

Group size versus territory size in group-living badgers: a large-sample field test of the Resource Dispersion Hypothesis

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Badgers (*Meles meles*) have been the focus for the development of a pervasive model of social grouping behaviour, relevant to a number of carnivore species and other taxonomic groups – the Resource Dispersion Hypothesis (RDH). The RDH hypothesises that the dispersion and richness of resources in the environment provide a passive mechanism for the formation of groups, even without any direct benefits of group living. However, few studies have tested the RDH in the field. The principal prediction is that, as opposed to enlargement of territory sizes to accommodate more members, territory size (TS) is independent of group size (GS). Instead, TS is determined by the spatial dispersion of resources, while GS is independently determined by the richness of those resources. However, these predictions provide only weak correlative tests, especially in non-experimental field studies. The first predicts an absence of correlation and is therefore prone to Type II error, especially given the small sample sizes and errors in estimating TS and GS of mammals in the field. We tested for independence of territory size and group size in all years with available data since the beginning of the long-term badger study in Wytham Woods in 1974. We used two methods of TS estimation, a sequential Bonferroni technique to adjust for multiple inference tests, a combined analysis and an analysis with pooled data. This prediction of the RDH could not be rejected on the basis of any of these analyses. Given this evidence that other processes are independently determining group size and territory size, further predictions of the RDH will be worth investigating in considerable detail.

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The Resource Dispersion Hypothesis (RDH) (Carr and Macdonald 1986, Macdonald and Carr 1989, Bacon et al. 1991) proposes that the spatiotemporal dispersion and richness of resources can lead to the passive formation and maintenance of animal groups, even in the absence of any direct benefits of group living per se. Thus, it provides a mechanism for the evolution of sociality outside specific selective pressures, such as those for group hunting or predator defence, that are evident in a majority of social animals (Bertram 1978, Bygott et al. 1979, Gittleman 1989, Packer et al. 1990,

Cooper 1991, Creel and Creel 1995). The RDH was first formalised by Macdonald (Macdonald 1981, 1983), and built on models developed on foraging in colonial bats (Bradbury and Vehrencamp 1976). Badgers (*Meles meles* L.) became a particular focus for attention as a model species (Stopka and Johnson 2000) after observations from our study site (Kruuk 1978a, b) highlighted the need for new explanations of sociality in this and other species that were group living but apparently non-cooperative (Woodroffe and Macdonald 1993, 2000). The RDH has been applied to various species,

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apart from the badger, including red foxes, *Vulpes vulpes* (Macdonald 1981), Blandford's fox, *Vulpes cana* (Geffen et al. 1992), arctic foxes, *Alopex lagopus* (Herrsteinsson and Macdonald 1982), brown hyenas, *Hyaena brunnea* (Mills 1982) and kinkajous, *Potos flavus* (Kays and Gittleman 1995, 2001). The RDH was later more explicitly described and statistical models showed it to be feasible under given conditions (Carr and Macdonald 1986), before it subsequently gained more rigorous support from mathematical modelling (Bacon et al. 1991). The RDH has since become widely recognised as a potential explanation for grouping behaviour in carnivores where no other functional behavioural benefits are evident, although its applicability may extend to a considerably wider range of taxa (Herrera and Macdonald 1989, Taber and Macdonald 1992, Davies et al. 1995). While RDH effects may be absent in many species, it remains a potential underlying influence on group size variation in many others, even if it is masked by much stronger selective pressures such as the need for cooperative hunting or predator defence. While it is, therefore, primarily important for apparently non-cooperative social animals, it remains a potentially additional explanatory factor of group size variation in other species. In general, the spatial dispersion, patchiness and variation of food resources are increasingly thought to have direct influences on group size variation among carnivore and primate species (Macdonald 1983, Wrangham et al. 1993, Chapman et al. 1994, Janson and Goldsmith 1995, Boesch 1996, Baker et al. 2000, Wrangham 2000).

