

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

Stacey E. Hewitt^{a,1}, David W. Macdonald^{a,1}, Hannah L. Dugdale^{a,b,*}

^aWildlife Conservation Research Unit, Department of Zoology, University of Oxford

^bNERC Molecular Genetics Facility, Department of Animal and Plant Sciences, University of Sheffield

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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

* Correspondence and present address: H. L. Dugdale, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K.

E-mail address: h.dugdale@sheffield.ac.uk (H.L. Dugdale).

¹ S. E. Hewitt and D. W. Macdonald are at the Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford OX1 3PS, U.K.

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

be expected to be most apparent during the spring period considered in this study.

We analysed each night's footage according to a strict ethogram with random tape checks between observers to confirm consistency (Dugdale 2007). We recorded the identity of the actors and receivers (as deduced from clip marks) involved in directed aggression, unreciprocated allogrooming and sequential allomarking. All are clear unidirectional behaviours, with one badger initiating the behaviour, and the other receiving it without reciprocating. Further detail is provided in the Appendix.

Genetic Analyses

We extracted DNA from hair samples using a Chelex protocol (Walsh et al. 1991) and from blood samples using a GFX genomic blood DNA purification kit (Amersham Biosciences, Little Chalfont, U.K.). We genotyped individuals for 22 microsatellite loci and assigned parentage using a likelihood-based approach; the methods are described in Dugdale et al. (2007). The Queller & Goodnight (1989) index of relatedness (R) was estimated for each badger dyad in this study using Relatedness 5.0.8 (<http://www.gsoftnet.us/gsoft.html>; see Dugdale et al. 2008 for details). R ranges from -1 (unrelated) to $+1$ (identical).

The breeding status of each group member was obtained from the parentage analysis, with badgers that had bred within their own social-group-year classed as reproductively active. Although males may father cubs outside their own group, such instances were excluded from analyses as such reproduction is outside the confines of any dominance hierarchy within the group. Group members were divided into three categories; breeding, nonbreeding or not capable of breeding (i.e. yearlings). Social-group-year compositions are provided in Table 1.

Statistical Analyses

We constructed actor–receiver matrices (Macdonald et al. 2000) for all instances of directed aggression that were recorded within

each social-group-year. All matrices were square, with an undefined diagonal (see Appendix, Fig. A1). To take into account variation between dyads in their opportunity to interact on camera, each matrix was also weighted by the number of 'bouts' in which each member of the dyad was seen. A bout is here defined as a period of badger activity captured on camera, ending when no further activity was detected within a minute of the last badger leaving the screen. Similar matrices were also created for all unreciprocated allogrooming and sequential allomarking events to investigate whether these were correlated with directed aggression.

Only badgers that were present, and identifiable, for the entire study period each year were included in the analyses (Table 1). Any unmarked individuals (those that eluded trapping or whose clip mark was lost through moulting) were excluded, as were all cubs. One badger was seen infrequently at P until early May 2004 and is thought to have subsequently died, while another individual (also from P) was found dead in April 2005. Both badgers were therefore excluded in these respective years. In addition, two males were excluded from the matrices for P 1995 and one female from the matrix for PO 2005 as their presence led to 'structural zeros' (where two individuals were never observed together and so did not have the opportunity to perform the behaviour). As such values would invalidate the matrix analyses as currently performed, the decision was made to exclude these badgers.

Analysis of dominance

We tested the directed aggression matrices for the presence of linear hierarchies using MatMan 1.1 (de Vries et al. 1993). Where there were unknown relationships between dyads the strength of linearity within each group was tested using the improved linearity index h' (de Vries 1995); otherwise Landau's h index was used. The significance of the degree of linearity was assessed by a two-step randomization test with 1000 randomizations (de Vries 1995). For groups where the degree of linearity was found to be significant, the matrices were then reordered using the I & SI method (de Vries 1998) to give the most consistent I&SI rank order for each group.

As the directed aggression matrix for PO in 2005 was made up of only five individuals, it was not possible to obtain a statistically significant level of hierarchy in this social-group-year when using either the h or h' index (Appleby 1983). Some authors (e.g. Isbell & Young 2002), however, have suggested that the directional consistency (DC) index (van Hooff & Wensing 1987) and transitivity of relationships across dyads may be used as an alternative to the h or h' indices. These values have been used to provide a measure of dominance in another study where group sizes were small (Archie et al. 2006).

