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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.

Keywords: dear enemy effect; Eurasian badger; faeces; field experiment; *Meles meles*; scent recognition; territoriality; wildlife disease

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^2, 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 (Brashares & 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 ± 0.8 badgers, and the mean group territory size was 0.53 km^2 (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 and autumn) and the nonbreeding seasons (summer and winter).

Faeces for display in the experiments were collected earlier on the same day to ensure they were fresh and that the ages of each sample were as equally matched as possible. All faecal samples were handled using disposable plastic gloves to minimize human scent and placed in sealed plastic bags for storage and transfer to the sett at which they would be displayed. Self-group scents and neighbour-group scents were collected from the main study setts, and alien-group scents were collected randomly from badger setts located approximately 5–8 km away from the study setts. This distance is equivalent to the diameters of at least 7 home ranges on the study site (mean home range size 0.53 km^2; Palphramand et al. 2007). Since dispersing badgers tend to move to neighbouring or nearby groups (Woodroffe et al. 1993; Rogers et al. 1998) and the furthest movement by a badger recorded on our site was 1.8 km from its main sett (K. Palphramand, unpublished data), there would be no expected previous contact between the study and alien groups.

Experimental Design

We used a paired-scent approach to investigate badgers' responses to neighbouring and alien scents relative to a self-group scent control. There were two treatments: 'alien treatment', involving the display of self-group scents with alien-group scents and 'neighbour treatment', involving the display of self-group scents with neighbour-group scents. We carried out two separate 3-day experiments at each of the three study setts during each of the four seasons. Only one main sett was the subject of an experiment during a single night.

Before each experiment, we established the locations of any radiocollared badgers present at the sett, to determine the entrance hole close to which the scents should be placed. First, this increased the chances of positioning the scents in an area where a badger was likely to emerge and investigate the scents. Second, badgers deposit dung in pits around the entrances of active holes to show ownership and so placing the scents in these 'latrine' areas would mimic natural badger behaviour. Third, it allowed the potential identification of individual badgers, if, as was often the case, only one collared badger had been using the hole as a day rest. If no collared badgers were present at the main setts, the scents were positioned near to a hole that was in regular use.

We placed equal-sized subsamples of faeces, normally representing a single defecation in volume, directly onto the ground from a storage bag, approximately 30 min before the start of each experiment. Samples were approximately 3 m apart, at a distance of 2–3 m from a main entrance hole to the sett. The positioning of the samples was randomised during the experiments to avoid any bias produced when the badgers approached the experimental set-up. Because the experiment was designed to test the reactions of badgers to faeces only, we avoided using any samples containing subcaudal and obvious anal secretions.

Monitoring Behaviour

We used remote infrared video surveillance to record the behaviour of badgers towards the scents over an 8-h period covering emergence times, and started filming between 1700 and 1800 hours GMT. Filming was carried out over 72 nights (18 per season), totalling 576 h of video footage. The equipment used was a Sony bullet monochrome waterproof camera attached to a 12 V 24-h timelapse video recorder (Real Time VCR, Henrys Electronics Ltd., U.K.) with a waterproof infrared light source (IR LED illuminator, Tracksys, U.K.). Both the camera and infrared lighting were attached to a tree close to the area under surveillance, approximately 1.5 m off the ground, to minimise their detectability by badgers. All appliances were powered by two 12 V 24Ah gel sealed lead acid batteries. The video and batteries were housed in camouflaged waterproof boxes, positioned away from the filming area.