Animals are expected to utilise home ranges that are 'minimum economically defensible' areas (Gill and Wolf 1975, Charnov et al. 1976, Maher and Lott 1995), but which are large enough to satisfy their metabolic needs over time (McNab 1963). If group size is increased via recruitment it follows that, all other things being equal, the territory must be enlarged to meet the increased metabolic requirements of more individuals. Contrary to these theoretical expectations, however, territory size (TS) does not increase with social group size (GS) in some carnivore species (Macdonald 1983). The RDH predicts that, if there is spatial or temporal heterogeneity in resource availability in the environment, rather than the enlargement of territory sizes to accommodate more members, territory size will be independent of group size. Instead, TS is hypothesised to be dependent on the spatial dispersion of resource patches, while GS will be dependent on the richness of those resource patches.

The hypothesis was initially criticised (von Schantz 1984) for lacking falsifiable predictions, and according to strict definitions (Peters 1991) it could be suggested not to meet the criteria of a predictive theory. Nevertheless, it provides, at the least, a useful model ('logical model' in Peter's terms), as an explanation for grouping by consideration of frequency distributions of food

resources in a variable environment (Macdonald and Carr 1989). However, there have been no other serious published falsifications or objections to the hypothesis in the twenty years since its appearance. Indeed, an ever increasing number of field studies are invoking the RDH as a fitting explanation of social grouping in various species (Arden-Clarke 1986, Geffen et al. 1992, Meia and Weber 1996, Brøseth et al. 1997, Johnson et al. 2001), even where sample sizes are small and habitat types are used as surrogate measures of resource patches. Most such studies do not specifically test the RDH predictions, but use it as an a posteriori explanation of observed patterns of social and spatial organisation.

Furthermore, few studies (especially of large mammals) offer the sample sizes necessary to support predictions of such hypotheses with confidence. This is partly because studies of carnivores (with which the hypothesis is usually associated) and methods of estimating territory size (usually labour intensive radio-tracking) constrain sample sizes. This is a particular problem for testing the prediction of independence of TS and GS, because Type II error (failure to reject the null hypothesis of no relationship) is likely if there is noise in the data from a variety of other possible sources, the problem being that it is precisely the lack of a relationship that is interpreted as support for the hypothesis. Many studies are also concentrated on one season, whereas it is explicit in the RDH that temporal as well as spatial variation in resource availability is crucial. Early reports on the hypothesis (Kruuk 1978a, Carr and Macdonald 1986) concentrated on variation over the scale of nights or days. However, there is no reason why the effect would not operate over much longer time-scales.

The variables in the latter two predictions (TS is dependent on dispersion of resources, GS is dependent on the richness of those patches), are difficult to measure accurately (Chapman et al. 1994), especially in badgers (Johnson et al. 2001), so in previous studies patches of habitat have often substituted for actual measurements of resource availability. However, despite the difficulties, these would be worth investigating in considerable detail if the first prediction (that TS and GS are independent) is met. Badgers offer an excellent opportunity to test this hypothesis because they have well-defined territory borders and, in our study site, there are several social groups with a range of group sizes. Badgers are well known for their marking behaviour at fixed 'latrine' sites (Roper et al. 1986, Kruuk 1989, Neal and Cheeseman 1996), many of which tend to be at the edges of their territories (Kruuk 1978b). This has led to well-established methods (since the work of Kruuk 1978b) of constructing maps of badger territory borders according to the distribution of these latrines. Bait, marked with plastic chips of different colours, can be put at each of the badger sett sites,

which are eaten by the badgers and subsequently deposited at their latrine sites. The locations of these 'bait-marks' can be found later on and recorded onto maps (a detailed methodology can be found in Delahay et al. 2000).

The population size and density of badgers has increased since the beginning of the study in Wytham Woods (Macdonald and Newman in press) so it was of interest to discover whether territory sizes have undergone changes during that time as well. Territory sizes were thought to have remained relatively constant since 1993, and this was an essential assumption in the calculation of an index of per-group densities in a recent study of density-dependent group effects in Wytham (Macdonald et al. in press). This had not been explicitly tested, however. Measuring a change in territory sizes over time is also important for two other reasons. Firstly, the more territory sizes change between years, the more pooled tests between years will represent more independent data (group sizes are also known to change considerably between years (Newman 2000) which will affect this as well). Secondly, it is of interest to know whether RDH predictions hold over a range of population densities, especially given that one recent study has explicitly suggested they may be density dependent (Baker et al. 2000).

