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Estimating group size and population density of Eurasian badgers *Meles meles* by quantifying latrine use

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Summary

1. Conservation issues and a potential role in disease transmission generate the continued need to census Eurasian badgers *Meles meles*, but direct counts and sett counts present difficulties. The feasibility of estimating social group size and population density of badgers by quantifying their use of latrines was evaluated.

2. The number of latrines, or preferably the number of separate dung pits, which were known from bait-marking to be used by members of a social group, was positively correlated with adult group size estimated from mark–recapture studies at Woodchester Park and North Nibley (south-west England). In the latter study area both latrine-use measures were also significantly associated with total group size (i.e. including cubs and adults).

3. In spring 1997 and 1998, we quantified latrine use along strip transects, following linear features across four and five areas, respectively, in England, where badger density in summer was known from mark–recapture/resight studies.

4. Seven latrine-use measures were evaluated with regard to their potential to predict badger density. Each measure separately explained between 62% and 91% of the variation in population density in a given year. The simplest measures (latrines km^{-1} and pits km^{-1}) were most stable between years.

5. For these two simple latrine-use measures, a linear model without an intercept term explained the highest proportion of variation in population density. A stepwise procedure to produce the best model selected only one (latrines km^{-1}) of the two measures as an explanatory variable, indicating that pits km^{-1} is colinear with the former variable.

6. A badger census technique based on simple measurements of latrine use has great promise but needs to be validated across a wider range of badger populations, habitats, years, seasons and weather conditions.

Key-words: bait-marking, census, demography, faecal count, population size.

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Introduction

Accurate information about population levels of Eurasian badgers *Meles meles* L. is important in monitoring the impact of human pressures on badger numbers, and understanding the role badgers play in the epidemiology of bovine tuberculosis and rabies. There have been many attempts to assess the distribution and status of the badger on international (Griffiths & Thomas 1993; Bevanger & Lindström 1995), national (Wiertz 1992; Smal 1993; Wilson, Harris & McLaren 1997) and more local levels (Aaris-Sorensen 1987; Skinner, Skinner & Harris 1991).

Direct counts of badger numbers are impractical on a large scale because of the animal's nocturnal and elusive lifestyle and because of the difficulty of identifying individuals within a population. Counting the number of badgers as they emerge from their setts significantly

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underestimates population size, and the degree of this error is likely to differ according to season, the field skills of the observer and the shyness of the badger population concerned (Macdonald, Mace & Rushton 1998). Badger population estimates are therefore almost invariably based on direct (Smal 1993; Wilson, Harris & McLaren 1997) or indirect (Thornton 1988; Macdonald, Mitchelmore & Bacon 1996) secondary indices of abundance, notably sett density. Sett surveys often rely on the differentiation of main setts from the other types of setts (annexe, subsidiary and outlier; *sensu* Wilson, Harris & McLaren 1997). Badger abundance is then estimated as the number of main setts multiplied by the average size of badger social groups derived from trapping studies. This method assumes that there is one main sett per social group and that surveyors are able to find, and classify correctly, all main setts in an area. Both assumptions may be invalid (Tuyttens *et al*. 2000a). Moreover, this method will work only in areas where the relationship between sett density and badger density is adequately known. This relationship may differ not only in space but also in time. The culling of badgers, for example as part of the UK government's policy to control the transmission of bovine tuberculosis from badgers to cattle, may substantially reduce badger abundance without altering the number of setts in the short to medium term (Tuyttens *et al*. 2000a). Furthermore, given the considerable variation in the size of badger social groups (ranging from one individual to more than 30), this method is only useful for estimating badger abundance over large areas. These misgivings support the conclusion by Macdonald, Mace & Rushton (1998) that there appears to be no reliable and cost-effective badger census technique at present that does not involve capture.

Indeed, the abundance of badgers in small intensively studied populations is usually estimated from mark–recapture studies (Rogers, Cheeseman & Mallinson 1997; Tuyttens *et al*. 1999b). These methods are believed to be reliable if the underlying assumptions are valid, if variations in capture probability are adequately controlled, and if an adequate proportion of the badgers is trapped over a sufficient number of trapping occasions (Tuyttens *et al*. 1999b; Tuyttens 2000). However, live trapping of badgers is expensive, labour-intensive, potentially disturbing to the badger population, and is illegal in many countries without a special permit.

