Habitat, food availability and group territoriality in the European badger, *Meles meles*

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**Abstract.** Since European badgers (*Meles meles* L.) form non-cooperative groups in parts of their geographic range, but are solitary elsewhere, their social systems have been at the centre of a debate about the evolution of group living in the Carnivora. In a recent review of models of non-cooperative sociality, Woodroffe and Macdonald (1993) presented evidence in favour of two hypotheses, which suggested that badger groups might form because either the distribution of blocks of food-rich habitat, or the economics of excavating new setts, prevented the division of group territories into individual territories. We present data upon the response of badger spatial organisation to a reduction in food-patch dispersion, brought about by the conversion of earthworm-poor arable land to earthworm-rich pasture over a 15-year period. This change in the distribution of earthworm-rich habitats was accompanied by territory fission, facilitated by the excavation of new setts. This indicates that the availability of sett sites had not constrained territory size at the start of the study. However, sett distribution did define the size and configuration of the daughter territories. We also show that variation among territories in the availability of food-rich habitats was reflected in the reproductive rates and body weights of the groups that inhabited them, although there was no detectable effect upon group size.

**Key words:** Territory – Sociality – Badger – *Meles meles* – Sett

European badgers, *Meles meles* L., are unusual among carnivores in general, and mustelids in particular, in that they form stable groups of mixed age and sex whose members share a territory and occupy a communal den. Such groups, ranging in size from 2 to 25 individuals, have been reported from several populations in Great Britain, but in some other parts of their broad geographic range badgers are pair-living or solitary (reviewed in Woodroffe and Macdonald 1993). This facultative sociality raises the question of the benefits, to individuals, of group living. Carnivore sociality has traditionally been explained in terms of cooperative hunting, vigilance or defence of the kill (Kruuk 1975; Gittleman 1989) but these explanations cannot be applied to species such as the European badger, which forage alone and have no major predators (Macdonald 1983).

Models of the evolution of such non-cooperative groups have focused upon the phenomenon of group territoriality, attempting to explain why an animal should hold a territory, presumably in response to competition, and then allow additional animals to share it. Most of the models assume that the retention of sexually mature offspring on the territory is favoured when the possibilities of dispersal elsewhere are limited (e.g. Emlen 1982; Lindström 1986). Discussion has therefore centred on the conditions leading to territories that can support animals in addition to the primary breeding pair (e.g. von Schantz 1984; Kruuk and Macdonald 1985; Carr and Macdonald 1986). In a recent review of models of non-cooperative sociality, Woodroffe and Macdonald (1993) showed that two hypotheses gave a good correspondence with the information available on badger social organisation in various areas.

The first of these, a form of the resource dispersion hypothesis, proposes that the size of the smallest territory that can be defended economically is inflated by the spatial distribution of food patches (Kruuk 1978b; Kruuk and Macdonald 1985). Badgers’ principal prey, the earthworm *Lumbricus terrestris*, is only available to badgers when it moves to the soil surface. This surfacing behaviour occurs in response to microclimatic conditions (Macdonald 1980); patches of surfacing earthworms therefore become available in different habitats at different times, so badgers may require several blocks of worm-rich habitat to provide a reliable food source. If patches are large or widely dispersed, the minimum ter-
ritory required by an individual will be highly contorted, and defence will therefore be costly. However, coalescence of several individual territories to form a single group territory would reduce individuals' defence costs while still providing access to several habitat blocks. In support of this hypothesis, Kruuk and Parish (1982) showed that, across several study sites in Britain, the distribution of blocks of worm-rich habitat correlated well with territory size.

The second model suggests that territory size is determined by the distribution of setts or sett sites. Doncaster and Woodroffe (1993) simulated territories from Dirichlet tessellations, which generated hypothetical borders equidistant between main setts. The proximity of actual border latrines to these hypothetical borders was compared with the distance from latrines generated by a model which placed setts in the middle of territories. The real borders lay closer than expected to the simulated borders in three of five British populations considered; that is, the size and configuration of territories could be predicted solely on the basis of sett location. Setts require a favourable coincidence of habitat and geology (Neal 1986), especially in modern agricultural landscapes where they are frequently restricted to hedgerows and small patches of woodland. Furthermore, setts represent a substantial resource once dug (Roper 1992), perhaps constraining badgers' ability to disperse away from areas occupied by other badgers. Under these conditions, territory size might be defined by the spatial distribution of setts or sett sites, perhaps leading to territories that can support more than one animal.