Although the RDH predicts that group size does not correlate with territory size, an alternative explanation for such a lack of fit is that if territories vary in quality, then variation in group size may just be a response to per capita territory quality, over and above any change in territory size itself. This is important because if the size of a territory is independent of its quality, GS could be hypothesised to be independent of TS as well. However, several previous studies in our study site reject this alternative. Former tests of this have failed to determine any relationship between group size and territory quality in Wytham Woods (Hofer 1988, Da Silva et al. 1993, Johnson et al. 2001), so we had reason to believe (including from recent data) that there were other independent factors responsible for the relationship between group size and territory size. This was also the original problem encountered in the first study there (Kruuk 1978a), a finding that led to the RDH as an alternative mechanism (Carr and Macdonald 1986) specifically to account for this. Furthermore, the only correlation between group size and the richness of a territory was that found between badger populations across the UK (Kruuk and Parish 1982), which are much more likely to experience different levels of resource availability. For these reasons, the establishment of whether GS and TS are robustly independent over all years is a crucial first step towards developing further tests of the RDH.

We present a multi-year test of the fundamental prediction of the RDH, that GS is independent of TS, for a well-known population in which there are up to

21 territories in any one year. Previous studies in Wytham Woods have investigated similar relationships (Kruuk 1978a, b, Hofer 1988) and some RDH predictions specifically (Da Silva et al. 1993, Johnson et al. 2001) (including one between-population study (Kruuk and Parish 1982)). All of these tests were, however, of small sample sizes and for single years only (Johnson et al. 2001). The results presented here therefore offer an improved test of this particular prediction, with relatively large sample sizes and multiple year tests, with corrected *P*-values for simultaneous inference testing and a pooled analyses, all of which serve to identify consistency and generality of the prediction between years. In addition, we conducted all tests using alternative methods of mapping territory borders to minimise bias in results due to methodology, since previous tests of this hypothesis have been crucially dependent on accurate estimates of territory sizes (Johnson et al. 2001).

Methods

Study site

Badgers have been studied since 1974 at Wytham Woods, 5 km NW of Oxford city (1° 18' W, 51° 46' N). The study site is a mixed-species deciduous woodland surrounded by pasture and arable farmland, with the river Thames to the north, Oxford to the west and major roads to the south and east. The wooded area of the study site lies on two hills and ranges from 60 to 165 m in altitude. Further details can be found elsewhere of the study site (Kruuk 1978b, Hofer 1988), and of the long term trapping study (Tuytens et al. 1999).

Badger group sizes

Adult badger group sizes were estimated from trapping studies conducted since 1974 (Kruuk 1978b, Hofer 1988, Da Silva 1989, Tuytens et al. 1999, Macdonald and Newman in press). There are three possible estimates of group sizes: (1) total number of different individuals caught in the setts of a social group in that year; (2) minimum number alive (MNA) which adds, post hoc, badgers not trapped that year but that were subsequently trapped (not necessarily in the same group) and therefore added to the estimate; (3) census data from a survey made during three nights in May each year by volunteer observers. All three estimates correlate closely (Newman 2000); however, we used actual number trapped, because census data has a number of sources of inherent bias and MNA estimates do not account for where untrapped badgers ranged during their absence (Macdonald et al. in press). Number of adults caught in the relevant territory during the

year reflect a resident group size, given that trapping efficiency remained high and similar between years (trapping success over the period 1987–1997 ranged from 83.2 to 100.0% (Newman 2000)). Moreover, MNA estimates were not available or calculable for the earlier studies. Therefore, actual number trapped provides estimates comparable over all study years.

Conversion of maps to a common format

Because maps of the badger groups' territory borders and latrine locations had been constructed in different formats since 1974, we needed to convert the existing maps (drawn on paper) of inconsistent scales into a common format for analysis. To do this, maps of territory borders from all years in which they were available were scanned (digitised at a resolution of 150 dots per square inch) from the original sources, and imported into a Geographic Information System (GIS) computer program ('ArcView GIS', ver. 3.2 ESRI). These were then resized so they would conform to an identical scale that followed the UK 'National Grid' co-ordinate system. The scaled images were then centred (put in the correct place) with reference to a feature in the study site with known co-ordinates, such that they overlaid each other precisely. Some discrepancies remained between the location of features on the old maps and their known co-ordinates on the modern map, so in order to minimise remaining errors in the placement of territory borders, old maps were 'rubber mapped' (which means they were stretched in two dimensions) to fit the modern 1:25 000 reference map (Ordnance Survey). This was carried out using a program specifically designed for this task (Spatial Tools Extension, ver. 3.3; a minimum of 50 'control points' and the 'second-order polynomial re-sampling' algorithm was used) (Hooge 1998).