Classification and Analysis of Behavioural Responses

Video footage was examined by K.L.P. to quantify behavioural responses to the scents. The randomisation of scent placement between different experiments meant that this scoring of tapes could be done 'blind', with the scorer being unaware of the relative placements of the different scents in individual experiments. A potential response event was defined as when a badger came within 1 m of either of the scents, at which distance it is very likely to have been able to detect the presence of the scent. We defined an actual response event as being initiated when the nose of a badger first came in close proximity (within 10 cm) to a scent (e.g. Sliwa & Richardson 1998). Behavioural responses to the scent were defined as occurring within approximately 50 cm of the scent and always following an initial response (e.g. Saunders 1992). A time period of 5 s after an initial response was used as a buffer zone for further behavioural patterns associated with that response event to occur. Any reactive behaviour occurring beyond this time window was defined as a new response event. During each individual response event, the following behavioural patterns were recorded: (1) the number of times a scent was investigated; (2) sniff duration, the time in seconds for which an investigating badger's nose was within 10 cm of a scent until it turned away; (3) the occurrence of overmarking with their own scent, and (4) any other responses in addition to sniffing, such as backing away from the scent.

We analysed the data within treatments, using linear mixed-effects models fitted by REML within Brodgar (Highland Statistics Ltd., Newburgh, U.K.), to determine the relative effects of scent type and season on aggregate behavioural patterns: (1) the number of contacts based on all potential response events and (2) the total duration of sniffing for those response events that involved sniffing. Data on sniff durations were log transformed before analysis to reduce non-normality (Zar 1999). In the mixed-effects models, season and scent type were treated as nominal fixed variables. It was not possible to

Table 1. The total number of successful footage nights at the three study groups during the different seasons

Group	Experimental treatment	Season				
		Autumn	Winter	Spring	Summer	Total
Pines	Alien	2	2	3	0	7
	Neighbour	2	1	3	3	9
Earthworks	Alien	2	1	3	3	9
	Neighbour	0	2	3	2	7
North Head	Alien	2	0	2	2	6
	Neighbour	0	0	1	2	3
Total		8	6	15	12	41

Three nights of filming were carried out per season for each treatment at each sett.

distinguish consistently between individuals and approximately half of the response events we recorded involved unknown individuals. Therefore, in the models, we treated social groups rather than individuals as random, repeated effects, to account for the use of repeated experiments conducted at the same setts. This approach was also appropriate because we were interested in behavioural patterns at the level of the group rather than at the level of the individual.

RESULTS

Badgers were filmed on 41 nights across the four seasons (Table 1). This provided 76 potential response events to each of the self and alien scents within the alien treatment (combined $N = 152$) and 41 potential response events to each of the self and neighbour scents within the neighbour treatments (combined $N = 82$).

Responses to Alien Treatments

The number of contacts per potential response event with scents in the alien treatments varied significantly with scent type (linear mixed-effects model fitted by REML: ANOVA for fixed effects: scent: $F_{1,146} = 9.14$, $P = 0.003$; Fig. 1). Badgers made significantly more close contacts with alien scents (mean ± SE: 0.64 ± 0.13) than with self scents (0.22 ± 0.06). The number of contacts made with different scents also varied significantly by season (season: $F_{1,146} = 7.53$, $P = 0.007$), and there was a significant interaction between scent type and season (scent*season: $F_{1,146} = 4.57$, $P = 0.034$). The mean number of contacts with alien scents in the breeding season was significantly higher than the numbers of contacts with alien scents in the nonbreeding season and self scents in both seasons (alien, breeding versus self, nonbreeding (reference combination): $t_{1,146} = -2.14$, $P = 0.034$).

Scent type had a significant effect on the aggregate time spent by badgers sniffing scents (linear mixed-effects model fitted by REML: ANOVA for fixed effects: scent: $F_{1,31} = 8.60$, $P = 0.006$; Fig. 2), with badgers spending a significantly longer mean time sniffing at nonself scents (10.12 ± 1.84 s) than self scents (3.38 ± 0.76 s). There was also an overall significant effect of season (season: $F_{1,31} = 4.58$, $P = 0.040$), with badgers spending a significantly greater mean time sniffing at scents during the breeding seasons (8.68 ± 1.52 s) than in the nonbreeding seasons (3.17 ± 1.14 s), although there was no significant interaction between scent type and season (season*scent: $F_{1,31} = 2.62$, $P = 0.116$).