The DC index ranges from 0 to 1 and was calculated across all dyads as: $(H - L)/(H + L)$, where H is the number of times the behaviour was performed in the main direction within each dyad and L is the number of times the behaviour occurred in the opposite direction. A high value therefore indicates that, for those individuals observed to interact multiple times, exchanges were highly unidirectional. The transitivity of relationships across dyads was measured as the number of circular triads observed within a social-group-year. A circular triad occurs when, for any three individuals in a social-group-year, A dominates B, B dominates C, but C dominates A. Therefore, at least one of these three pairs will be inconsistent with a linear order. The observed number of circular triads in a group can be compared with that expected if relationships within the group were totally random. A smaller than expected number of observed triads indicates transitive relationships, and the strength of linearity in the group increases as the number of circular triads decreases.

Measuring the DC index and transitivity of relationships therefore provides a means of commenting on dominance structure in the smallest group in this study, even if it cannot be tested for the presence of significant linearity. However, the former value can be

Table 1
Social-group-year compositions

	1995		2004		2005	
	P	SH	P	PO	P	PO
Breeding female	4	2	2	1	4	1*
Nonbreeding female	3	1†	2‡	3	1	1
Yearling female	0	1	0	0	2	1
Breeding male§	0*	1	0	1	0	0
Nonbreeding male	2*†	5	3‡	1‡	1‡	2
Yearling male	0	4	0	1	1	0
Total	9	14	7	7	9	5
Unmarked (seen on screen)**	5	4	2	1	2	3
Badgers known to be unmarked††	8 ^a	4 ^b	1 ^c	1 ^d	0	3 ^e
Sex ratio (proportion male, including unmarked)	0.24	0.72	0.38	0.50	0.22	0.50

* An additional badger was removed from the analyses as it led to structural zeros.

† One (P 1995) or two (SH 1995) additional marked badgers were present in this category, but they were not seen on screen, so were excluded from the analyses.

‡ Additional badgers were not present for all of the study period, either because they were found dead (one nonbreeding male in both P 2004 and P 2005) or presumed dead as they were only seen for a maximum of 3 days and then not seen again (two nonbreeding females in P 2004 and one nonbreeding male in PO 2004).

§ Breeding male refers to males that sired cubs within their own social-group-year only.

** Estimated by the maximum number of unmarked badgers seen on screen at any one time.

†† Resident adults and yearlings known to be unmarked for all or most (one breeding male, one nonbreeding male and one nonbreeding female at SH in 1995 were not clip marked until May) of the study, from trapping records are: ^a one breeding male, one nonbreeding male and six nonbreeding females; ^b three nonbreeding males and one yearling female; ^c one nonbreeding female; ^d one nonbreeding male; and ^e one breeding male, one nonbreeding male and one breeding female. Marked badgers from neighbouring social groups were excluded from the analyses.

greatly affected by dyads in which the behaviour is performed frequently, suggesting caution should be used in its interpretation.

Finally, we calculated the steepness of each dominance hierarchy based on the directed aggression matrices, using the R package *Steepness 0.1* written by D. Leiva (Department of Methodology of the Behavioural Sciences, Faculty of Psychology, University of Barcelona, Spain) and H. de Vries (Department of Behavioural Biology, Utrecht University, The Netherlands). The package calculates a dyadic dominance index D_{ij} , in which the proportion of wins and losses are corrected for the chance occurrence of these events (de Vries et al. 2006). D_{ij} is then used to calculate the normalized David's score (DS) for each individual, with values varying between 0 and $N - 1$, where N is the number of individuals in the group (de Vries et al. 2006). Ranking the normalized DSs provides the DS rank. Regressing the DS ranks against the normalized DS values provides the slope or steepness of the hierarchy, which varies between 0 (an egalitarian hierarchy) and 1 (a despotic hierarchy). The significance of this steepness was assessed through 10 000 randomizations of the observed directed aggression matrices.

