study site/year).

spacing pattern is more important than the actual number of fresh feces in each latrine.

#### *Latrines followed a regular spacing pattern*

NNA R-values indicated that between 78% and 89% (mean  $84.4\% \pm 4.35\%$  SD) of group ranges, at all four study sites, across all years, exhibited a regular latrine distribution pattern, while only 16% (mean  $15.60\% \pm 4.35\%$  SD) of ranges had latrines spaced randomly. This

tendency for a regular latrine pattern applied irrespective of group range area (Fig. 4). By contrast, the same analysis applied to the randomly generated simulated MCP dataset for E1<sub>2002</sub> (Fig. 5) resulted in a very different outcome: only 25% (mean  $24.55\% \pm 21.07\%$  SD) of these MCPs exhibited a regular latrine distribution, whereas 71% (mean  $70.98\% \pm 25.95\%$  SD) had latrines spaced randomly. This evidences that badgers locate their latrines

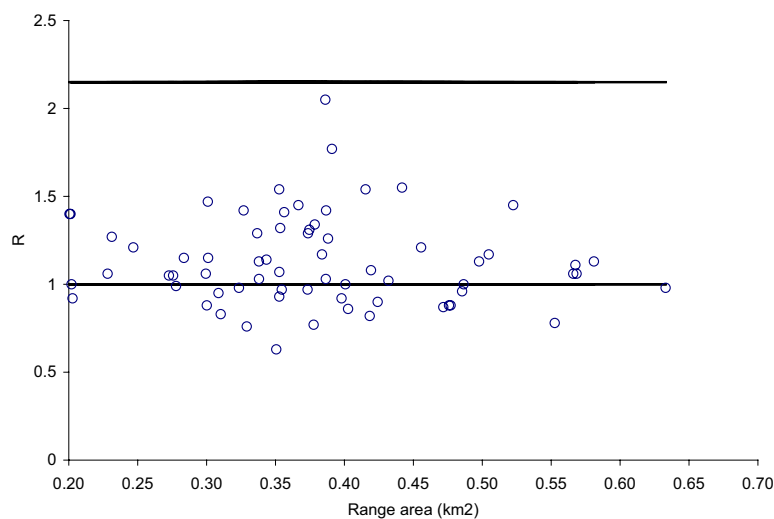


Fig. 5. R values resulting from nearest-neighbor analyses carried out for latrines within randomly positioned MCPs plotted against area of randomly positioned MCP (data from all group ranges are combined for each study site/year).

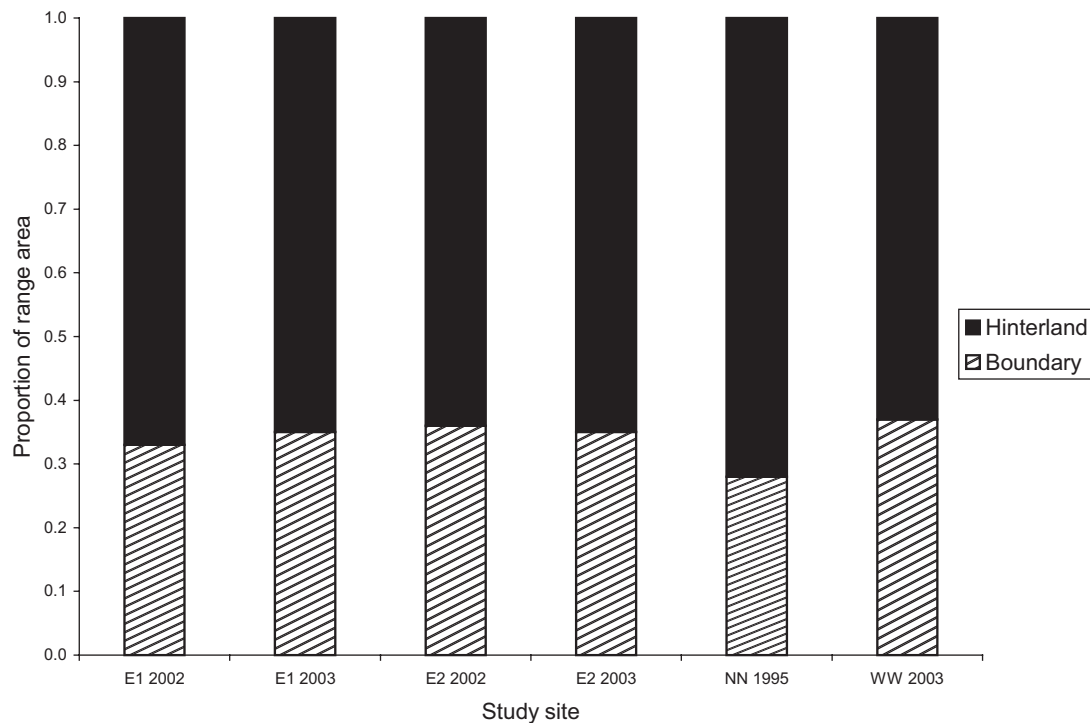


Fig. 6. The proportional area of boundary and hinterland regions in each study site / year (data from all group ranges combined for each study site / year).