Within the alien treatments, only one of the 17 actual response events associated with self-group scents (Table 2) induced any response other than sniffing, which was overmarking. In contrast, out of the 49 response events associated with alien-group scents, we recorded five instances of overmarking and nine instances of other reactive

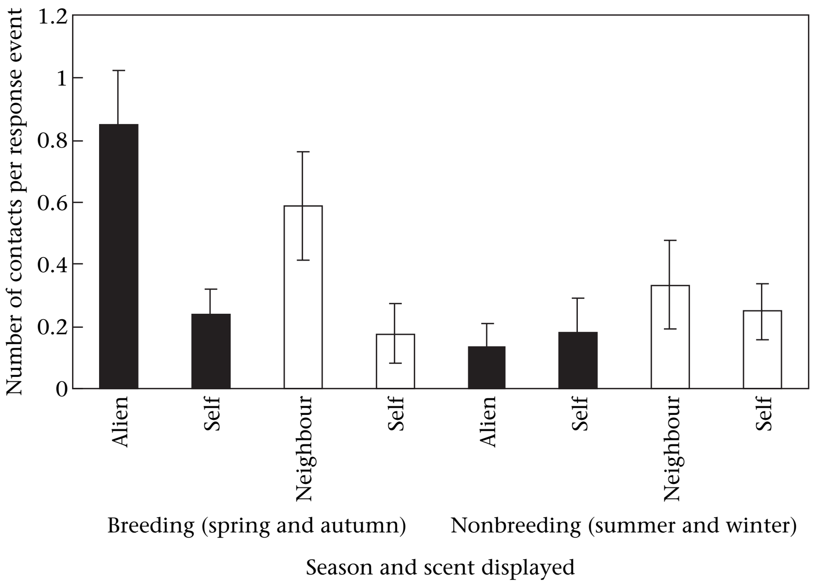

Figure 1. Number of contacts per response event with alien-group versus self-group scents (■) and neighbour-group versus self-group scents (□) within (spring and autumn) and outside (summer and winter) the breeding season. Vertical bars indicate standard error of the mean.

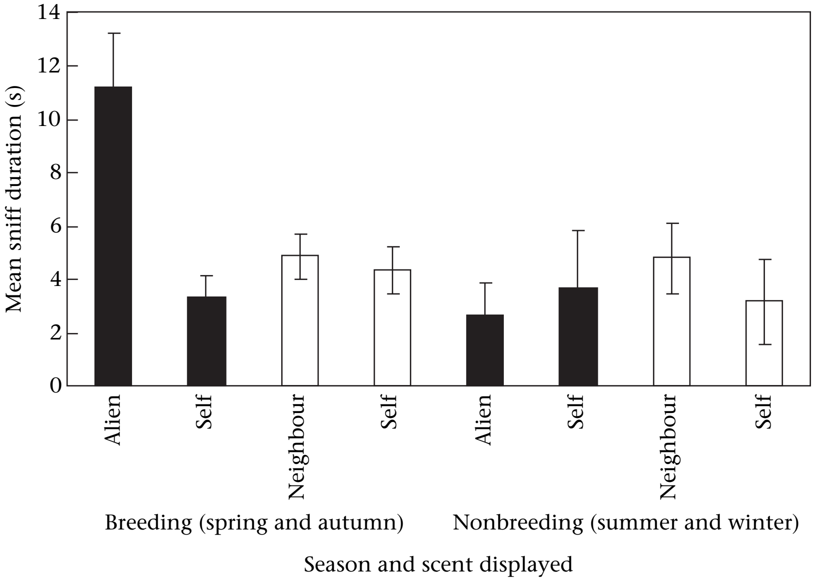

Figure 2. Aggregate time spent by badgers investigating alien-group versus self-group scents (■) and neighbour-group versus self-group scents (□) within (spring and autumn) and outside (summer and winter) the breeding season. Only those scents that were contacted are included. Vertical bars indicate standard error of the mean.