Maps of territory borders and territory sizes

Interpolated (INT) mapping method

Three methods of mapping each badger groups' territory borders were used. First, interpolated (INT) maps were constructed, according to the well-established methods of bait-marking and interpretation of field signs for this species (Kruuk 1978b, Delahay et al. 2000). Territory borders were then drawn over the underlying territory maps, as digital lines (in ArcView GIS). These borders were subsequently corrected for remaining errors by hand at a scale of about 1:6000. For example, in some places on older maps, uncorrected territory borders ran along the 'wrong' sides of rivers or major roads. Where outer boundaries of territories at the edge of the woods were unknown, outer limits were constrained by a 100-m buffer from the

woodland edge, beyond which latrines were rarely found. Territory areas using this method, and those below, were calculated using an ArcView algorithm (to 0.1 m²).

Minimum convex polygon (MCP) method

Secondly, for comparison, and to avoid subjective inference errors associated with the first method (Johnson et al. 2001), 100% Minimum Convex Polygons (MCP) were constructed using another extension to the ArcView GIS program ('Animal Movement' (Hooge and Eichenlaub 1997)), which constructs a convex polygon around the latrines – outer-most from each sett – that were found containing marked bait.

Dirichlet tessellation (TES) method

Finally, the third method constructed territories according to a mathematical rule known as a Dirichlet tessellation (TES) (Blackwell and Macdonald 2000), which constructs borders at the mid-points between all neighbouring setts. These borders then run perpendicular to the straight line between those neighbouring setts, until they meet another border, from an adjacent territory. The resulting pattern is a matrix of convex polygons (the territories) that contain all points which are nearer to the sett in the centre of the polygon than to any other neighbouring sett. Main sett locations were those recorded in the year 2000 (which have changed little for several years). Dirichlet tessellations have been a point of contention in past studies of badgers in this and other study sites, because they provide a method of mapping territories merely from knowledge about main sett locations, without having to carry out the labour intensive bait-marking experiments required to follow the traditional method (Delahay et al. 2000). Aside from this practical importance, Dirichlet tessellations are also the centre of a theoretical debate about how animals construct and configure their territories (Blackwell and Macdonald 2000), the resolution of which has implications for theories of spacing patterns including the RDH (Doncaster and Woodroffe 1993). We therefore included Dirichlet tessellations here as a type of 'control' for comparison with the other methods but, because their biological significance is unclear, we did not test them against GS.

Results

Comparison of territory mapping methods

Both MCP and INT territories had positively skewed distributions, so data were log-transformed before further comparisons were made, and very small outliers were removed. These outliers resulted from MCPs constructed around too few latrines that had identifiable bait-mark retrievals, and all deviated in slope and dis-

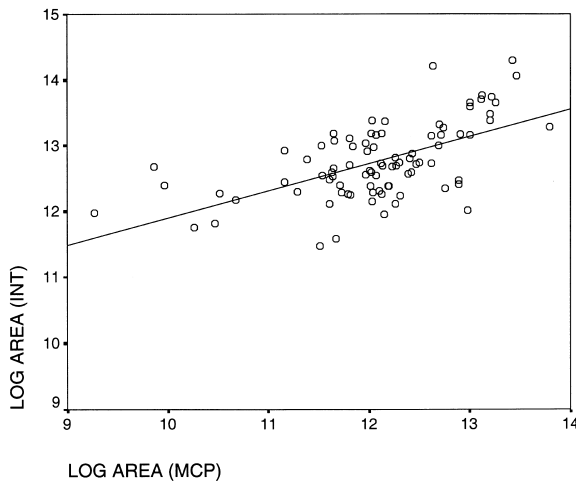


Fig. 1. Significant positive correlation between territory sizes as estimated by the interpolation (INT) method and Minimum Convex Polygon (MCP) method ($F_{1,85} = 45.3$, $P < 0.0001$).