according to a strategic design, likely evolved to optimize latrine detectability by the intended recipients of the signals.

#### *Badgers marked boundaries at a higher rate than hinterlands*

Combining all years and sites, latrine distribution defined a peripheral border zone (specified as a 30 m strip on either side of the edge of bait-marking-derived MCPs) that comprised ~30% of mean group range, with the remaining 70% as hinterland (Fig. 6).

Despite this majority of range being hinterland, just over half (=53.3%) of the active dung pits were apportioned to border areas (Fig. 7). Thus, significantly more dung pits were positioned at boundaries compared with hinterland latrines (Wilcoxon signed-ranks test:  $T = 21$ ,  $N = 6$ ,  $P = 0.028$ ), evidencing that badgers prioritize border marking.

## GENERAL DISCUSSION

Badger latrines were not distributed randomly throughout group ranges, but conformed to a

regular spacing pattern, within which more latrines were positioned along the borders of group ranges than in their hinterland. While larger group ranges were ringed by more border latrines than were smaller ones, these contained, per latrine, fewer fresh feces. These traits in latrine distribution are apparent across populations of different densities in different regions of southern England.

The concentration of latrines at the interface between groups has been documented repeatedly in high-density badger populations, and interpretations have generally been predicated upon the concepts of territoriality and group exclusivity (Roper et al. 1986, Stewart et al. 1997, 2001, Allen et al. 1999, Kilshaw et al. 2009), either by active (Kruuk 1978) or passive defense (Stewart et al. 2001) mechanisms. Kilshaw et al. (2009) observed that badgers often defecated along a different border stretch than that closest to their current feeding areas, and interpreted this as evidence for a division of labor in border marking. In contrast, Stamps and Buechner (1985) suggested that the maintenance of border latrines might

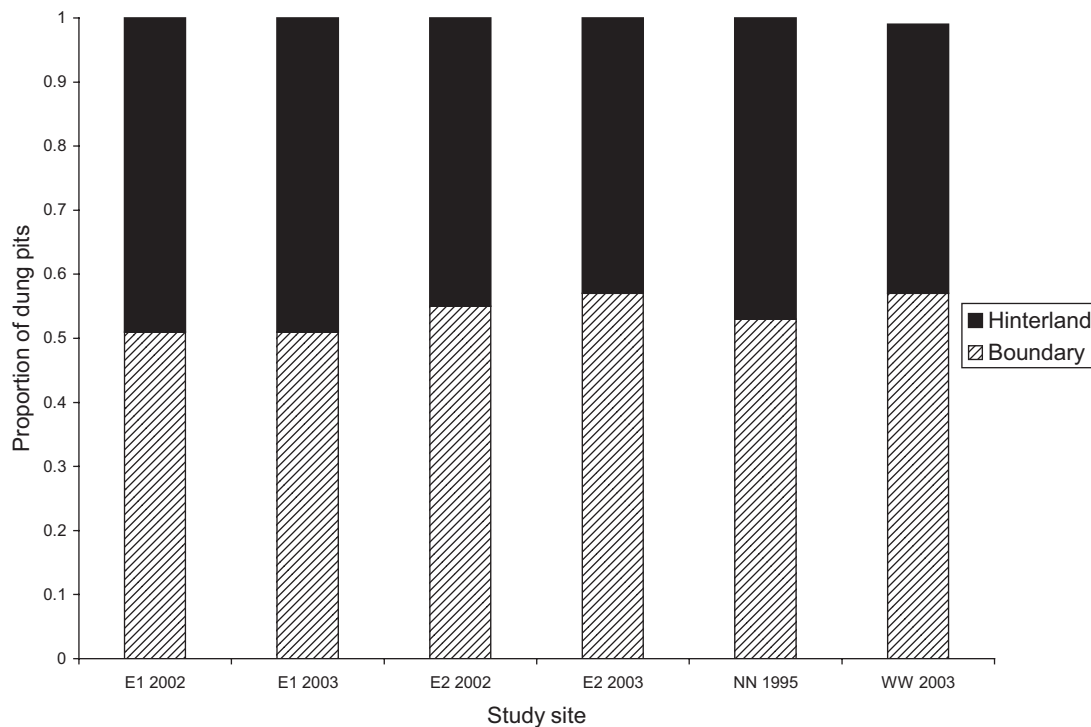


Fig. 7. Proportion of total number of dung pits per social group range that were placed in boundary areas and hinterland areas of the group range (data from all group ranges are combined for each study site / year).