behaviour. Ten collared adult badgers out of an estimated total of 18 adult badgers across the three social groups (Palphramand et al. 2007) were identified during the video surveillance trials (four male adults and six female adults). This was not a sufficient sample to analyse statistically for sex-related differences in behaviour, but males and females appeared to spend similar amounts of time investigating scents, and overmarking of alien scents was done by both males (three occasions) and females (two occasions). Eight of the 10 instances of multiple investigations towards scents (where a badger returned to the same scent on more than one occasion) were recorded for alien scents. Self-group scents were never returned to once they had been investigated. For multiple investigations towards alien scents, there was a significant trend for the mean sniff duration to decline with successive contacts (Spearman rank correlation: $r_s = -0.30$, $N = 50$, $P < 0.05$; Fig. 3).

Responses to Neighbour Treatments

Within the neighbour treatments, we observed nine response events directed towards self-group scents and 18 directed towards neighbour-group scents. The aggregate number of contacts per response event within the neighbour treatments was not significantly affected by scent type or season and neither was there any significant interaction between scent type and season (linear mixed-effects model fitted by REML: ANOVA for fixed effects: scent: $F_{1,76} = 3.07$, $P = 0.084$; season: $F_{1,76} = 1.10$, $P = 0.298$; scent*season: $F_{1,76} = 1.67$, $P = 0.201$; Fig. 1). There were also no significant effects of scent type or season on the aggregate time spent by badgers investigating scents within the neighbour treatments (scent: $F_{1,16} = 0.60$, $P = 0.451$; season: $F_{1,16} = 1.68$, $P = 0.214$; scent*season: $F_{1,16} = 0.31$, $P = 0.586$; Fig. 2).

Within the neighbour treatments, of the nine response events associated with self-group scents, one evoked an over-marking response by a female and of 18 response events associated with neighbour-group scents, one evoked an over-marking response by a male and five evoked other forms of reactive behaviour (Table 2).

DISCUSSION

Scent Recognition

This was the first experimentally controlled investigation into the responses of badger groups, including known individuals, to scents of different origin (i.e. self-group,

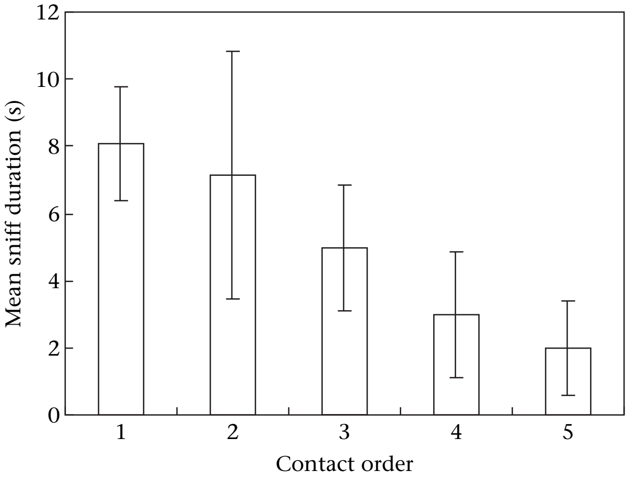

Figure 3. Relationship between the order of successive contacts and the mean duration of sniffing during each contact, for multiple investigations towards alien-group scents in the alien treatments. Successive contacts: order 1, $N = 12$, order 2, $N = 7$, order 3, $N = 3$; order 4, $N = 3$, order 5, $N = 2$. Vertical bars indicate standard error of the mean.

Table 2. Number of potential and actual response events observed in the alien and neighbour treatments

	Alien treatment			Neighbour treatment		
	Self scent	Alien scent	Total	Self scent	Neighbour scent	Total
Potential response events	76	76	152	41	41	82
Breeding season	54	54	108	17	17	34
Nonbreeding season	22	22	44	24	24	48
Actual response events	17	49	66	9	18	27
Breeding season	13	46	59	3	10	13
Nonbreeding season	4	3	7	6	8	14

For definitions, see text.

neighbouring-group and alien-group) across a seasonal spectrum. Badgers showed heightened behavioural responses towards alien-group compared with self-group scents, but there was no significant difference in the responses to neighbour-group relative to self-group scents. The relative responses towards alien-group scents were greatest during the breeding seasons, but there were no seasonal differences in the responses to neighbour-group versus self-group scents. There were also no discernible differences in responses between males and females, although sample sizes for observations of badgers of known sex were small.

