An analysis of social spacing in the European badger (*Meles meles*) in the UK

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Summary

Classical explanations of sociality focus on identifying functional benefits that favour individuals living in a group. Several candidate behaviours have been investigated in our study population, including alloparental care, allogrooming, cooperative sett site maintenance and increased mating opportunities. In contrast, the resource dispersion hypothesis (RDH) suggests that group-living may result passively, as a consequence of patchy and unpredictable food resources. The RDH has received most attention in explaining the highly social grouping behaviour observed in British badgers, which are otherwise solitary or pair living over the remaining great majority of their distribution.

Unfortunately, the RDH has proved difficult to test empirically, especially in the field. We have put territory and sett site data onto digital maps using GIS (Geographic Information System) software in order to test the hypothesis that the distribution of resources can explain variation in the spatial organisation of badger groups. In support of the prediction of the RDH, group sizes were independent of territory sizes. However, in contrast to other RDH predictions, an index of total resource richness did not correlate positively with group size, nor did variables indexing the dispersion of patches correlate positively with territory size. We suggest some deficiencies and assumptions of the analysis that need to be addressed if future studies are to improve as valid tests of the RDH.

1. Introduction

Ninety percent of the Carnivora are defined as not being 'social' (Gittleman 1989) and there is a considerable literature on the possible explanations for why the remaining 10% make exception to this general rule. For many of the social species, evidence for particular benefits for group living have been demonstrated,

for example, the benefits of cooperative hunting (MILLS 1989) or alloparental be-haviour (CREEL & CREEL 1991). However, several other social species exist whose reasons for grouping are not understood – they forage alone and there appear to be none of the numerous other potential advantages documented for group living (KREBS & DAVIES 1993; WOODROFFE & MACDONALD 2000). One concept that does provide a good explanation for such spatial groups of animals is the Resource Dispersion Hypothesis (RDH) (MACDONALD, 1983; CARR & MACDONALD 1986). This proposed that animals could have overlapping home ranges (i.e. a group forms) where 'resources are dispersed such that the smallest economically defensible ter-ritory for a pair ... can also sustain additional animals'; this may occur where resource availability is spatially or temporally heterogeneous. In such a scenario, even a single animal would have to use a home range encompassing several pat-ches to ensure a certain guarantee of finding enough food. Thus, assuming some distribution of patch availability, for much of the time more than enough patches would be available. Consequently, there would be very little cost to the original territory resident through interference or exploitation competition if other indivi-duals joined the territory.

This hypothesis has developed as a potential model for spatial groups of sever-al carnivore species (MACDONALD 1983) and may facilitate a distinction between 'expansionist' or 'contractionist' societies, depending on the pattern of food avai-lability (KRUUK & MACDONALD 1985). The RDH could explain, for example, why coyotes *Canis latrans* and lions *Panthera leo* increase their ranges with group size, while there is no correlation between group size and territory size in red foxes *Vulpes vulpes* or badgers *Meles meles* (KRUUK & PARISH 1982; MACDONALD 1983). Predictions of the hypothesis were initially developed from a discrete model of resource richness (CARR & MACDONALD 1996; MACDONALD & CARR 1989), and a more detailed mathematical analysis showed that a continuous model supported the original predictions and was robust to parameter changes (BACON *et al.* 1991a; BACON *et al.* 1991b).

However, VON SCHANTZ (1984) criticised the RDH for being too all-encompas-sing, because it allows an array of possible conditions and variations that make it difficult to falsify in experimental situations. For example, patches could operate on a time scale of days, months or even between years, and these patches could be of nutrients rather than measurable prey abundance or availability. Another pro-blem is that even if the predictions are not falsified, the original mechanisms for group formation may now be overshadowed by other sociological benefits that evolved in the meantime. It is, therefore, difficult to discount any underlying effect of the hypothesis on the grounds of no evidence even within one's own study. Many hypotheses in evolutionary biology suffer from such a 'chicken and egg' conundrum, but a hypothesis should, nevertheless, have the property of being fal-

sifiable else it cannot be of use in furthering the understanding of ecological me-
chanisms (PETERS 1991). KRUUK & MACDONALD (1985) and VON SCHANTZ (1984)
himself suggested some field experiments with which the hypothesis can be expo-
sed to some degree of testing, but these have largely not been done.