Faecal counts have frequently been used as a measure of animal abundance (Neff 1968; Putman 1984; Krebs *et al*. 1986; Sutherland 1996; Plumptre 2000). As badgers defecate in characteristic 'latrines', or clusters of dung pits, their excreta are not only easily distinguished from other species but are also relatively easy to find. Several workers have realized that badger density could be estimated if only there was an easy and reliable way of counting these latrines in the field (Brown 1993; Hutchings 1996). This paper reports the feasibility of a badger census method based on the quantification of latrine use. We first tested whether the size of social groups can be predicted from bait-marking studies, and then evaluated whether measurements of latrine use along strip transects correlated with population density in study areas in England where the density of badgers is known from mark–recapture/resight studies.

Methods

LATRINE USE AND SOCIAL GROUP SIZE

A standard bait-marking trial (Kruuk 1978) was conducted in the North Nibley study area (Gloucestershire, south-west England, National Grid reference ST74,96; for details see Tuyttens *et al*. 1999b) in the spring of 1996. In February–March a mixture of peanuts, golden syrup and indigestible plastic chips was put down at each active non-outlier sett in the study area in the late afternoon for a period of about 3 weeks. The bait was covered by stones or inserted directly in the sett entrances, in order to reduce uptake by other species. Each sett was given its unique colour of plastic chips. The study area was then surveyed for badger latrines. From the colour of the plastic chips recovered from the faeces it was possible to determine which setts belonged to each social group and which latrines were used by each group (Tuyttens *et al*. 2000b). For each latrine we recorded the number of pits that contained faeces and the colour of the plastic chips in them (if any). A similar bait-marking and latrine survey took place at Woodchester Park (Gloucestershire, south-west England, National Grid reference SW81,01; for details see Delahay *et al*. 2000), where the bait was provided for about a fortnight starting at the end of March.

We fitted generalized least-square models (which give unbiased coefficient estimates in the case of heteroscedasticity) to investigate the relationship between group size and the number of latrines or number of separate pits used by each social group, for both study areas separately. The number of latrines or pits used by a social group was defined as the total number of latrines or pits found during the survey that contained faeces with plastic returns of that group (irrespective of whether or not the latrine or pit also contained returns from other social groups). Group size was estimated from mark–recapture studies. Badgers were cage-trapped three times a year (late spring, summer and autumn) at North Nibley and at least four times a year (additional trap-up in winter) at Woodchester Park, using standard procedures (Rogers, Cheeseman & Mallinson 1997; Tuyttens *et al*. 1999a). Social group size was calculated as the number of different cubs (0–1 years) and adults (≥ 1 years) captured during any of the trap-ups of that year, plus the number of animals that were not caught that year but in the previous and subsequent years (1995–98 data only). If an animal was captured in two different groups within a year, it was counted as half a badger in both groups.

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LATRINE USE AND POPULATION DENSITY

From mid-April until mid-May of 1997 and 1998, strip transects 6 m wide, arranged in a stratified-random design, were searched on foot for badger latrines in areas in England where badger density was known from mark–recapture (North Nibley, Wytham Woods, National Grid reference SP46,08, and Woodchester Park) or mark–resight studies (Kettering, National Grid reference SP81,76, and Yeovil, National Grid reference ST51,18). Population estimates at Yeovil were only available for 1998. The boundaries of each study area were drawn along the outside boundaries of the ranges of peripheral social groups as estimated from bait marking (Tuyttens *et al.* 2000b). Population size at the time of the summer following the bait-marking trial was estimated using the methods explained in Tuyttens *et al.* (1999b). It was found previously that at North Nibley there was a good correspondence between mark–resight and mark–recapture badger population estimates (Tuyttens *et al.* 1999b). However, the mark–resight estimates could estimate only total badger density because cubs and adults could not be distinguished reliably when resighted at that time of year.