The lack of a significant difference in the number of contacts and the time spent investigating neighbour-group versus self-group scents suggests that badgers were equally familiar (or equally unfamiliar) with both types of scent. However, badgers were less familiar with the alien-group scents, so investigated these more frequently and for a greater length of time relative to self scents. Kruuk et al. (1984) argued that badgers spent a long time sniffing alien scent marks to familiarize themselves with the smell to aid in future encounters. Our results provide some evidence for this in that the duration of time spent sniffing alien-group scents decreased progressively during successive contacts. It is likely that the duration of sniffs reflects the time required by an individual to identify the scent mark donor and after sniffing the first mark, the individual gradually habituates to subsequent investigations (Sliwa & Richardson 1998).

The reactive responses displayed by the badgers towards neighbour-group scents were weaker and less aggressive than has been suggested by two previous studies (Neal 1986; Christian 1993). However, Christian's (1993) study was carried out within a provisioned food patch, and the behaviour he observed may therefore have been partly or wholly in response to the presence of food rather than solely in response to different scents. Our results were more consistent with those of Kruuk (1978), who found that badgers showed only limited responses to faeces from neighbouring groups placed on a main sett. Kruuk argued that (1) the effects of faeces from other groups only became apparent during subsequent interactions with the alien intruder, (2) the function of faeces alone was to advertise the presence of other more specific information contained in glandular secretion or (3) faeces only had a specific effect in an appropriate context (i.e. boundary latrine marking). However, Kruuk's results can now also be interpreted in the context of badgers displaying familiarity with the scent of known neighbours.

There may be a number of reasons why overmarking of alien faeces, as predicted by Gosling (1982), was observed only rarely during our study. First, faecal marking is constrained by the actual production of faeces and their availability may limit the marking rate in species that use them to demarcate territorial boundaries (e.g. Peters & Mech 1975; Macdonald 1979). The limited group size of the badgers at the study site (average of 5.5 adults/group; Palphramand et al. 2007) may mean that faecal resources from all group members need to be conserved for marking in an appropriate, higher-priority context, such as boundary marking, consistent with Kruuk's (1978) theory. In addition, if faeces and anal secretion represent a uniform group scent, it is more advantageous to the group to deposit these scents around territory boundaries. Second, the observed scent marking during the present study involved setting scent with the subcaudal gland. Subcaudal secretion is commonly used by badgers (Gorman et al. 1984) and is not constrained by the amount produced, making it readily available to mark objects frequently. It is often used to mark the sett area and territorial boundaries (Gorman et al. 1984), and is more likely to convey individual information about the owner than other forms of scent mark (Gorman et al. 1984; Kruuk et al. 1984; Buesching et al. 2002). Subcaudal secretions deposited by a resident badger provide a priori indication of that individual's status, so an intruder can assess the potentially costly aggressive interaction in the absence of the signaller (Gorman et al. 1984). They may also serve to reiterate to other group members information on the resident badger's own quality, especially for males signalling to females.

Seasonal Patterns in Behaviour towards Scents

The badgers showed a greater degree of investigation of alien- relative to self-group scents during the breeding seasons (spring and autumn), when the potential threat posed by itinerant or dispersing animals is highest (Roper et al. 1986; Cheeseman et al. 1988). During these seasons, there were only a few occasions when badgers ignored the scents. These findings are consistent with the observation that badger mating seasons are accompanied by an increase in subcaudal scent-marking activity (Kruuk 1978). The number of contacts with neighbour- relative to self-group scents was higher during the breeding season, although this difference was not quite significant at the $P = 0.05$ level. However, it does suggest that this may be a time when near enemies are not so 'dear' and is consistent with the AntiKleptogamy Hypothesis (Roper et al. 1986). The lack of any difference in the length of time spent investigating neighbour versus self-group scents at any time of year is likely to be because badgers were already familiar with the donor of these scents and could therefore identify them quickly.