aid in the defense of food resources, which has been proposed as the main latrine function also in the more solitary hog badger *Arctonyx collaris* (Zhou et al. 2015). Roper et al. (1986) suggest that range exclusivity maintained by border-latrines may serve in mate defense (antikleptogamy hypothesis); nevertheless, recent genetic evidence has revealed a promiscuous, polygynandrous mating system with high rates of extra-group paternity in high-density badger populations (Woodchester Park: Carpenter et al. 2005, Wytham Woods: Dugdale et al. 2007, 2011). In WW, approximately 48% of cubs are fathered by extraterritorial males, the majority (approximately 86%) from neighboring groups, but also from more distant liaisons (Dugdale et al. 2007, Annavi et al. 2014), and trapping reveals that ~19% of badgers are caught in temporary cross-boundary excursions (Macdonald et al. 2008, see also Huck et al. 2008).

In contrast, studies conducted in low-density areas, for example in Portugal (Rosalino et al. 2004) or in Switzerland (Do Linh San et al. 2007), did not find conclusive evidence of consistent group

ranges marked with border latrines; instead concluding that the predominant function of latrines is the exchange of olfactory information between individuals, especially in the context of reproduction (see also Kaneko et al.'s (2009) study on the closely related Japanese badger *Meles anakuma*). A further complication to seeking a consilient function for latrine marking is that different individuals may communicate different information, sometimes at different locations, and there could be very different variations on a single theme, ranging from threat to advertisement (Buesching and Macdonald 2001). Although we confirmed that, in all four study areas, borders between adjacent groups were defined by a high-density ring of latrines connected by well-traveled paths, we found no evidence that they functioned to maintain exclusive group range borders.

## CONCLUSION

As predicted by the RDH, our findings support that the mechanism determining population density and group size (see comparison of study

sites in Table 1) is different from the mechanism determining group area, i.e., patch richness vs. patch dispersion (review see Macdonald and Johnson 2015). A corollary of the non-defense-based RDH model of territoriality appears to be its effect on feces availability: under conditions supporting high-density groups, i.e., rich patches with low dispersion, as seen in WW, a smaller group range area to group membership ratio leads to a prolific supply of feces, allowing badgers to maintain more latrine sites with more fresh fecal input. At the opposite end of this scale, where resource conditions dictated a high(er) group range area to membership ratio, conditions of fecal constraint (*sensu* Macdonald 1980) were associated with a decrease in the *use* of latrines (i.e., the number of feces deposited), and not the *number* of latrines. On this basis, our results imply that badgers occupying larger group ranges seek to maintain inter-latrine spacing patterns, plausibly to optimize latrine detection rates by conspecifics (Buesching and Jordan, *in press*). Under conditions of fecal constraint, however, badgers may have to compromise the number of pits used per latrine as well as fecal renewal rates, where replenishment intervals are likely detectable from the odor profile (Buesching et al. 2002).

Overarchingly, we conclude that latrine maintenance and fecal scent-marking activity in badgers involves a trade-off between group size and group range area, while energetic costs of signaling the intended message (Alberts 1992) are minimized (Maynard Smith 1974, Taylor and Jonker 1978).

## ACKNOWLEDGMENTS

We are very grateful to the PTES for their ongoing long-term support for the badger research programme at Wytham Woods. Research in North Nibley and at E1 and E2 was supported by MAFF (now Defra) and carried out with support from the Central Science Laboratory (now FERA) at Woodchester Park, for which we are grateful to Dr Dez Dealhay and Dr Chris Cheeseman. We thank Dr Bart Harmsen and Ms Emma Fordham for their contribution to data collection at E1 and E2, and Dr Frank Tuytens at North Nibley along with numerous other volunteers in all sites. We also thank the landowners and tenants in the study areas for their co-operation during fieldwork.