The strip transects were drawn along linear features (habitat boundaries, roads, tracks, fences, hedges and so on) of the habitat following as closely as possible all east–west and north–south Ordnance Survey map gridlines (1 km apart) that crossed the study areas. In the smaller study areas (Kettering and Yeovil), additional transects, half-way between the original ones, were chosen randomly so that a minimum of 20 km of transect had been surveyed in each study area. For every latrine containing badger faeces we recorded the number of pits, the number of pits containing faeces (except at Wytham and Nibley in 1997), the number of pits containing fresh faeces, the volume of faeces in each pit (except at Wytham and Nibley in 1997) and the volume of fresh faeces in each pit. Pits not containing badger faeces were discriminated from diggings by other animals (mainly rabbits and squirrels) by comparing the size and shape with pits that did contain badger faeces. The volume of faeces was estimated by comparing the amount of faeces in each pit with plasticine moulds of known volume. Soft, smelly and moist faeces were considered to be fresh. Older faeces were usually harder and drier and sometimes had mould on them. For each study area we calculated the mean number of latrines with faeces, number of pits, number of pits with faeces, number of pits with fresh faeces, volume of faeces and volume of fresh faeces, per km of transect searched, for 1997 and 1998 separately. These latrine-use measures were then plotted against the known densities of total badgers in summer. Regression analyses were used to identify which measures predicted badger density most accurately in 1997 and 1998.

In order to test whether the relationships between latrine-use measures and badger density differed between years, two linear regression models were fitted to the various latrine measures. In the full model the year by measure interaction was included as an explanatory variable, while in the reduced model only the measure variable was included. An ANOVA was carried out to evaluate whether there were any significant differences in the relationship between latrine-use measure and density between the years. The R^2 values of both models were compared due to the small number of observations used to fit the models (i.e. statistical tests unlikely to be significant), to see whether the quality of the model was affected by allowing the relationship between latrine measure and density to depend on year.

The two latrine-use measures that best predicted badger density and that were not subject to year effects were selected as the most promising predictor variables. We investigated whether setting an intercept term at zero improved these models. We used ANOVA to test whether including an intercept term significantly improved the fit of the models. As before, we also compared the R^2 values of the models with and without an intercept term. Next we investigated whether population density could have been non-linearly related to either latrine-use measure. This was explored by fitting linear models to the log-density and comparing the R^2 values of these models to those of the same models fitted to the untransformed density. In this case it was not possible to use an ANOVA as the models were non-nested.

Finally, we investigated whether it would be more informative to incorporate both latrine-use measures into a single model for predicting badger density. This was tested by first fitting a linear regression model using year, with both latrine-use measures as predictor variables. This model was then updated using a stepwise procedure to produce the best model for total badger density using the available explanatory variables and two-factor interactions. If both latrine use variables were more informative than either measure alone, the stepwise procedure should select both variables in the final model.

Results

LATRINE USE AND SOCIAL GROUP SIZE

Figure 1 shows that there were significant positive associations between both latrine-use measures and the estimated number of adult badgers per social group at North Nibley and Woodchester Park in 1996. The data were analysed using a generalized least-squares approach instead of a linear regression approach because there appeared to be some inequality of variances among samples (heteroscedasticity). The P-values given in Fig. 1 are for the test that the slope = 0 or not, and therefore indicative of whether or not the latrine-use measures were useful predictors of density. The number of pits with returns was a consistently better predictor of badger group size than the number of latrines with returns. The lines of best fit differed

