



## Context-dependent linear dominance hierarchies in social groups of European badgers, *Meles meles*

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A social hierarchy is generally assumed to exist in those mammalian societies in which the costs and benefits of group living are distributed unevenly among group members. We analysed infrared closed-circuit television footage, collected over 3 years in Wytham Woods, Oxfordshire, to test whether social groups of European badgers have dominance hierarchies. Analysis of directed aggression between dyads revealed linear dominance hierarchies in three social-group-years, but patterns within social groups were not consistent across years. Dominance hierarchies were significantly steeper than random in five out of six social-group-years. In those social-group-years where a linear hierarchy was determined, there was an effect of sex on dominance rank, with females gaining significantly higher rank than males in two social-group-years. Overall, rank was not related to age, nor did it appear to affect the likelihood of an individual being wounded, or an individual's breeding status. The latter resulted from nonorthogonality between sex and breeding status, as there were only two breeding males. Overall, hierarchies were primarily dominated by breeding females, and may occur when breeding competition arises. Relatedness, unreciprocated allogrooming and sequential allomarking were not consistently related to levels of directed aggression across social-group-years. We suggest that dominance structures within European badger groups may be context dependent, with future study required to complete our understanding of where, and when, they arise.

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Group living is hypothesized to evolve when individuals derive net benefits from group membership, which enhance their fitness above the level that they would achieve as solitary individuals (Alexander 1974). Benefits arising from group living may include increased vigilance and protection from predation (Rasa 1986), or increased resource acquisition (Creel & Macdonald 1995). Once a group has been established, these benefits may then be further enhanced by the development of social behaviour (Alexander 1974). However, within a group certain individuals may exert disproportionate influence over others and competitive asymmetries may generate a social hierarchy, with those individuals that monopolize contested resources classed as dominant. The definition of dominance often varies between studies, leading Drews (1993, page 308) to suggest the following structured definition: 'Dominance is an attribute of the pattern of repeated, agonistic interaction between two individuals, characterised by a consistent

outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation'.

Dominance hierarchies can be described using two characteristics: linearity and steepness (de Vries et al. 2006). The former is an ordinal measure and provides information on the consistency of the direction of dyadic interactions, whereas the latter requires a cardinal rank measure, which quantifies the rank distances between individuals based upon their relative likelihood of winning dominance encounters (de Vries et al. 2006; Vervaecke et al. 2007). Where rank distances are large the hierarchy is steep and despotic; where they are small it is shallow and egalitarian (de Vries et al. 2006). Where dominance hierarchies are apparent, the costs and benefits of group living may be divided unequally between group members dependent upon their position within the group. These differences in dominance status may be related to factors such as size (e.g. McElligott et al. 2001) or age (e.g. Berdoy et al. 1995) and may have large consequences for the fitness of individuals.

Dominance hierarchies are generally assumed to exist in mammalian societies and have been demonstrated in, for example, brown hyaenas, *Hyaena brunnea* (Owens & Owens 1996) and patas monkeys, *Cercopithecus patas* (Goldman & Loy 1997). Hierarchies

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may also be limited to one sex within a species, as is the case in male capybaras, *Hydrochaeris hydrochaeris* (Herrera & Macdonald 1993); or hierarchies may be detected separately in each gender, as in mountain goats, *Oreamnos americanus* (Cote 2000; Mainguy et al. 2008) and bighorn sheep, *Ovis canadensis* (Festa-Bianchet 1991; Pelletier & Festa-Bianchet 2006). We investigated whether evidence can be found of dominance hierarchies within social groups of the European badger.

European badgers show marked intraspecific variation in their behavioural ecology across the species' extensive geographical range (Johnson et al. 2002). In lowland Britain they live at high densities in both urban and rural areas (Huck et al. 2008), forming social groups of up to 29 individuals of both sexes (da Silva et al. 1994). Groups appear to form by the retention of offspring in their natal territory (da Silva et al. 1994), with low dispersal rates, which are not sex biased, among adults (Pope et al. 2006). Individuals in groups share communal setts, within which they sleep by day, and are sociable around sett entrances, where they greet, mark, groom and play with each other. However, individuals typically spend much of their time foraging alone (Kruuk 1978a) and there is limited evidence that group members benefit from cooperation (Woodroffe & Macdonald 1992). This, together with the fact that group living is rare in mustelids, has led to the suggestion that social structures may not yet be well established within European badger groups (da Silva et al. 1994).

The degree of sociality found in European badgers also varies across their geographical range, with individuals in continental Europe commonly living alone or in pairs, while within the British Isles badgers are more typically group living (Johnson et al. 2000). Kruuk (1978b) first proposed that the resource dispersion hypothesis (Macdonald 1983) explained why badgers form groups in some areas. This hypothesis suggests that if resources are heterogeneous in space and time, this may enable several individuals to share them without imposing large costs on each other. Ecological constraints may also play a role in group formation by the costs that they impose on dispersal and independent breeding (da Silva et al. 1994). However, while the role of ecological factors in the formation of groups in this species has been explored (Johnson et al. 2002), the factors influencing the evolution of behaviour within these social groups are less well understood.