tance from the majority of the data in normal probability plots. Fig. 1 shows there was a significant positive correlation between territory sizes as estimated by INT and MCP methods ($F_{1,85} = 45.3$, $P < 0.0001$). However, there was considerable scatter, only 34.8% of the variance is explained, and the slope of 0.41 is significantly lower than the value of 1.0 that would be expected if both methods provided equal, linear estimates ($t_{84} = -9.62$, $P < 0.001$). Overall, there was a significant difference between all three estimation methods (Fig. 2) (one-way ANOVA: $F_{2,229} = 21.5$, $P < 0.0001$). Tukey's post hoc tests for multiple comparisons shows that this is mainly due to the significant difference between the

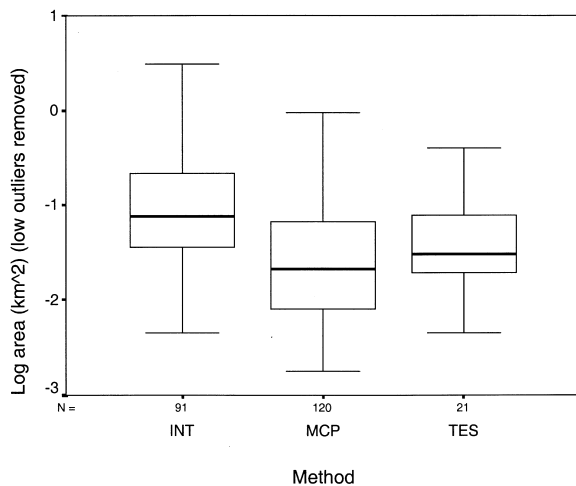


Fig. 2. Significant difference in mean territory size among the three estimation methods (interpolation (INT), Minimum Convex Polygon (MCP) and Dirichlet tessellation (TES) methods). One-way ANOVA: $F_{2,229} = 21.5$, $P < 0.0001$. The box represents the interquartile range; line is median; whiskers are the highest and lowest values.

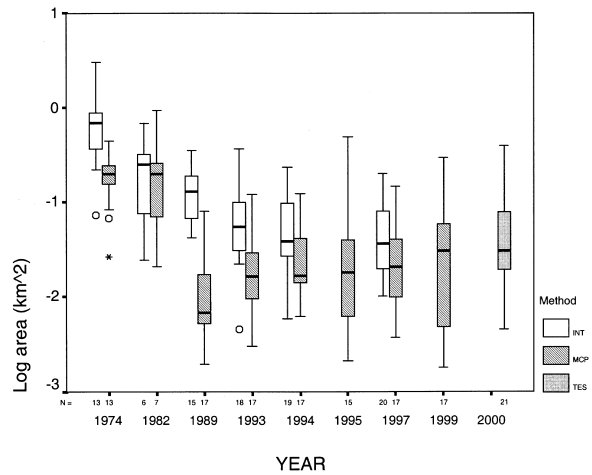


Fig. 3. Boxplot split by year (x -axis not linear) and method (interpolation (INT), Minimum Convex Polygon (MCP) and Dirichlet tessellation (TES) methods). The box represents the interquartile range; line is median; whiskers are the highest and lowest values, excluding outliers (outliers are either: open circles, $1.5-3.0 \times$ boxlengths from interquartile range, or asterisks, > 3.0 boxlengths).

INT and MCP methods ($P < 0.0001$). INT was nearly significantly different from the TES method as well ($P = 0.052$), but the MCP method was not ($P = 0.307$).

Sample size is limited where territories could only be constructed by one method in some years (for example, where there were too few latrines with identifiable marked bait to construct polygons). The tessellation method generates only few territories ($N = 21$), because the main sett sites themselves have hardly changed. Nevertheless, these are representative for most years where the 'main setts' were the same within that territory, the case for most at least since 1993.