Sex-specific Responses to Scents

There are very few data in previous literature regarding the behaviour of individual badgers towards scent categories, especially sex-related differences. Our results, although relatively sparse, suggested no apparent difference between the responses of male and female badgers in terms of the number or duration of investigations of neighbour- or alien-group scents relative to self-group ones. Males were responsible for five of the seven reactive responses of known individual badgers. Scent marking is done more frequently by males (Gorman et al. 1984), with the group composite scent usually dominated by that of the alpha male (Kruuk et al. 1984), which may explain this observed behaviour. Females are likely to be responding to nonself scents for different reasons. There is evidence that adult badgers interact with members of other groups more than previously thought, including breeding (Evans et al. 1989; Woodroffe et al. 1993). Female residents may therefore be assessing nonself scents with the potential to secure opportunistic matings within their own territory.

This study focused on behaviour at the level of the social group. At this level, badgers clearly showed heightened behavioural responses towards alien- relative to neighbour-group scents compared with self-group scent controls. However, it is likely that there will be variation between individuals in their responses towards different scents, which will depend on their own status in the group, the status of the signalling individual and also on the nature of the scent being displayed. In future studies, the behaviour of resident animals towards identifiable scents collected from individuals of known sex and age (such as subcaudal secretion, which may be capable of advertising individuality; Buesching et al. 2002) would confirm whether sex-related or status-related differences are apparent. The experimental design we have used would provide a means of investigating this in a robust manner. Using this approach, it would be possible to link the observed behaviour of marked individuals to their status and likely motivations. Longitudinal studies may reveal further information about how social groups and hierarchies are maintained, and also about the driving forces behind behavioural patterns at the population level, such as dispersal.

Implications for Population Management

Badgers in the U.K. have long been identified as a wildlife reservoir of *Mycobacterium bovis*, the causative agent of bovine tuberculosis (TB) in cattle (Muirhead et al. 1974). As a consequence, they have been the focus of management strategies aimed at reducing the risk of TB transmission to livestock (Krebs et al. 1997), the primary means being culling based on trapping around setts. Recent large-scale experimental field trials have shown that badger culling can actually lead to an increase in the levels of infection in cattle (Donnelly et al. 2003; Godfray et al. 2004). One possible contributory factor is that culling disrupts badger social groups, resulting in increased movement and fighting among badgers (Rogers et al. 1998; Tuyttens et al. 2000). The difference in behaviour shown by badgers towards familiar neighbours and strangers provides a potential mechanism for the effects of culling-induced perturbation in amplifying disease risks to cattle. The same mechanisms may act to reduce the efficiency of disease management strategies in other parts of the world where group-living animals serve as wildlife hosts for diseases of humans or livestock.

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References

Bee, M. A. 2003. A test of the ‘‘dear enemy effect’’ in the strawberry dart-poison frog (*Dendrobates pumilio*). *Behavioral Ecology and Sociobiology*, **54**, 601–610.

Brashares, J. S. & Arcese, P. 1999. Scent marking in a territorial African antelope: II. The economics of marking with faeces. *Animal Behaviour*, **57**, 11–17.

Brown, R. E. & Macdonald, D. W. 1985. *Social Odours in Mammals*. Oxford: Oxford University Press.

Buesching, C. D., Newman, C. & Macdonald, D. W. 2002. Variations in colour and volume of the subcaudal gland secretion of badgers (*Meles meles*) in relation to sex, season and individual-specific parameters. *Mammalian Biology*, **67**, 147–156.

Carpenter, P. J., Pope, L. C., Greig, C., Dawson, D. A., Rogers, L. M., Erven, K., Wilson, G., Delahay, R., Cheeseman, C. L. & Burke, T. 2005. Mating system of the Eurasian badger, *Meles meles*, in a high density population. *Molecular Ecology*, **14**, 273–284.