Traits correlated with rank

For those social-group-years where significant linear hierarchies were found using the directed aggression matrices, we analysed the relationship between I&S rank and four traits: sex, minimum age (considered to be 1 year if first trapped as an adult), wounding status (classified as wounded or unwounded from the presence of fresh wounds in the January and June trapping data; see Macdonald et al. 2004) and breeding status (did or did not breed, with yearlings excluded). We also analysed these four traits against the DS rank. We used Spearman rank correlations and unequal variance t tests. Zimmerman & Zumbo (1993, cited in Ruxton 2006) argued that, when carried out on ranked data, the unequal variance t test performs better than the Mann–Whitney U test when variances are unequal. This test was therefore considered preferable here. All analyses were conducted in SPSS 15 (SPSS Inc., Chicago, IL, U.S.A.).

Relatedness and directed aggression

As individuals might be expected to show lower levels of directed aggression towards relatives, we entered R into matrices for all social-group-years and Kendal's (K_r) row-wise correlations (de Vries 1993) were used to compare the resulting relatedness matrices with those for directed aggression. To assess the significance of the resulting K_r statistic we used a permutation procedure, in which the rows and columns were permuted simultaneously 10 000 times, from MatMan 1.1 (de Vries et al. 1993).

Behaviours correlated with directed aggression

Finally, we investigated whether individuals were more likely to direct aggression at partners that they allomarked more often, or whether they received more unreciprocated allogrooming from those partners to which they directed more aggression. To achieve this, we used K_r row-wise correlations to compare the matrices for directed aggression with their corresponding matrices for unreciprocated allogrooming and allomarking. We observed a total of 659 instances of directed aggression, 838 of unreciprocated allogrooming and 1476 of sequential allomarking.

RESULTS

Dominance Hierarchies

Three of the six social-group-years showed a significant degree of linearity (Table 2). Two social-group-years (P 1995 and PO 2004) showed no significant linear hierarchy while one further social-group-year (PO 2005) contained too few individuals for testing using this method (Table 2). Two of the five linearity tests were not independent, as some individuals were present in both P 2004 and P 2005. When we excluded P 2004, or P 2005, Fisher's method of combining probabilities showed an overall significant effect ($\chi^2_8 = 18.5$ or 20.6, respectively, $P < 0.02$). The frequency of directed aggression observed per h of footage analysed did not differ between groups with or without a hierarchy, although the sample size was small (unequal variance t test: $t_1 = 0.0$, $P = 1.0$, excluding either P 2004 or P 2005 to maintain independence, and PO 2005 in which no hierarchy could be tested). The sex ratio of a social-group-year did not appear to affect the presence of a hierarchy, as the social-group-years with the lowest and highest sex ratios (P 2005 and SH 1995, respectively) had significant hierarchies, whereas the two that did not have hierarchies (P 1995 and PO 2004) had intermediate sex ratios (Table 1).

DC indices for the six social-group-years were high (0.7–1.0), with a DC index of 0.84 for PO in 2005 suggesting a high degree of unidirectionality within dyads (Table 2). The number of circular triads observed was also smaller than expected in all social-group-years, except P 1995 (Table 2). The number was not greatly smaller in PO 2005 (Table 2), suggesting that its members had asymmetric relationships, although the degree of linearity within the social-group-year may be low.

The hierarchies were significantly steeper than random in five of the six social-group-years, including all three social-group-years with significantly linear hierarchies (Table 2). The steepest hierarchy was seen in P 2004, which also had the most linear hierarchy. The shallowest hierarchy was seen in the group with the least linear

Table 2
Results of the dominance hierarchy linearity and steepness analyses

	1995		2004		2005	
	P	SH	P	PO	P	PO*
Total observation time (h)	1383	1242	2444	798	3872	1491
Directed aggression events observed	8	122	164	118	198	37
Number of individuals	9	14	7	7	9	5
Linearity index (h' or h)†	0.27	0.39	0.93	0.61	0.68	—
Directional consistency index	1	0.85	0.70	0.74	0.85	0.84
Number of circular triads observed	29.25	79	1	6.75	11.5	1.75
Number of circular triads expected	21	91	8.75	8.75	21	2.5
$P_{\text{right}}‡$	0.61	0.040	0.007	0.20	0.020	—
Steepness of dominance hierarchy	0.05	0.21	0.63	0.43	0.46	0.51
P	0.41	0.0001	0.0002	0.005	0.0001	0.035

Significant results ($P < 0.05$) determined by permutation tests are shown in bold.