## LITERATURE CITED

- Alberts, A. C. 1992. Constraints on the design of chemical communication systems in terrestrial vertebrates. *American Naturalist* 139:62–89.
- Allen, J. J., M. Bekoff, and R. L. Crabtree. 1999. An observational study of coyote (*Canis latrans*) scent-marking and territoriality in Yellowstone National Park. *Ethology* 105:289–302.
- Annavi, G., C. Newman, C. D. Buesching, D. W. Macdonald, T. Burke, and H. L. Dugdale. 2014. Heterozygosity–fitness correlations in a wild mammal population: accounting for parental and environmental effects. *Ecology and Evolution* 4:2594–2609.
- Bodin, C., S. Benhamou, and M. L. Poulle. 2006. What do European badgers (*Meles meles*) know about the spatial organisation of neighbouring groups? *Behavioural Processes* 72:84–90.
- Brown, R. E., and D. W. Macdonald. 1985. *Social odours in mammals*. Oxford University Press, Oxford, UK.
- Buesching, C. D., and N. R. Jordan. *In press*. The function of small carnivore latrines: case studies and a research framework for hypothesis-testing. *In* E. Do Linh San, J. J. Sato, J. L. Belant, and M. J. Somers, editors. *Small carnivores: evolution, ecology, behaviour & conservation*. Wiley-Blackwell, Oxford, UK.
- Buesching, C. D., and D. W. Macdonald. 2001. Scent-marking behaviour of the European badger (*Meles meles*): resource defence or individual advertisement. Pages 321–327 *in* A. Marchlewska-Koj, J. L. Lepri, and D. Müller-Schwarze, editors. *Chemical signals in vertebrates 9*. Kluwer Academic/Plenum, New York, New York, USA.
- Buesching, C. D., J. P. Waterhouse, and D. W. Macdonald. 2002. Gas chromatographic analysis of the subcaudal gland secretion of the European badger (*Meles meles*) Part II: time-related variation in the individual-specific composition. *Journal of Chemical Ecology* 28:57–69.
- Buesching, C. D., C. Newman, and D. W. Macdonald. 2014. How dear are deer volunteers: the efficiency of monitoring deer using teams of volunteers to conduct pellet group counts. *Oryx* 48:593–601.
- Carpenter, P. J., L. C. Pope, C. Greig, D. A. Dawson, L. M. Rogers, K. Erven, G. J. Wilson, R. J. Delahay, C. L. Cheeseman, and T. Burke. 2005. Mating system of the Eurasian badger, *Meles meles*, in a high density population. *Molecular Ecology* 14:273–284.
- Cavallini, P. 1994. Feces count as an index of fox abundance. *Acta Theriologica* 39:417–424.
- Delahay, R. J., J. A. Brown, P. J. Mallinson, P. D. Spivee, D. Handoll, L. M. Rogers, and C. L. Cheeseman. 2000. The use of marked bait in studies of the