Cheeseman, C. L., Cresswell, W. J., Harris, S. & Mallinson, P. J. 1988. Comparison of dispersal and other movements in two badger (*Meles meles*) populations. *Mammal Review*, **18**, 51–59.

Christian, S. F. 1993. The behavioural ecology of the Eurasian badger, *Meles meles*: space use, territoriality and social behaviour. D.Phil thesis, University of Sussex.

Cresswell, W. J., Harris, S. & Cheeseman, C. L. 1992. To breed or not to breed: an analysis of the social and density-dependent constraints on the fecundity of female badgers (*Meles meles*). *Philosophical Transactions of the Royal Society of London, Series B*, **338**, 393–407.

Daly, M. 1977. Some experimental tests of the functional significance of scent marking by gerbils (*Meriones unguiculatus*). *Journal of Comparative Physiology and Psychology*, **91**, 1082–1094.

Davies, J. M., Lachno, D. R. & Roper, T. J. 1988. The anal gland secretion of the European badger (*Meles meles*) and its role in social communication. *Journal of Zoology*, **216**, 455–463.

DeVries, A. C., Johnson, C. L. & Carter, C. S. 1997. Familiarity and gender influence social preferences in prairie voles (*Microtus ochrogaster*). *Canadian Journal of Zoology*, **75**, 1082–1094.

Donnelly, C. A., Woodroffe, R., Cox, D. R., Bourne, J., Gettinby, G., Le Fevre, A. M., McInerney, J. P. & Morrison, W. I. 2003. Impact of localized badger culling on tuberculosis incidence in British cattle. *Nature*, **426**, 834–837.

Estes, R. D. 1991. *The Behaviour Guide to African Mammals*. Los Angeles: University of California Press.

Evans, P. G. H., Macdonald, D. W. & Cheeseman, C. L. 1989. Social structure of the Eurasian badger (*Meles meles*): genetic evidence. *Journal of Zoology*, **218**, 587–595.

Ferkin, M. H. 1988. The effect of familiarity on social interactions in meadow voles, *Microtus pennsylvanicus*: a laboratory and field study. *Animal Behaviour*, **36**, 1816–1822.

Fisher, J. 1954. Evolution and bird sociality. In: *Evolution as a Process* (Ed. by J. Huxley, A. C. Hardy & E. B. Ford), pp. 71–83. London: Allen and Unwin.

Godfray, H. C. J., Curnow, R. N., Dye, C., Pfeiffer, D., Sutherland, W. J. & Woolhouse, M. E. J. 2004. *Independent Scientific Review of the Randomised Badger Culling Trial and Associated Epidemiological Research*. London: Defra.

Gorman, M. L., Kruuk, H. & Leitch, A. 1984. Social functions of the sub-caudal scent gland secretion of the European badger *Meles meles* (Carnivora: Mustelidae). *Journal of Zoology*, **204**, 549–559.

Gosling, L. M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, **60**, 89–118.

Hyman, J. 2005. Seasonal variation in response to neighbors and strangers by a territorial songbird. *Ethology*, **111**, 951–961.

Johnson, D. D. P., Jetz, W. & Macdonald, D. W. 2002. Environmental correlates of badger social spacing across Europe. *Journal of Biogeography*, **29**, 411–425.

Johnston, R. E. 1993. Memory for individual scent in hamsters (*Mesocricetus auratus*) as assessed by habituation methods. *Journal of Comparative Psychology*, **107**, 201–207.

Krebs, J. R., Anderson, R. M., Clutton-Brock, T., Morrison, I., Young, D. & Donnelly, C. 1997. *Bovine Tuberculosis in Cattle and Badgers*. London: Ministry of Agriculture, Fisheries and Food.

Kruuk, H. 1978. Spatial organisation and territorial behaviour of the European badger *Meles meles*. *Journal of Zoology*, **184**, 1–19.