The RDH predicts that '...territory size is constrained by the dispersion of pat-
ches of available food, whereas group size is independently limited by the richness
of these patches' (CARR & MACDONALD 1986: 1541; see also BACON et al. 1991b).
This gives three predictions that we tested in the field and analysed on digital
maps: (1) territory size is independent of group size. Instead, (2) group size is
dependent on the resource richness of all patches in the territory, while (3) territory
size is dependent on the spatial distribution and or number of resource patches.
The first is tested through trapping and bait-marking experiments. The second is
tested using estimated potential food availability within the territory. The third is
tested by multiple regression of several potential indices of resources and their
dispersion, with territory size as the dependent variable. Our study has detailed
long-term data for 21 groups of badgers in Wytham Woods, Oxfordshire. We assu-
me in this stage of our ongoing analyses that resource patches can be equated with
habitat patches.

2. Materials and Methods

2.1 Territories

Territories were mapped using bait-marking (methodology described by Kruuk
1978a; Delahay et al. in press) in spring 1997. The principal habitats and the terri-
tories on the study site are shown in figure 1.

2.2 Group sizes

Badgers were trapped near their setts and individually marked four times in
1997, in January, May, August and October, using the methods of CHEESEMAN &
HARRIS (1982). Group size is the sum of all adult badgers caught exclusively there,
plus the fraction of any badgers caught partly there and partly at another sett, ha-
ving moved between them (a more realistic estimate of per capita resource usage
per territory).

2.3 Habitat

Habitat types were classed into the four major types: woodland, arable, pasture
and urban, plus 'scrub' (all other habitats) and created as digital maps. The propor-
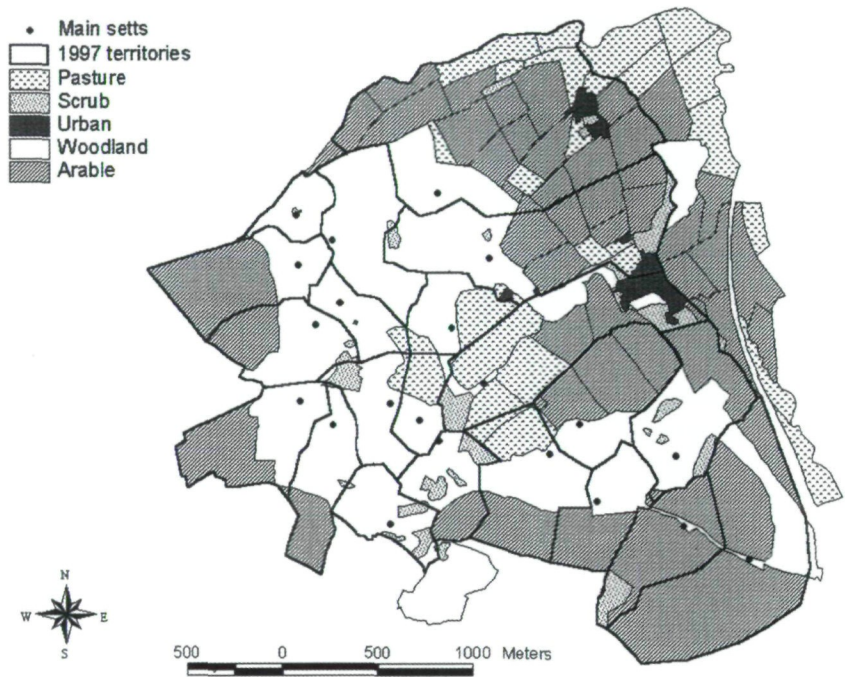tion of these in each territory was calculated, as well as total territory area.