Changes in territory sizes over time

Territories decreased in size over the study period from 1974 to 1997 (INT method: mean of 0.9 to 0.3 km²; MCP method: mean of 0.5 to 0.2 km²), while group sizes increased from the mean of 5.8 in 1974 (Kruuk 1978b) to 9.0 in 1997. Applying a linear regression model, this decrease over time was significant, both according to the INT method (ANOVA $F_{1,89} = 87.3$, $P < 0.0001$) and the MCP method (ANOVA $F_{1,118} = 27.2$, $P < 0.0001$).

However, further investigation of a boxplot split by year and method (Fig. 3) shows that territory sizes underwent a large decrease from 1989 to 1993 (territories have only recently been regularly mapped, so the x -axis is not linear). Thereafter, from 1993 until 1999, territories remained relatively constant according to both methods (one-way ANOVAs: $F_{2,54} = 0.73$, $P = 0.49$, INT method; $F_{4,78} = 0.28$, $P = 0.89$, MCP method).

Table 1. Independent regressions of group size against log territory size for each year and each method. Cases are ranked by their normal P -values. None of the tests are significant under the new critical P -values calculated using the sequential Bonferroni adjustment for multiple testing (Rice 1989).

Year	Method	Normal P -value	Rank	New critical P -values	Beta (standardized regression slope)
1989	MCP	0.005	1	0.0038	0.723
1993	MCP	0.107	2	0.0042	0.433
1997	INT	0.129	3	0.0045	0.351
1974	MCP	0.141	4	0.0050	0.57
1997	MCP	0.230	5	0.0056	0.308
1982	INT	0.324	6	0.0063	-0.562
1995	MCP	0.364	7	0.0071	0.252
1982	MCP	0.365	8	0.0083	-0.523
1993	INT	0.394	9	0.0100	0.214
1989	INT	0.466	10	0.0125	0.204
1994	INT	0.529	11	0.0167	0.154
1994	MCP	0.762	12	0.0250	-0.082
1974	INT	0.950	13	0.0500	0.026

Group size and territory size

In analyses conducted separately for each year, only a single one of 12 independent regressions of GS against log TS was significant at the 0.05 level (Table 1 and Fig. 4). We then applied a sequential Bonferroni technique for multiple comparisons, which controls for the increased number of Type I error rates (false rejections of the null hypothesis) in a posteriori multiple significance testing (Rice 1989). Standard Bonferroni tests are not adequate, because they increase Type II error rates where more than one component hypothesis is false (i.e. they reduce power in detecting significant results). In this case, none of the tests are significant under the newly derived significance levels (Table 1), judged by a test of $P_i \leq \alpha/(1+k-i)$ where each P -value is ranked in ascending order ($P_1, P_2 \dots P_i$) for k tests. The adjustment thus gives a different critical P -value for each test.

Given that a number of other confounding variables may mask an underlying trend, not evident in individual tests each year, we applied a method to analyse the slopes from all regressions at once. In a nested ANOVA, where years were included as indicator variables, we tested the null hypothesis that the slopes of all relationships between GS and TS were equal to zero (Sokal and Rohlf 1995), which could not be rejected for either territory estimation method (INT method: $F_{5,73} = 0.55, P = 0.95$; two-tailed; MCP method: $F_{5,96} = 0.66, P = 0.89$, two-tailed). Thus, there is still no evidence for any of the slopes being significantly different from zero when all the variance is analysed together. Ten of the total thirteen slopes were positive, however.

Group size was also independent of log territory size when all data were pooled across years (INT method: $F_{1,83} = 0.17, P = 0.68$; MCP method: $F_{1,87} = 1.38, P = 0.24$) (Fig. 5). Since the combined data in this test are not necessarily independent if territory size and group size of the same social group are related between years, we focus all our conclusions on the separate within-year tests presented above (Table 1 and Fig 4). We did,

however, investigate support for the independence of data in this pooled analysis. Data from different years are separated by at least 2 year-intervals (except 1995 MCP data) during which time territory sizes did shift and, in particular, the sizes of many groups are known