Kruuk, H., Gorman, M. L. & Leitch, A. 1984. Scent-marking with the subcaudal gland by the European badger, *Meles meles*. *Animal Behaviour*, **32**, 899–907.

Langen, T. A., Tripet, F. & Nonacs, P. 2000. The red and the black: habituation and the dear–enemy phenomenon in two desert *Pheidole* ants. *Behavioral Ecology and Sociobiology*, **48**, 285–292.

Leiser, J. K. & Itzkowitz, M. 1999. The benefits of dear enemy recognition in three-contender convict cichlid (*Cichlasoma nigrofasciatum*) contests. *Behaviour*, **136**, 983–1003.

Macdonald, D. W. 1979. The flexible social system of the golden jackal, *Canis aureus*. *Behavioral Ecology and Sociobiology*, **5**, 17–38.

Muirhead, R. H., Gallagher, J. & Burn, K. J. 1974. Tuberculosis in wild badgers in Gloucestershire: epidemiology. *Veterinary Record*, **95**, 552–555.

Neal, E. 1986. *The Natural History of Badgers*. Beckenham: Croom Helm.

Neal, E. & Cheeseman, C. L. 1996. *Badgers*. London: T & AD Poyser.

Palphramand, K. L., Newton-Cross, G. A. & White, P. C. L. 2007. Spatial organization and behaviour of badgers (*Meles meles*) in a moderate-density population. *Behavioral Ecology and Sociobiology*, **61**, 401–413.

Peters, R. P. & Mech, R. D. 1975. Scent marking in wolves. *American Scientist*, **63**, 628–637.

Pratt, A. E. & McLain, D. K. 2006. How dear is my enemy: intruder–resident and resident–resident encounters in male sand fiddler crabs (*Uca pugilator*). *Behaviour*, **143**, 597–617.

Revilla, E. & Palomares, F. 2002. Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*. *Journal of Animal Ecology*, **71**, 497–512.

Rogers, L. M., Delahay, R., Cheeseman, C. L., Langton, S., Smith, G. C. & Clifton-Hadley, R. S. 1998. Movement of badgers (*Meles meles*) in a high-density population: individual, population and disease effects. *Proceedings of the Royal Society of London, Series B*, **265**, 1269–1276.

Roper, T. J., Shepherdson, D. J. & Davies, J. M. 1986. Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour*, **97**, 94–117.

Roper, T. J., Tait, A. I., Fee, D. & Christian, S. F. 1991. Internal structure and contents of three badger (*Meles meles*) setts. *Journal of Zoology*, **225**, 115–124.

Roper, T. J., Conradt, L., Butler, J., Christian, S. E., Ostler, J. & Schmid, T. K. 1993. Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. *Behaviour*, **127**, 289–307.

Rosell, F. & Bjorkoyli, T. 2002. A test of the dear enemy phenomenon in the Eurasian beaver. *Animal Behaviour*, **63**, 1073–1078.

Saunders, G. 1992. Urban foxes (*Vulpes vulpes*): implications of their behaviour for rabies control. Ph.D. thesis, University of Bristol.

Sliwa, A. & Richardson, P. R. K. 1998. Responses of aardwolves, *Proteles cristatus*, Sparrman 1783, to translocated scent marks. *Animal Behaviour*, **56**, 137–146.

Tuyttens, F. A. M., Delahay, R. J., Macdonald, D. W., Cheeseman, C. L., Long, B. & Donnelly, C. 2000. Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *Journal of Animal Ecology*, **69**, 815–828.

Vestal, B. M. & Hellack, J. J. 1978. Comparison of neighbor recognition in two species of deer mice (*Peromyscus*). *Journal of Mammalogy*, **59**, 339–346.

Woodroffe, R., Macdonald, D. W. & Da Silva, J. 1993. Dispersal and philopatry in the European badger, *Meles meles*. *Journal of Zoology*, **237**, 227–239.

Zar, J. H. 1999. *Biostatistical Analysis*. 3rd edn. London: Prentice-Hall.