Fig. 1: Wytham Woods badger territories, main setts and habitat types

2.4 Resource richness

Predicted earthworm biomass per territory was calculated by multiplying mean earthworm biomass per unit area for each habitat type by its area within that territory. Biomass data come from Kruuk (1978b) for the three major habitat types only, woodland (80000 kg/km^2), arable (48648 kg/km^2) and pasture (97619 kg/km^2). Hofer (1988) reports a very similar earthworm biomass in deciduous woodland.

2.5 Resource patch abundance and dispersion

Several measures of the dispersion and abundance of resource patches were calculated; (1) Distance from the main sett to the three major habitat types (edge of woodland, arable fields and pasture); (2) The numbers of arable fields, pasture and patches of scrub within the territory; (3) The numbers of pasture and fields adjacent to the territory (the two particularly important feeding habitats); (4) A habitat heterogeneity index. This was the sum of the number of separate habitat areas, excluding woodland and urban, divided by the territory area.

3. Results

3.1 Group size and territory area

Group size was independent of territory size ($F_{1,19}$ = 0.7, P = 0.4) see figure 2. However, a stepwise multiple regression of group size on the areas of the five main habitat type areas per territory identified woodland area as a significant explanatory variable ($F_{1,19}$ = 8.28, P < 0.001; see figure 3); there was, however, considerable scatter in this relationship. No other variables qualified (at a significance level of 0.05) for the regression model (area of arable, pasture, urban or scrub). For each sex separately, a woodland only regression showed a significant relationship with the number of males in the territory ($F_{1,19}$ = 8.71, P = 0.008) while the significance level was borderline for females ($F_{1,19}$ = 4.34, P = 0.051). Area of woodland was not related to the number of cubs in the territory ($F_{1,19}$ = 0.00, P = 0.98). None of the other habitat proportions correlated with the size of any other age-sex class (all correlation coefficients < 0.3). Considering all 25 possible correlations (5 habitats and 5 age-sex classes), the Dunn-Šidák corrected significance level for k tests (α' = 1 − (1 − α)$^{1/k}$) (SOKAL & ROHLF 1995) is 0.002, so strictly, the relationships between woodland area and male and female numbers become insignificant.
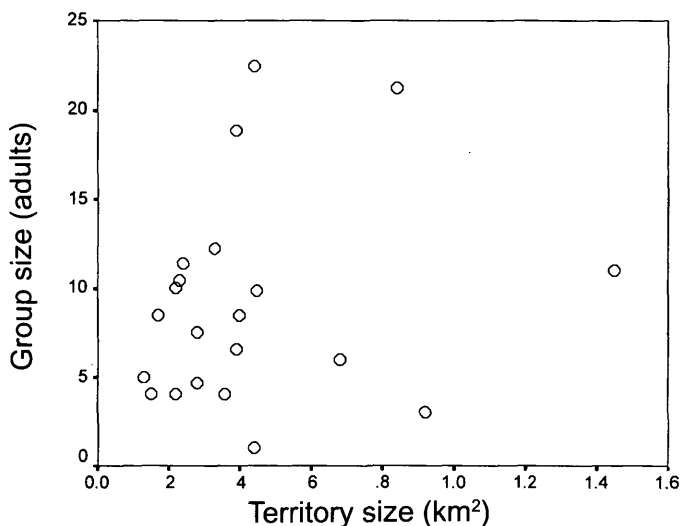