- territorial organization of the European Badger (*Meles meles*). *Mammal Review* 30:73–87.
- Do Linh San, E., N. Ferrari, and J.-M. Weber. 2007. Spatio-temporal ecology and density of badgers *Meles meles* in the Swiss Jura Mountains. *European Journal of Wildlife Research* 53:265–275.
- Dugdale, H. L., D. W. Macdonald, L. C. Pope, and T. Burke. 2007. Polygynandry, extra-group paternity and multiple-paternity litters in European badger (*Meles meles*) social groups. *Molecular Ecology* 16:5294–5306.
- Dugdale, H. L., D. Davison, S. E. Baker, S. A. Ellwood, C. Newman, C. D. Buesching, and D. W. Macdonald. 2011. Females teat size is a reliable indicator of annual breeding success in European badgers: genetic validation. *Mammalian Biology* 76:716–721.
- Gittleman, J. L. 1989. Carnivore group living: comparative trends. Pages 183–207 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Vol. 1. Cornell University Press, Ithaca, New York, USA.
- Gompper, M. E., R. W. Kays, J. C. Ray, S. D. Lapoint, D. A. Bogan, and J. R. Cryan. 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. *Wildlife Society Bulletin* 34:1142–1151.
- Gorman, M. L., and B. J. Trowbridge. 1989. The role of odor in the social lives of carnivores. Pages 57–88 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Vol. 1. Cornell University Press, Ithaca, New York, USA.
- Gosling, L. M. 1981. Demarkation in a gerenuk territory: an economic approach. *Zeitschrift für Tierpsychologie* 56:305–322.
- Gosling, L. M. 1985. The even-toed ungulates: order Artiodactyla. Pages 550–618 in R. E. Brown, and D. W. Macdonald, editors. *Social odors in mammals*. Oxford University Press, Oxford, UK.
- Gosling, L. M., and S. C. Roberts. 2001. Testing ideas about the function of scent marks in territories from spatial patterns. *Animal Behaviour* 62:7–10.
- Gosling, L. M., S. C. Roberts, E. A. Thornton, and M. J. Andrew. 2000. Life history costs of olfactory status signalling in mice. *Behavioral Ecology and Sociobiology* 48:328–332.
- Huck, M., A. C. Frantz, D. A. Dawson, T. Burke, and T. J. Roper. 2008. Low genetic variability, female-biased dispersal and high movement rates in an urban population of Eurasian badgers *Meles meles*. *Journal of Animal Ecology* 77:905–915.
- Johnson, R. P. 1973. Scent marking in mammals. *Animal Behaviour* 21:521–535.
- Johnson, D. D., D. W. Macdonald, C. Newman, and M. D. Morecroft. 2001. Group size versus territory size in group-living badgers: a large-sample field test of the Resource Dispersion Hypothesis. *Oikos* 95:265–274.
- Kaneko, Y., T. Suzuki, and O. Atoda. 2009. Latrine use in a low density Japanese badger (*Meles anakuma*) population determined by a continuous tracking system. *Mammal Study* 34:179–186.
- Kendall, K. C., L. H. Metzgar, D. A. Patterson, and B. M. Steele. 1992. Power of sign surveys to monitor population trends. *Ecological Applications* 2:422–430.
- Kilshaw, K., C. Newman, C. D. Buesching, J. Bunyan, and D. W. Macdonald. 2009. Coordinated latrine use by European badgers, *Meles meles*: potential consequences for territory defense. *Journal of Mammalogy* 90:1188–1198.
- Kimura, R. 2001. Volatile substances in feces, urine and urine-marked feces of feral horses. *Canadian Journal of Animal Science* 81:411–420.
- Kohn, M. H., and R. K. Wayne. 1997. Facts from feces revisited. *Trends in Ecology & Evolution* 12:223–227.
- Krebs, C. J. 1999. *Ecological methodology*. Addison Wesley Longman, Menlo Park, California, USA.
- Kruuk, H. 1978. Spatial organization and territorial behaviour of the European badger *Meles meles*. *Journal of Zoology* 184:1–19.
- Kruuk, H. 1989. *The social badger*. Oxford University Press, Oxford, UK.
- Lubowski, D. Z., R. J. Nicholls, M. Swash, and M. J. Jordan. 1987. Neural control of internal anal sphincter function. *British Journal of Surgery* 74:668–670.
- Macdonald, D. W. 1980. Patterns of scent marking with urine and feces amongst carnivore communities. *Proceedings of the Symposia of the Zoological Society of London* 45:107–139.
- Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379–384.
- Macdonald, D. W. 1985. The carnivores: order Carnivora. Pages 619–722 in R. E. Brown, and D. W. Macdonald, editors. *Social odours in mammals*. Clarendon Press, Oxford, UK.
- Macdonald, D. W., and D. D. P. Johnson. 2015. Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. *Journal of Zoology* 295:75–107.
- Macdonald, D. W., and C. Newman. 2002. Population dynamics of badgers (*Meles meles*) in Oxfordshire, UK: numbers, density and cohort life histories, and a possible role of climate change in population growth. *Journal of Zoology* 256:121–138.
- Macdonald, D. W., C. Newman, J. Dean, C. D. Buesching, and P. J. Johnson. 2004. The distribution of Eurasian badger, *Meles meles*, setts in a high-density area: field observations contradict the sett dispersion hypothesis. *Oikos* 106:295–307.
- Macdonald, D. W., P. Riordan, and F. Mathews. 2006. Biological hurdles to the control of TB in cattle: a test of two hypotheses concerning wildlife to explain the failure of control. *Biological Conservation* 13:268–286.