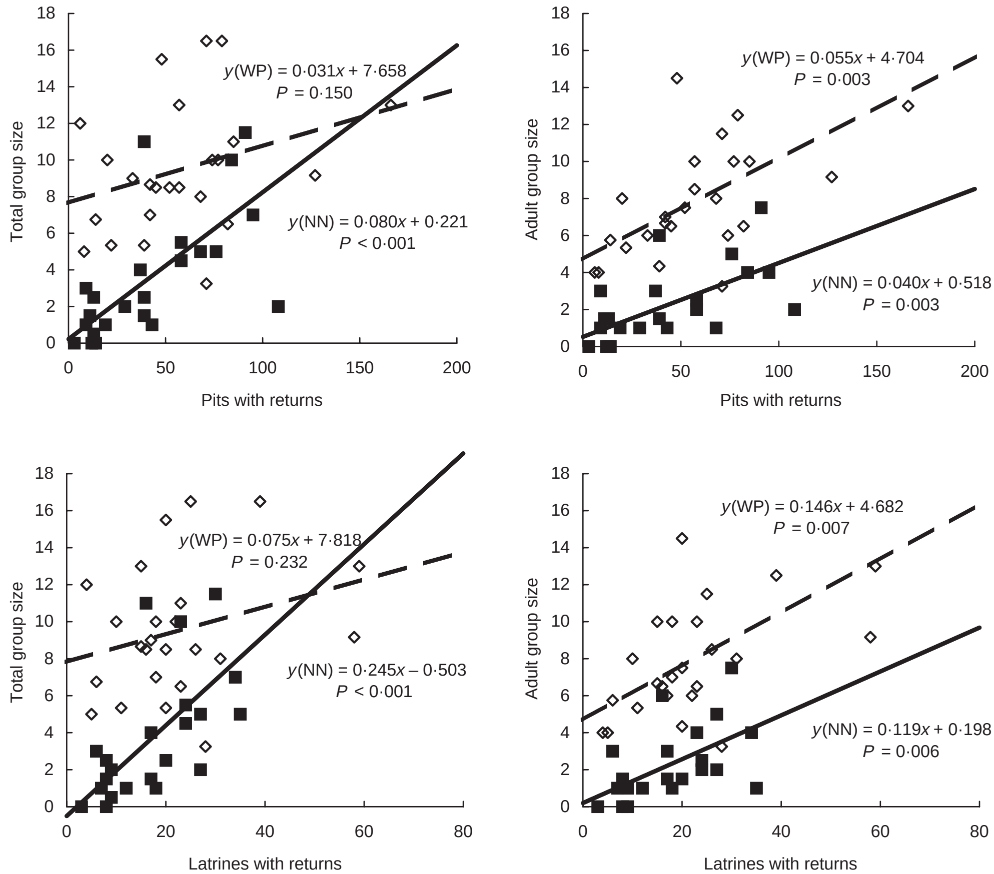

Fig. 1. Relationship between the number of pits or latrines used by a social group and the estimated number of adult, or total, badgers in each social group. Dashed (1997) and solid (1998) straight lines are the lines of best fit for the badger groups at Woodchester Park (WP, open diamonds) and North Nibley (NN, filled squares), respectively, using a generalized least-squares algorithm to adjust for heteroscedasticity.

considerably between study areas. Intriguingly, at Woodchester Park the latrine-use scores were significantly associated only with adult group size but not with total group size. At Nibley, on the other hand, both latrine-use characteristics were more closely associated with total group size than with adult group size.

LATRINE USE AND POPULATION DENSITY

Within a single year, all latrine-use measures were positively associated with population density and all were at least close to statistical significance (Fig. 2). The R^2 values indicated that the various latrine-use measures could explain between 62% and 91% of the variation in population density. The best relationship was between the number of pits containing fresh faeces per km transect and population density in 1997. However, in 1998 the relationship between these variables was quite different. Indeed, Table 1 shows that the year variable was a significant predictor of badger density in the model for pits with fresh faeces. Although year was not a statistically significant predictor of density in the other models, the R^2 values of most dropped considerably when this variable was not included, implying a worse fit. The difference between years seemed most pronounced for the more complex latrine-use measures that required an estimate of faecal volume and/or differentiation between fresh and old faeces. In fact, only in the models for the latrines km^{-1} and pits km^{-1} measures were there no real differences between years. As these were the most (if not the only) stable density predictors with respect to time, we selected them for further analyses.

Table 2 shows that the R^2 clearly improved for the models without an intercept term, although not quite significantly. In other words, models that predict no badgers in the area if no latrines or pits are found along the transects produced a slightly better fit than models with an intercept $\neq 0$.