Fig. 2: 1997 Territory size is independent of group size in the Wytham Woods badger population. Dependence is expected if food resources across the territory are randomly continuously distributed, rather than patchily distributed as in the RDH model
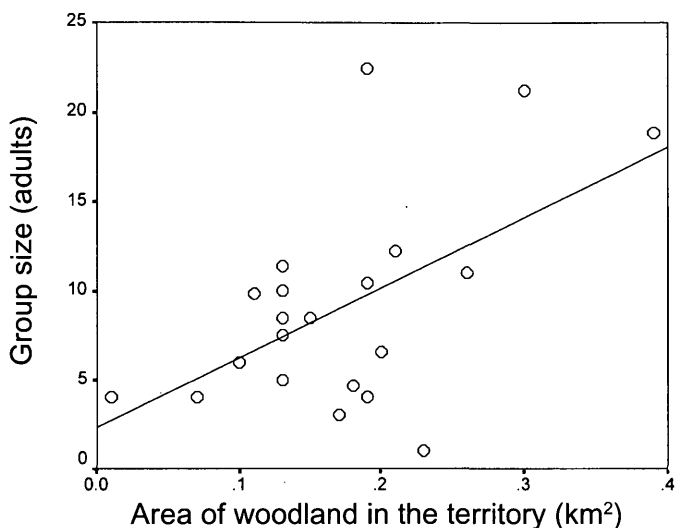
Fig. 3: Area of woodland in the territory is significantly related to group size $(F_{1,19} = 8.28, P < 0.001)$
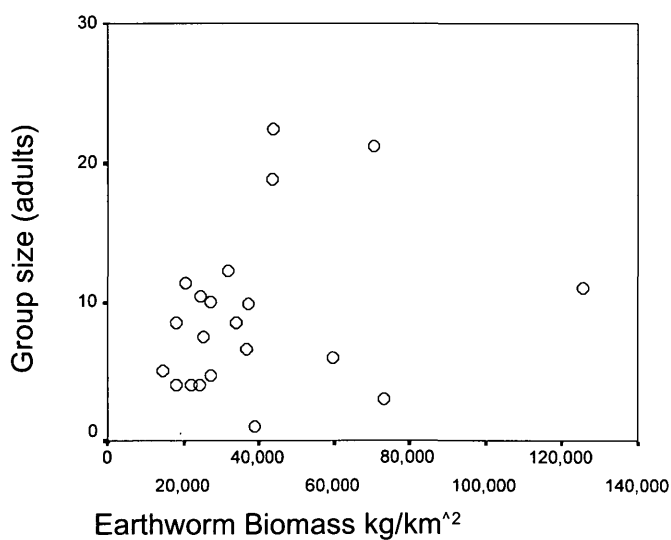

Fig. 4: Group size is not a significant correlate of predicted earthworm biomass, nor when the outlier at the far right is removed

3.2 Group size and resource richness

Group size was not significantly related to total predicted earthworm biomass for the territory as a whole ($F_{1,19}$ = 1.39, P = 0.25, figure 4), nor was the number of any age or sex class (P > 0.1 in all cases) or mean adult body condition ($F_{1,19}$ = 1.69, P = 0.21) or body mass ($F_{1,19}$ = 2.93, P = 0.10).

3.3 Territory size and resource patch dispersion

A stepwise multiple regression revealed that territory size was significantly related to the number of arable fields within and adjacent to it ($F_{2,18}$ = 61.52, P < 0.0001). No other variables qualified for the regression model. From figure 1, this may be expected as larger territories are likely to encompass more fields. However, omitting the territory TC, which was particularly large and contained very many fields, the regression model was still significant with the same independent variables ($F_{2,17}$ = 21.52, P < 0.001). No variables qualified for a stepwise multiple regression model if group size was tested as the dependent variable.

4. Discussion

Group size was independent of territory size, as predicted by the RDH. This has previously been shown between populations (KRUUK & PARISH 1982) and in Wytham but with smaller sample sizes, 10 and 20 years ago (HOFER 1988; KRUUK 1978a).