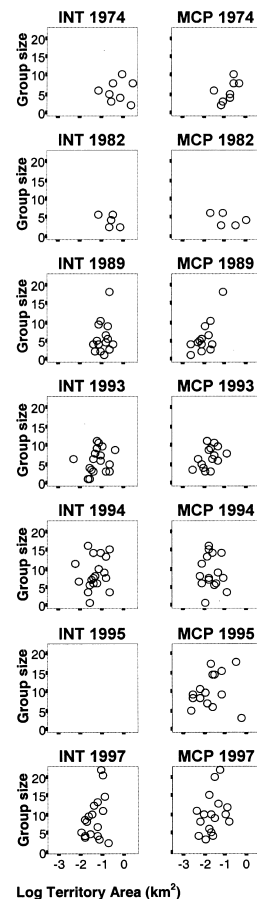
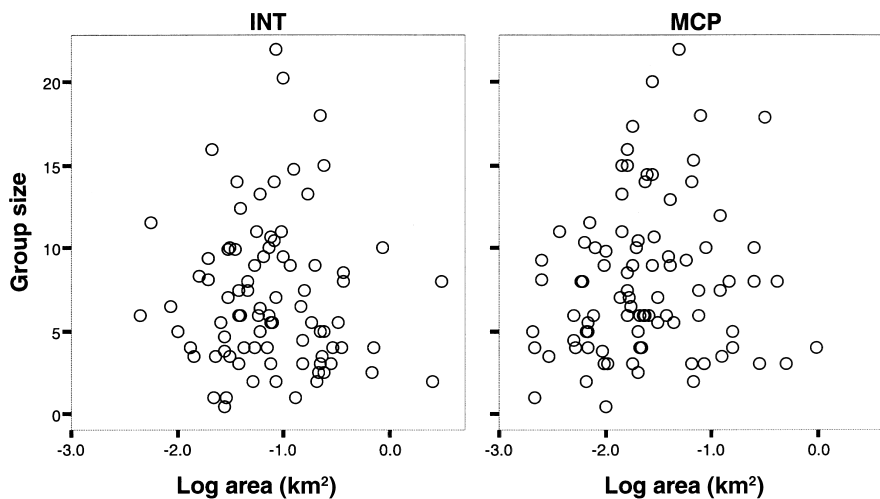


Fig. 4. Group sizes against territory sizes for all years and split by interpolation (INT) and Minimum Convex Polygon (MCP) estimation methods (statistical tests in Table 1).

Fig. 5. Combining all data (and assuming independence), group size is not significantly predicted by territory size using either territory size estimation method.



to have changed considerably with the large and long-term population increase (Newman 2000, Macdonald and Newman in press). We used a one-way ANOVA with social group as the categorical predictor variable as a test of whether, across all years, variance in TS (or GS) was greater between social groups than within them (Sokal and Rohlf 1995). A non-significant result means that within-group variance is comparably large, thus providing some support for the assumption that, in the average social group, log TS (or GS) is independent between years. Only social groups that appeared in the data at least twice were included. The result was non-significant for the MCP method (MCP: $F_{20,76} = 1.13$, $P = 0.34$), supporting independence across years of MCP territory size within a social group. There was, however, evidence that TS was not independent between years with the INT method (INT: $F_{22,64} = 3.21$, $P < 0.001$) as there was with group size ($F_{22,142} = 7.24$, $P < 0.0001$), since the variance was significantly greater between social groups than within them. This test is potentially confounded because groups that appear only a small number of times are likely to have inaccurate estimates of their mean, but will nevertheless constitute another group (and another degree of freedom), increasing the chance of a rejection of the null hypothesis. A repeat test including only social groups represented at least five times in the data provided evidence for independence in territory size data estimated by both methods (INT: $F_{8,36} = 0.99$, $P = 0.45$; MCP: $F_{16,78} = 1.08$, $P = 0.39$), although the test for group size was still significant ($F_{17,94} = 5.37$, $P < 0.0001$). Thus, there is only mixed evidence that the pooled test of GS against TS constitutes independent data. Nevertheless, this does not affect our conclusions because, as stated above, we only refer to the clear results found in the separate tests for each year (Table 1) in drawing conclusions about the relationship between GS and TS.