* Social-group-year contained too few individuals for testing the linearity of the hierarchy.

† The improved linearity index h' was used where there were unknown relationships between dyads (SH 1995, P 1995, P 2005 and PO 2004); otherwise Landau's h index was used (P 2004).

‡ P_{right} tests whether a hierarchy is significantly linear. It provides the probability that a randomly generated dominance matrix has a degree of linearity \geq the linearity in the observed dominance matrix.

hierarchy (P 1995). The smallest number of directed aggression events was observed in this group; however, the group with the second smallest number of directed aggression events observed (PO 2005) had the second steepest hierarchy (Table 2). When we removed nonindependent tests at random, Fisher's method of combining probabilities showed an overall significant effect ($\chi^2_8 = 43.9$, $P < 0.001$).

Traits Correlated with Rank

Females had significantly higher I&SI ranks than males in two social-group-years, but not in the third social-group-year for which linear hierarchies were detected (Table 3, Fig. 1). While there was no significant difference between male and female I&SI or DS rank in P 2005 (Table 3), sexually mature females did occupy the top ranks in this social-group-year, although the sexually immature female yearlings were ranked bottom (Fig. 1c). There was no significant difference between the DS ranks of males and females in the three social-group-years in which no linear hierarchy was detected (Table 3).

Age was not related to I&SI rank in any of the social-group-years, but was in one case when DS rank was analysed (Table 3).

A significant relationship between I&SI rank and breeding status was seen in only one social-group-year (Table 3). A significant result was obtained for this and one other social-group-year using DS rank (Table 3). The small sample sizes, however, were likely to have been influential. There also appears to be nonorthogonality

between sex and breeding status in these social-group-years, with only two males seen to reproduce within their own groups (Table 1). Thus any apparent relationship between rank and breeding status may well be artificial, instead reflecting the difference in rankings between males and females (Fig. 1).

Small sample size was also problematic for these analyses when we tested the relationship between rank and wounding status, with no badgers documented as wounded in 2005. No significant relationship was found between the two variables in the remaining social-group-years (Table 3).

Relatedness and Directed Aggression

The K_r statistic was negative for levels of directed aggression and relatedness in the three social-group-years that were structured according to linear dominance hierarchies, but this was significant for only P 2005 (Table 4). The remaining three social-group-years showed no significant relationship (Table 4).

Behaviours Correlated with Directed Aggression

In some social-group-years badgers were more likely to receive unreciprocated allogrooming from those individuals to which they directed more aggression, but not in all. Positive K_r statistics for these two behaviours were seen in four social-group-years, although these were significant for only P 1995 and PO 2004 (Table 4). Five of the six social-group-years had a positive K_r statistic for levels of directed aggression and sequential allomarking. This relationship was,

Table 3

Unequal variance t tests of rank, obtained from the linear hierarchies (I&SI rank) and from David's scores (DS rank), according to gender, reproductive status (in which yearlings were excluded) and wounding status and Spearman rank correlations of rank against age

	1995		2004		2005	
	P	SH	P	PO	P	PO
N_{males}	2	10	3	3	2	2
N_{females}	7	4	4	4	7	3
I&SI rank and gender	t	—	4	—	1.6	—
	df	—	5	—	7	—
	P	—	<0.001	0.01	—	0.16
DS rank and gender	t	0.0	2.4	1.0	1.6	0.0
	df	1	5	3	7	3
	P	1.00	<0.001	0.07	0.39	0.16
$N_{\text{nonbreeders}}$	5	6	5	4	2	4
N_{breeders}	4	3	2	2	4	1
I&SI rank and breeding status	t	—	4.0	—	2.9	—
	df	—	5	—	2	—
	P	—	0.012	—	0.11	—
DS rank and breeding status	t	0.7	4.0	−0.2	3.7	1.7*
	df	7	5	1	4	3
	P	0.49	0.25	0.012	0.90	0.024
$N_{\text{nonwounded}}$	6	8	5	5	9	5
N_{wounded}	3	6	2	2	0	0
I&SI rank and wounding status	t	—	−1.8	—	—	—
	df	—	11	—	—	—
	P	—	0.81	0.13	—	—
DS rank and wounding status	t	0.4	−1.2	−1.2	—	—
	df	3	11	2	2	—
	P	0.69	0.42	0.36	0.36	—
I&SI rank and age	r_s	—	−0.28	0.22	—	−0.63
	N	—	14	7	—	9
	P	—	0.33	0.63	—	0.07
DS rank and age	r_s	0.07	−0.47	0.37	−0.02	−0.70
	N	9	14	7	7	9
	P	0.85	0.09	0.41	0.97	0.037