Further evidence in favour of Doncaster and Woodroffe's hypothesis comes from long-term studies of badger spatial organisation. Several authors have commented upon the stability of territory borders in the face of changing food availability (e.g. Roper et al. 1986; Cheeseman et al. 1987). When badgers were removed from an area of Gloucestershire, animals moving in to recolonise the cleared area replaced territory borders almost exactly where they had been prior to the removal (Cheeseman et al. 1993). The configuration of territories just after recolonisation showed a particularly good fit to the Dirichlet model (Doncaster and Woodroffe 1993).

Woodroffe and Macdonald (1993) found it difficult to compare the effects of food patch dispersion and sett distribution upon badger spatial organisation, partly because the two factors are expected to act together. The rolling topography likely to lead to abundant sett sites is also characterised by small fields, and thus short distances between food patches. In this paper we attempt to separate the effects of food patch distribution and the availability of sett sites, by presenting data upon the response of badger spatial organisation to a change in the distribution of habitat blocks. Conversion of worm-poor arable land to worm-rich pasture in the Wytham Estate, Oxfordshire, led to a reduction in patch dispersion over a 15-year period. Under these conditions, the patch distribution hypothesis would predict a reduction in territory size. However, since the geology of the area and the availability of cover remained constant, there was no change in the availability of sett sites.

Both of the hypotheses predict that group size should be determined by food availability within the territory, rather than territory size or richness being adjusted to an optimal group size. We therefore investigate the effect of variation in territories' habitat composition on the size and structure of the groups that inhabit them.

**Methods**

**Study area**

Wytham Woods, southern England, occupies approximately 6 km² of mainly deciduous woodland surrounded by farmland. Kruuk (1978a) and Hofer (1988) give details of the site's soil and vegetation characteristics as they relate to badger ecology. Changes in land use and the vegetation cover in Wytham since 1974 were determined from the Oxford University Farm Records and from information provided by C.W.D. Gibson, the warden of Wytham Woods. Kruuk and Parish (1982) measured the distribution of food patches in Wytham in 1974 by calculating the distance from ten random points to the five nearest blocks of worm-rich habitat (pasture and deciduous woodland). We repeated this calculation of the "five-food-patch distance" for Wytham in 1988, following the conversion of large areas of arable land to pasture.

**Sett activity and population size index**

Data on changes in the activity of main setts, and the size of the badger population in Wytham 1976–1998, were taken from the Annual Wytham Badger Census, organised by the Department of Zoology, University of Oxford. In this census, the study area was surveyed for active setts in early May each year. One to four observers were then stationed at each active sett for three evenings, and asked to count the number of adults and cubs seen. Cubs are weaned by this time of year, but can easily be distinguished from adults. The maximum number of each age class seen in one evening at each sett was summed across setts to give an index of the size of the badger population.

For 1974, the population size index was taken from Kruuk (1978a), who gives the number of badgers trapped or seen in each territory. The census data are broadly comparable within themselves, although perhaps not directly comparable with Kruuk's 1974 value.

**Defining territory borders**

Territory borders were mapped in 1987, 1988 and 1989 using bait-marking (Kruuk 1978a). Trapping data (see below) were used to resolve any ambiguity in the interpretation of bait-marking results. The locations of territories in 1974 and 1982 are from Kruuk (1978a) and Hofer (1988), respectively, who used a combination of bait-marking and radio-tracking to determine territory borders. Bait-marking provides a quick and accurate method of defining borders for many territories, and the results of this method correspond closely with those of radio-tracking (Kruuk 1978a; Cheeseman and Mallinson 1980; Parish and Kruuk 1982).

**Calculating food availability in territories**

It is difficult to measure the distribution of earthworm patches directly (Kruuk 1978b). However, the abundance of earthworms varies markedly among vegetation types (Kruuk 1978a; Hofer 1988), and, following Kruuk and Parish (1982), we have therefore considered blocks of worm-rich habitat to estimate the food available within group territories. The area of each habitat type within