Discussion

Long-term changes and mapping methodology

Territory sizes have decreased over the duration of the long-term badger study at Wytham, although there was considerable scatter. Comparing methods, while they did correlate (Fig. 1), the INT method resulted in larger estimates of territory size than the MCP method. This is due to the inferred element of the INT method, which extends territory borders out to landscape features where outer boundaries are not entirely known. The INT method also makes the assumption that all territories tessellate, although in Wytham this is increasingly unlikely to be the case because overlap is common (unpubl. data). While overlap may be common, however, 'unused' gaps of habitat, between territories, are not likely to be common. The large change between 1974 and 1993 may partly reflect a change in protocol rather than real changes in badger territories. This is because territories were originally assumed to extend to limits of the local population, a major river in the North, and major roads in the South and East (Kruuk 1978b). This fitted with the scale of the much larger territories in the woods at the time. This assumption is no longer made, however, and furthermore latrines are rarely found > 100 m from the woodland. The accurate estimation of territory sizes and configurations is crucial to good tests of the RDH and other models of spacing behaviour.

Implications for the RDH

An increase in the size of a group results in a larger biomass per unit area. Thus, to sustain per capita energy intakes the amount of available resources must be increased. The initial prediction is, therefore, that as group size increases there should be a corresponding

increase in territory area. This has been demonstrated within several species of carnivores (Macdonald 1983), and reflects a general inter-specific allometric principle spanning several mammalian orders and includes the mustelid family (Gittleman and Harvey 1982, Reiss 1988, Gompper and Gittleman 1991, Johnson et al. 2000, Johnson and Macdonald unpubl.). However, this process is based on a fundamental assumption: that resources are homogeneously or randomly distributed in the environment. In reality, resources are very likely to be 'patchy' or 'clumped' (spatially aggregated). It has been shown that, at a certain level of this patchiness, and with a certain variance in food availability of those patches, groups may form with no direct costs to the original territory owners, hence the Resource Dispersion Hypothesis (Carr and Macdonald 1986, Macdonald and Carr 1989, Bacon et al. 1991).

For social species that do not appear to cooperate or derive benefits from group-living (Woodroffe and Macdonald 2000), especially the badger (Kruuk 1989), the RDH may appear to be the most parsimonious explanation (Woodroffe and Macdonald 1993). However, the fundamental, and initially paradoxical, prediction of that hypothesis, that group size should be independent of territory area, is rarely tested with large sample sizes or for robustness between years. This study demonstrates that, for a population which stimulated part of the original thinking behind the RDH (Kruuk 1978a, b), this prediction is consistently met over several territories over the course of nearly two decades. We can therefore conclude that such independence was not a peculiarity of those short periods in which this hypothesis was tested before (Kruuk and Parish 1982, Hofer 1988, Johnson et al. 2001). Group sizes and territory sizes do indeed appear to be determined by another, or other, independently varying factors.

Future studies should test what these factors might be. The RDH further predicts that: (1) TS is dependent on dispersion of resources and (2) GS is dependent on the richness of those resources. The latter (prediction (2)) was supported by a study which compared means from different populations (Kruuk and Parish 1982) but not by studies in Wytham (Hofer 1988, Da Silva et al. 1993, Johnson et al. 2001) (although Da Silva et al. op cit. found per group cub production was a correlate of 'worm rich' habitat area in the territory, as was mean male weight). Prediction (1) was again supported by the inter-population study (Kruuk and Parish 1982), and by a study of artificial manipulation of habitat types around Wytham (Da Silva et al. 1993) but other studies were inconclusive on this point (Hofer 1988, Johnson et al. 2001).

Derivation of these RDH predictions rest on certain other assumptions, such as that the spatial dispersion of patches is independent of their richness, and that there is sufficient variation in resource richness between patches (Bacon et al. 1991). Future studies should test

these underlying assumptions using estimates of resource availability and detailed mapping of resource patch locations. With regard to the other two predictions themselves (GS correlates with resource richness, TS with resource dispersion), it is interesting to consider that only the inter-population study (Kruuk and Parish 1982) was able to demonstrate support for these two further predictions of the RDH. This suggests that there may be insufficient variation within one single population to detect underlying relationships between these variables; especially if there is a relatively large amount of noise in the data from other sources. These other two predictions must also, therefore, be tested in Wytham with larger sample sizes and using data from multiple years. Further exploration of the variation between different populations across Europe may also, however, be the best method of maximising the power of such tests (Stopka and Johnson 2000). The RDH offers an alternative explanation of sociality that is potentially applicable to a wide range of species, but there remains a distinct lack of field tests to evaluate the validity of its predictions.

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