It is very difficult, without additional data, to determine whether the relationships between the latrine-use measures and density are linear or exponential. The R^2 values indicated, however, that linear models produced better fits than exponential models for both latrines km^{-1} (linear: $R^2 = 0{\cdot}936$; exponential: $R^2 = 0{\cdot}735$) and pits km^{-1} (linear: $R^2 = 0{\cdot}954$; exponential: $R^2 = 0{\cdot}730$).

Finally, the stepwise procedure to produce the best model for badger density did not select both latrine-use measures as explanatory variables (Table 3). Instead, this analysis produced models that used only latrines km^{-1} as an explanatory variable. The model with an intercept term predicted that the number of badgers

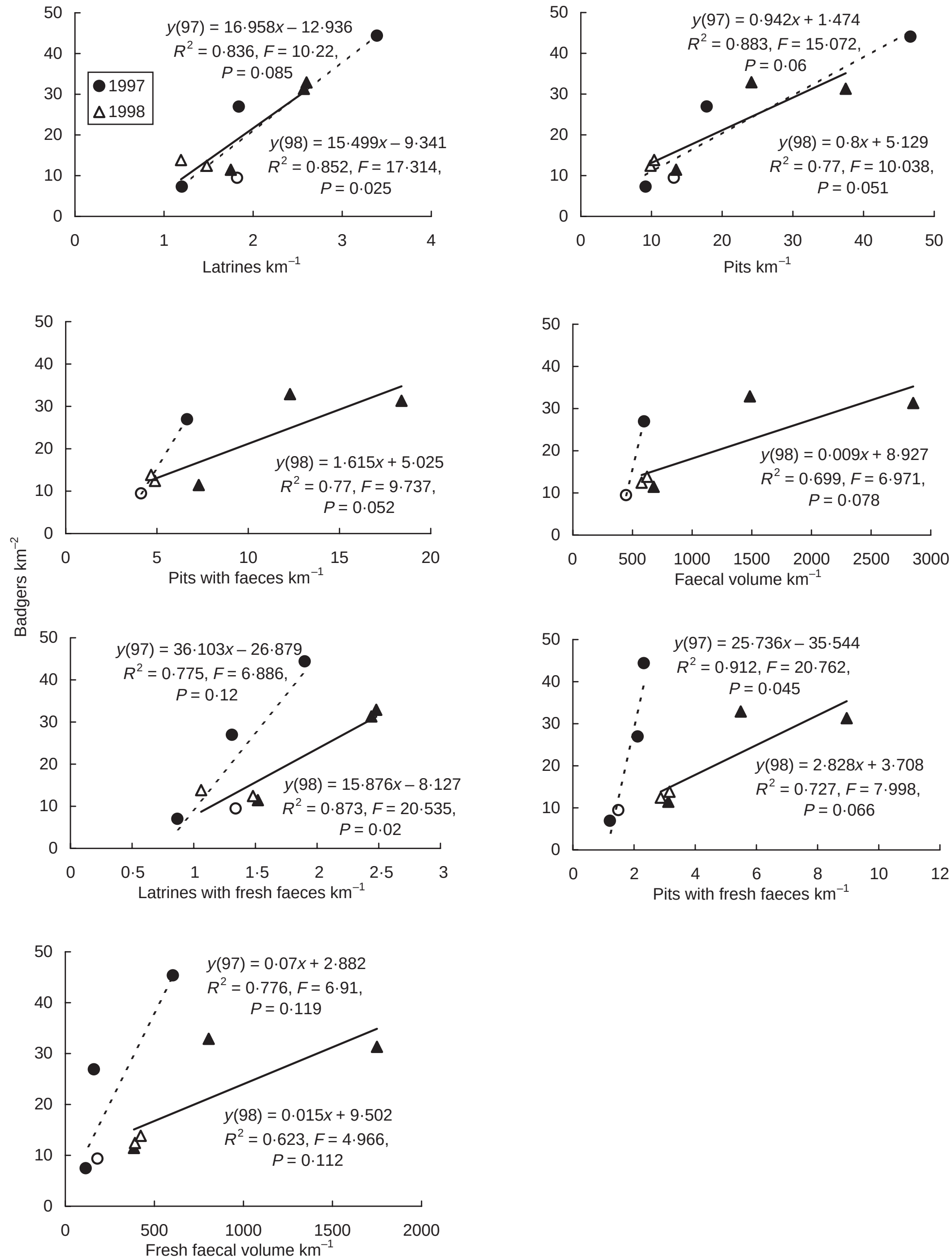

Fig. 2. Relationship, and test statistics of the regression analyses, between the seven latrine-use measures and the estimated density of badgers in the different study areas in 1997 (circles and dashed lines) and 1998 (triangles and solid lines). Population density was estimated by mark–recapture (filled symbols) or mark–resight (open symbols).

km^{-2} = 16·3–11·3 (latrines km^{-1}). The model without an intercept term predicted that the number of badgers km^{-2} = 11·3 (latrines km^{-1}). These results indicated that the extra potential information that may come from pits km^{-1} is colinear with that from latrines km^{-1}.

Discussion

We have illustrated that both social group size and population density of badgers can be estimated by quantifying their use of latrines. First, it was illustrated that counting the number of latrines or, even better, pits with returns used by a social group during a bait-marking trial can yield an approximation of the number of adult badgers living in that social group. Both latrine-use measures were also significantly associated with total group size (i.e. including cubs) at North Nibley, but not at Woodchester Park. The Woodchester Park results make most sense biologically because at the time