



## Badgers, *Meles meles*, discriminate between neighbour, alien and self scent

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For group-living animals, the ability to discriminate between familiar individuals and strangers may allow reduced agonistic behaviour between holders of neighbouring territories, termed the 'dear enemy' effect. We tested the hypothesis that Eurasian badgers can discriminate between self-, neighbour- and alien-(unknown) group faeces placed near their main sett. We carried out a series of controlled field experiments over a 12-month period at the main setts of three badger groups occupying contiguous territories. The experimental design used two different treatments: 'alien treatment' involved the display of self-group scents with alien-group scents and 'neighbour treatment' involved the display of self-group scents with neighbour-group scents. Badgers showed heightened behavioural responses towards alien- compared with self-group scents, but there was no significant difference in response to neighbour- relative to self-group scents. The relative responses towards alien-group scents were greatest during the breeding seasons, but there were no significant seasonal differences in the responses to neighbour-group versus self-group scents. In undisturbed badger populations, levels of aggression between neighbouring territory-holders are likely to be kept relatively low through neighbour recognition. However, increased levels of aggression will be shown towards dispersing or itinerant (alien) badgers, especially during periods such as the breeding season when the potential threats to the long-term fitness of territory owners are greatest. This behaviour may reduce the effectiveness of management strategies involving the culling of group-living wildlife hosts to reduce levels of livestock or human disease.

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Many territorial animals are able to discriminate between familiar individuals and strangers. This is thought to be beneficial since it allows them to avoid costly territorial conflicts with neighbours (Vestal & Hellack 1978; Ferkin 1988), with whom recognition relationships have already been established and which may pose little threat to stable territory ownership (Bee 2003). As a consequence, the level of agonistic behaviour between holders of neighbouring territories may be reduced relative to that between strangers. This phenomenon has been termed the 'dear enemy' effect (Fisher 1954) and has been observed in a variety of taxa (Leiser & Itzkowitz 1999;

Langen et al. 2000; Rosell & Bjorkoyli 2002; Pratt & McLain 2006).

The threat posed by both familiar individuals and strangers to the long-term fitness of a territory holder is likely to vary according to the social environment (Hyman 2005). In particular, it may be greater at certain times of the year, such as during the breeding season. At this time, the potential benefits to be gained from direct aggression are likely to become greater relative to the potential costs, and aggression towards all individuals from other groups may be expected to peak. For example, the incidence of bite wounds in both foxes and badgers show increases during the breeding seasons (Cresswell et al. 1992). Therefore, while familiar (neighbouring) enemies may face reduced aggression from territory holders for much of the year, they may not be held so 'dear' during the breeding season, and an increased level of aggressiveness may be displayed towards them by territory

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holders. There may also be sex-related differences in behavioural responses, depending on the mating system of the species involved. However, the individual-level behavioural mechanisms underlying temporal variations in wounding rates at the population level have received little attention to date.

To display differences in levels of aggression towards familiar individuals and strangers, animals must be able to discriminate, recognize and distinguish familiar individuals from unfamiliar ones (Johnston 1993). For mammals, this is mostly achieved through olfactory communication (Daly 1977; DeVries et al. 1997). This ability for neighbour recognition suggests that, in undisturbed situations, groups of social, territorial mammals may exist as an interlocking social network across the landscape, maintained primarily by ritualized behaviour rather than through direct aggression.

The Eurasian badger is a group-living carnivore, widely distributed throughout the western Palearctic, ranging from Ireland, across Europe and Asia, to Japan. Within this geographical range, the group size of badgers varies between 2 and 25 individuals and territory size ranges from 0.14 to 14 km<sup>2</sup>, according to a combination of ecological (resource-related), demographic and behavioural (philopatry versus dispersal) constraints (Johnson et al. 2002; Revilla & Palomares 2002; Palphramand et al. 2007). Badger groups normally occupy a single main burrow system or 'sett' (Roper et al. 1991) and members of the same social group familiarise themselves by regular 'allomarking' (Kruuk et al. 1984). Badgers, like many social carnivores, use a number of different scent marks to signal their presence. The most visually obvious scent marks used by many species to demarcate territorial boundaries are faeces (Brown & Macdonald 1985; Estes 1991). Although the use of faeces is constrained by their rate of production, which limits their availability for marking (Bra-shares & Arcese 1999), they incur minimal energetic costs to the signaller (Gosling, 1982).

Individual badgers frequently occupy the same territories for their entire life, and they can inflict serious injuries on another during fights (Cresswell et al. 1992; Neal & Cheeseman 1996). Badgers would be expected to be able to distinguish between neighbour and stranger scents, since this would allow them to show the dear enemy effect as an evolutionary response to the potential high cost of aggression and the benefits of more ritualised encounters. Dispersing animals moving across an occupied landscape in search of an opportunity to become established within a territory pose a more significant threat to territory holders. These animals will be perceived as strangers, not familiar to the resident animals, so a higher level of aggression might be expected towards them. Although most social groups maintain a well-defined territory throughout the year (Neal & Cheeseman 1996), interbreeding does occur, especially between close neighbouring groups (Evans et al. 1989; Carpenter et al. 2005). Badgers have two peaks of ovulation, in spring (the main breeding season) and autumn (Cresswell et al. 1992; Roper et al. 1986). At these times of year, the potential benefits of direct aggression may be greater and the

dear enemy effect may be reduced. If females are a limiting resource for badgers (Roper et al. 1986, 1993), the responses of males to nonself scents should also be stronger than those of females.

In this study, we tested whether badgers possessed the capacity to display the dear enemy effect by showing differences at the group level in their responses to self-, neighbour- and alien- (unknown) group faeces placed close to their main sett. Faeces are thought to represent a group composite scent (Davies et al. 1988) and therefore the use of faeces in our study avoided potential biases that might have resulted from using other forms of scent, such as subcaudal secretion or urine, which may contain individual information (Buesching et al. 2002). We also investigated seasonal and sex-related differences in responses. We tested the specific hypotheses that: (1) badgers would display an increased level of investigation towards scents from strangers than those from familiar neighbours, and (2) the level of investigation of scents from both familiar individuals and strangers would be increased during the breeding season, especially by male badgers.

## METHODS

### Study Site

Our study was carried out in Dalby Forest, situated in the North York Moors National Park, in northeast England. This is predominantly coniferous plantation woodland, interspersed with broadleaved woodland, including oak, *Quercus* spp., and beech, *Fagus sylvatica*, and grassland. During 2001–2003, the mean adult group size at the study site was  $5.5 \pm 0.8$  badgers, and the mean group territory size was 0.53 km<sup>2</sup> (Palphramand et al. 2007). Three badger groups forming an interlocking neighbouring network were selected for the scent recognition experiments. Within these groups, the identity of a number of individuals was known, either recognizable from fur-clips or radiocollar frequencies.

### Collection of Scents

To establish whether badgers could discriminate between self-group scents, neighbour-group scents and alien-group scents, we carried out a series of experiments over a 12-month period (autumn 2003 to autumn 2004) at the main setts of the three social groups. The experiments were carried out across all four seasons of the year to incorporate changes in patterns of badger behaviour: spring (March to May), the peak breeding season; summer (June to August), when young animals range more widely through the territory and food is most limiting; autumn (September to November), covering the secondary breeding season and the period over which the animals need to build up their fat reserves for the winter; and winter (December to February), when activity is reduced in response to food shortage and severe conditions (Neal & Cheeseman 1996). These four seasons were aggregated into two seasons for analysis: the breeding seasons (spring

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