Although it is often implied in the literature that dominance hierarchies exist within European badger social groups (by allusion to dominant group members), no empirical evidence of such hierarchies has yet been found (Macdonald et al. 2002). This aspect of the structuring of badger societies therefore remains open to question. The costs and benefits of group living to badgers remain uncertain (Woodroffe & Macdonald 1992). Understanding whether these costs and benefits may be equally distributed among group members or skewed across a hierarchy therefore has important implications, and also, more widely, it may offer important insights into the evolution of mammalian societies.

We examined directed aggression between dyads in six social-group-years in Wytham Woods, Oxfordshire, U.K., to investigate whether: (1) hierarchies exist within badger social-group-years, as is often implied but has never been demonstrated (Macdonald et al. 2002); (2) males gain higher rank than females (as is generally the case in mammals, Kappeler 2000) and rank is positively correlated with age (e.g. Berdoy et al. 1995; Archie et al. 2006); (3) high-ranking individuals gain breeding status (e.g. Mainguy et al. 2008) and low-ranking group members suffer from increased bite wounds; (4) levels of directed aggression in dyads decrease with increased relatedness (as seen in female Japanese macaques, *Macaca fuscata*, Belisle & Chapais 2001); and (5) levels of directed aggression in these badgers are positively related to other behaviours, such as allogrooming (as seen in meerkats, *Suricata suricatta*, Kutsukake & Clutton-Brock 2006) and sequential allomarking.

## METHODS

### Study Site

This study was conducted in Wytham Woods, an area of mostly deciduous woodland 5 km northwest of the city of Oxford, U.K. A detailed description of the site is given by Kruuk (1978a). European badgers in this area have been studied since the 1970s and trapping events have occurred annually since 1987 (Macdonald & Newman 2002). Territory borders are mapped every 2 years using bait-marking techniques (Kruuk 1978b). Fieldwork was carried out under Home Office and English Nature licences.

Filming was carried out at three social groups of European badgers within Wytham Woods: Sunday's Hill (SH), Pasticks (P) and Pasticks Outlier (PO). Pasticks Outlier was originally contained within Pasticks; however, badger groups may undergo fission (da Silva et al. 1994) and bait-marking and trapping records showed that Pasticks and Pasticks Outlier were separate stable groups by 2003.

### Data Collection

Badgers were trapped at least four times a year, generally around January, June, August and November (Macdonald & Newman 2002). Individuals were caught using swing-door box traps that were baited with peanuts (Tuytens et al. 1999). Badgers were sedated by an intramuscular injection of approximately 0.2 ml ketamine hydrochloride (Vetlar; Pharmacia and Upjohns, Crawley, U.K.) per kg bodyweight. All badgers were marked with a unique tattoo number upon first capture. Individuals from the three social groups studied here were also given unique clip marks to allow identification on camera (Stewart et al. 1999). Badgers were allocated to social groups based on where they were most frequently trapped. A range of measurements were also taken from each badger, providing information on sex, age and any visible fresh wounds (Macdonald et al. 2004). In addition, guard hairs or a blood sample (approximately 3 ml from the jugular vein) were collected from each individual for genetic analyses.

Filming was carried out using infrared CCTV equipment (Stewart et al. 1997), with cameras set up to record all nocturnal, above-ground activity in the locations selected. As behaviour occurred sporadically, with periods of no activity, passive infrared (PIR) detectors were used so that video recording (in 3 h real-time mode) was triggered only when activity was detected.

In this study, we analysed video footage from 3 years of filming (1995, 2004 and 2005). Cameras were placed at two social groups each year: SH and P in 1995 and P and PO (by this point a separate group) in 2004 and 2005. Each camera was placed to capture social behaviour in the vicinity of the sett entrances. As there were more sett entrances at P than the other setts, three cameras were placed at P and one camera at SH and PO per year. Although this led to a small sample size, it is better to gain a detailed picture of social interactions in a few groups, rather than greater replication but reduced detail (Oksanen 2001).

### Behavioural Analyses

We analysed 960 videotapes (corresponding to 319 calendar nights or 11 230 h), from 1 February to 31 May each year. Cubs are born underground around February, and breeding females immediately enter a period of postpartum oestrus (Cresswell et al. 1992). Although mating can occur all year round, this is the first of two distinct peaks in mating activity, with a second period of oestrus in late summer/autumn; however, not all males remain fertile for this second period (reviewed in Yamaguchi et al. 2006). As males may compete for access to females, while females compete for breeding status (Woodroffe & Macdonald 1995), dominance hierarchies may

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