- Macdonald, D. W., C. Newman, C. D. Buesching, and P. J. Johnson. 2008. Male-biased movement in a high-density population of the Eurasian badger (*Meles meles*). *Journal of Mammalogy* 89:1077–1086.
- Macdonald, D. W., C. Newman, P. M. Nouvellet, and C. D. Buesching. 2009. An analysis of Eurasian badger (*Meles meles*) population dynamics: implications for regulatory mechanisms. *Journal of Mammalogy* 90:1392–1403.
- Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology* 47:209–221.
- Olsson, C., and S. Holmgren. 2011. Autonomic control of gut motility: a comparative view. *Autonomic Neuroscience* 165:80–101.
- Peters, R. P., and L. D. Mech. 1975. Scent-marking in wolves: radio-tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well. *American Scientist* 63:628–637.
- Pigozzi, G. 1990. Latrine use and the function of territoriality in the European badger, *Meles meles*, in a Mediterranean coastal habitat. *Animal Behaviour* 39:1000–1002.
- Putman, R. J. 2008. Facts from faeces. *Mammal Review* 14:79–97.
- Riordan, P., R. J. Delahay, C. Cheeseman, P. J. Johnson, and D. W. Macdonald. 2011. Culling-induced changes in badger (*Meles meles*) behaviour, social organisation and the epidemiology of bovine tuberculosis. *PLoS ONE* 6:e28904.
- Roper, T. J. 2010. Badger (Collins New Naturalist Library, Vol. 114). Harper Collins, New York, UK.
- Roper, T. J., D. J. Shepherdson, and J. M. Davies. 1986. Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour* 97:94–117.
- Roper, T. J., L. Conradt, J. Butler, S. E. Christian, J. Ostler, and T. K. Schmid. 1993. Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. *Behaviour* 127:3–4.
- Roper, T. J., J. R. Ostler, and L. Conradt. 2003. The process of dispersal in badgers *Meles meles*. *Mammal Review* 33:314–318.
- Rosalino, L. M., D. W. Macdonald, and M. Santos-Reis. 2004. Spatial structure and land-cover use in a low-density Mediterranean population of Eurasian badgers. *Canadian Journal of Zoology* 82:1493–1502.
- Sillero-Zubiri, C., and D. W. Macdonald. 1998. Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *Journal of Zoology* 245:351–361.
- Stamps, J. A., and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *Quarterly Review of Biology* 60:155–181.
- Stewart, P. D., C. Anderson, and D. W. Macdonald. 1997. A mechanism for passive range exclusion: evidence from the European badger (*Meles meles*). *Journal of Theoretical Biology* 184:279–289.
- Stewart, P. D., D. W. Macdonald, C. Newman, and C. L. Cheeseman. 2001. Boundary faeces and matched advertisement in the European badger (*Meles meles*): a potential role in range exclusion. *Journal of Zoology* 255:191–198.
- Stewart, P. D., D. W. Macdonald, C. Newman, and F. H. Tattersall. 2002. Behavioural mechanisms of information transmission and reception by badgers, *Meles meles*, at latrines. *Animal Behaviour* 63:999–1007.
- Taylor, P. D., and L. B. Jonker. 1978. Evolutionary stable strategies and game dynamics. *Mathematical Biosciences* 40:145–156.
- Tuytens, F. A. M., D. W. Macdonald, R. Delahay, L. M. Rogers, P. J. Mallinson, C. A. Donnelly, and C. Newman. 1999. Differences in trappability of European badgers *Meles meles* in three populations in England. *Journal of Applied Ecology* 36:1051–1062.
- Tuytens, F. A. M., R. J. Delahay, D. W. Macdonald, C. L. Cheeseman, B. Long, and C. A. Donnelly. 2000. Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *Journal of Animal Ecology* 69:815–828.
- Tuytens, F. A. M., B. Long, T. Fawcett, A. Skinner, J. A. Brown, C. L. Cheeseman, A. W. Roddam, and D. W. Macdonald. 2001. Estimating group size and population density of Eurasian badgers *Meles meles* by quantifying latrine use. *Journal of Applied Ecology* 38:1114–1121.
- Wronski, T., M. Islam, and M. Plath. 2012. Latrine survey as a method to estimate the population size of Arabian gazelles (*Gazella arabica*). *Mammalian Biology* 78:226–230.
- Zhou, Y., C. D. Buesching, C. Newman, Y. Kaneko, Z. Xie, and D. W. Macdonald. 2013. Balancing the benefits of ecotourism and development: the effects of visitor trail-use on mammals in a protected area in rapidly developing China. *Biological Conservation* 165:18–24.
- Zhou, Y., W. Chen, C. D. Buesching, C. Newman, Y. Kaneko, M. Xiang, C. Nie, D. W. Macdonald and Z. Xie. 2015. Hog badger (*Arctonyx collaris*) latrine use in relation to food abundance: evidence of the scarce factor paradox. *Ecosphere* 6:art19.