of bait-marking badger cubs were not yet contributing many faeces to above-ground latrines. At North Nibley, however, the range of adult group sizes was limited because its badger population not only was at much lower density than at Woodchester Park but also consisted of a much higher proportion of cubs (Tuyttens *et al*. 2000c). Hence including cubs increased the range of different group sizes, particularly at North

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Table 1. Comparison of the variation in population density explained by the various latrine-use measures when year was included (R^2_{years}) or excluded ($R^2_{no\ year}$) in the models. The ANOVA test results indicate whether year was a significant predictor

Predictor	R^2_{years}	$R^2_{no\ year}$	Test statistic	*P*
Latrines km^{-1}	0·843	0·840	0·038	0·963
Pits km^{-1}	0·845	0·839	0·098	0·908
Pits with faeces km^{-1}	0·825	0·635	1·625	0·333
Latrines with fresh faeces km^{-1}	0·809	0·529	3·665	0·105
Pits with fresh faeces km^{-1}	0·850	0·189	11·022	0·015
Faecal volume km^{-1}	0·776	0·526	3·986	0·092

Table 2. Comparison of the variation in population density explained by the two chosen latrine-use measures when an intercept term was included ($R^2_{int.}$) or excluded ($R^2_{no\ int.}$) in the models. The ANOVA test results indicate whether excluding the intercept term significantly improved the models

Predictor	$R^2_{int.}$	$R^2_{no\ int.}$	Test statistic	*P*
Latrines km^{-1}	0·840	0·936	3·970	0·087
Pits km^{-1}	0·839	0·954	0·918	0·396

Table 3. Test statistics of the models with (a) and without (b) an intercept term for predicting badger density using a stepwise procedure to select the explanatory variables (latrines km^{-1} and/or pits km^{-1})

Coefficient	Value	SE	*t*	*P*
(a) Intercept ≠ 0 ($R^2 = 0·840$, $F_{1,7} = 36·8$, $P = 0·0005$)				
Intercept	–11·273	5·658	–1·992	0·0866
Latrine km^{-1}	16·342	2·695	6·064	0·0005
(b) Intercept = 0 ($R^2 = 0·936$, $F_{1,8} = 117·6$, $P < 0·0001$)				
Latrines km^{-1}	11·272	1·039	10·846	< 0·0001