Group size, the numbers of any age or sex class, adult mass and body condition were independent of total resource richness per unit area using our index of predicted earthworm biomass. Confidence in this result relies on our index being a realistic estimate of resource richness. The data were not collected simultaneously, and clearly new data on contemporary earthworm biomass are needed. If the index is accurate, one alternative explanation for the lack of any relationship is that food may be so plentiful that variation in richness between territories is not limiting to the number of potential group members. KRUUK (1978b) found that earthworm biomass from a single feeding patch of $20m^2$ could greatly exceed the nutritional requirements of 30 badgers. In addition, the large (three-fold) population increase in Wytham over the last two decades suggests that food has not been limiting to density. Nevertheless, correlations have previously been shown between both badger density and earthworm biomass among populations and between earthworm biomass and group size per territory (KRUUK & PARISH 1982).

Among animals with homogeneous resources, group size should be at least partly determined by territory size (KRUUK & MACDONALD 1985; MACDONALD 1983).

The RDH predicts that in other situations, where resources are heterogeneous, territory size depends instead on the spatial distribution of resources (CARR & MACDONALD 1986; MACDONALD & CARR 1989). Numerous studies have identified pasture as the principal food 'patches' for badgers in Wytham (KRUUK 1978a,b, HOFER 1988, DA SILVA et al. 1993). In contrast to the prediction however, we found that territory size was not significantly related to any of our indices of spatial distribution of resources.

Territory size was significantly related to the number of arable fields within it and the number adjacent to it. This variable is likely to be autocorrelated with territory size, especially at the periphery of the woods, so it may not be very meaningful. Group size was, incidentally, also unrelated to any patch number or patch dispersion variables that we measured.

Interestingly, area of woodland in the territory was a significant predictor of group size (figure 3). It is feasible that woodland area provides a more reliable index of actual territory size because the uncertainty of territory borders increased with distance from the woodland edge. This is mainly because latrines were less likely to exist or to be found on an ever-increasing arc away from the focal area (badgers tend to establish latrines between adjacent territories, whereas at the edge of the woodland there are no adjoining clans to communicate with). A previous study from the same population showed that adult male body mass was significantly correlated with area of deciduous woodland (DA SILVA et al. 1993). However, we found no significant relationships between adult body mass or body condition (split by sex and season) and any of the habitat areas.

In this study we tested three predictions of the RDH in 21 adjacent territories in a semi-closed high-density badger population. Data have been collected in this population since the 1970s so it has become particularly interesting to see which relationships remain true after considerable territory fission, changes of group membership and population increases since then. For this year, and with these indices, only the first prediction of the RDH was fulfilled: (1) group size did not depend on territory size. However, the other two predictions were not borne out. Group size cannot be predicted by (2) our measure of resource richness, nor was (3) territory size related to our measures of resource dispersion. Territory size was only significantly related to the number of one type of resource patch, arable fields, which provide important foraging sites during the dry periods of summer when earthworms are less accessible (KRUUK 1978, DA SILVA et al. 1993). However, this is likely to be autocorrelated with territory size, so we are not convinced of a useful interpretation of that particular result.

The endorsement of three particular assumptions inherent in this, and other, analyses of RDH predictions struck us as important targets for further research: (1) Other variables, overlooked in habitat classifications, such as underlying geology or soil type may also lead to spatial variation in resource availability, or temporal variation under interaction with different climatic conditions. For example, during very wet periods, only well-drained areas might provide good feeding areas; or, pasture on shallow soil may be relatively poor in terms of earthworm abundance. (2) Further caution must be applied in these sorts of studies because the assumption of 'patches of habitat' equating to 'resource patches' may be false. Further studies are needed to test for intra- and inter-habitat variation and spatial aggregation of resources. If it is a false assumption, a different resolution of feeding patches will be needed to investigate these relationships. The woods do indeed have a considerable degree of within-habitat heterogeneity with varying vegetational communities, some of which may be more resource rich than others. (3) Another critical assumption, on which valid tests of RDH predictions depend, is that the territory estimations were accurate. Although bait marking has a well-established methodology (see DELAHAY *et al.* in press), future studies should compare results using alternative estimation methods.

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