Nibley. In addition, at North Nibley the mark–recapture estimates of total group size may have been more accurate than the adult group size estimates because the trapping probability of adult badgers in this study area was comparatively low (Tuyttens *et al.* 1999a). This difference in trappability may also explain why the lines of best fit predict higher (adult) group sizes at Woodchester Park than at North Nibley for a given latrine-use score. The differences between the study sites could also be a consequence of (minor) logistical differences in the bait-marking methodology. The groups were fed for longer with the peanut–treacle–plastic bait at Nibley than Woodchester; bait-marking took place earlier in the year; it seemed that the bait was less readily consumed; and, despite our efforts, it is difficult to be sure that both sites were searched with equal effectiveness during the latrine surveys. Differences in habitat and in the time that had elapsed between feeding and latrine survey may cause additional biases in the latrine-use scores of the various social groups. Latrines are more easily found in open pasture than dense woodland and in early spring than late spring. The probability of finding plastic returns in faeces also diminishes as time elapses since bait placement (Delahay *et al.* 2000).

Alternatively, the difference between both sites might have a true biological explanation. For example, there might be a threshold effect such that at a certain group size the number of latrines or pits no longer increases. Faeces from large social groups may be concentrated in a relatively small number of heavily used latrines and pits, while faeces from small groups of badgers might be spread more thinly in a relatively large number of latrines or pits. If so, we would have expected that the more complex measures of latrine use (e.g. those that estimate faecal volume) would better predict badger density than the coarser measures. There was little evidence, however, that this was the case. In both 1997 and 1998, simple latrine-use measures such as latrines km^{-1} or pits km^{-1} were as good at predicting density as the more detailed measures. It is possible, however, that the potentially greater discriminating power of the more complex measures was not realized because they were more prone to measurement errors and observer biases. The latter measurements may also have been confounded more by potential differences in the badger's diet. Furthermore, if there were such differences in defecation patterns between low and high density badger populations, as suggested above, we would have expected exponential rather than linear relationships between the coarser latrine-use measures and badger density. For the populations considered in the present study, however, linear models produced a better fit. It is possible that an exponential relationship would be observed if more populations with a greater range in density had been included in the study. Our results suggest, nevertheless, that even coarse latrine-use measures can be used to estimate the abundance of very high density populations (Wytham Woods and Woodchester Park harbour the highest densities of wild badgers known in Europe).

In addition, the coarse latrine-use measures appear to be of most practical value for predicting badger abundance in the future because these measures were most stable with respect to time. Models for the more complex latrine-use measures, on the other hand, differed considerably between 1997 and 1998. Stricter procedures for quantifying faecal volume and for differentiating between fresh and old faeces might partly solve this problem.

The present evidence suggests that quantifying the number of latrines along strip transects is a very promising new badger census technique that warrants further investigation. Laymen can be successfully trained to do this within a couple of hours. We estimated that, on average, one person needed an hour to survey a transect of about 0·7 km. At this speed all transects in 1 km^2 were covered in about 5 h. This compares favourably with the time required to survey 1 km^2 for badger setts. During the National Badger Survey, volunteer fieldworkers were encouraged to cover 1 km^2 in 1 day (Wilson, Harris & McLaren 1997). During our own sett survey in North Nibley at least two people were required to cover 1 km^2 in a day. In the present study we surveyed for badger latrines only along narrow strips following linear features of the habitat, because it is along these linear features that the majority of badger latrines are positioned (White, Brown & Harris 1993). Hence, this stratified-random design has three important advantages. First, it increases the time-effectiveness of the method because it maximizes the number of latrines found per distance walked. Secondly, it reduces the problem of edge effects because it is exceptional to find latrines that are only partly within the 6-m wide boundaries of the transect. Thirdly, as the boundaries of the transects were so narrow and well-defined, the chance that latrines would be overlooked was minimal.

To conclude, our study suggests that a badger census technique based on the quantification of simple latrine-use measures along strip transects has great promise. However, further research is needed in order to validate the relationships between the various latrine-use measures and badger density across a wider range of badger populations, habitats, years, seasons and weather conditions. More complex measures of latrine use may enhance the predictive power of the analyses but require refined, standardized and very strict measurement procedures. Similarly, it is likely that social group size could be estimated more precisely by quantifying latrine use if more standardized bait-marking and latrine survey protocols were adhered to.

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