Significant results are shown in bold. A dash indicates a test was not run because of a nonlinear hierarchy or no data.

* Equal variance t test used.

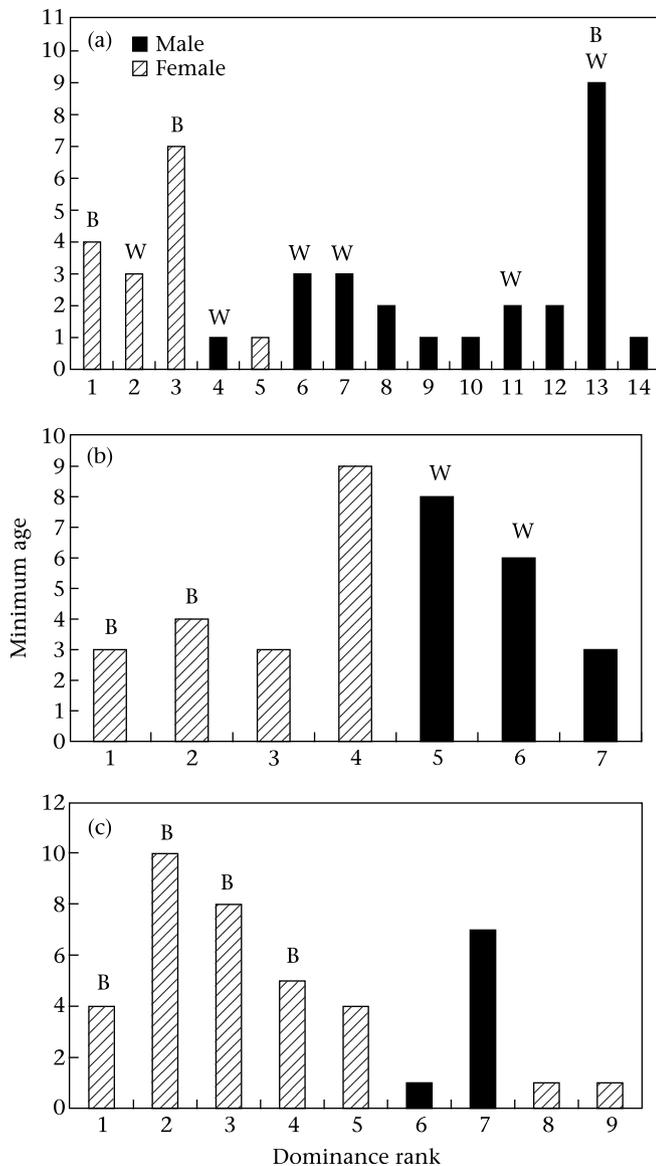


Figure 1. The age (years), sex, breeding status and wounding status of badgers of each I&SI rank in the dominance hierarchy in (a) SH 1995, (b) P 2004 and (c) P 2005. A rank of 1 is the highest rank. Ages are a minimum (with an individual considered to be at least 1 year old if first trapped as an adult). Individuals that successfully bred in each social-group-year are indicated by a B, wounded individuals by a W.

however, significant for only one group (P 2005), showing that badgers more frequently allomarked individuals towards which they directed more aggression in this social-group-year (Table 4).

DISCUSSION

Although dominance hierarchies are often alluded to in studies of the European badger (Woodroffe & Macdonald 1995; Revilla & Palomares 2002), empirical evidence of such hierarchies has proved elusive (Macdonald et al. 2002). Here we have presented evidence of significant linear dominance hierarchies in three of six social-group-years, or in two of three independent social groups, as determined from analyses of directed aggression around sett entrances. Furthermore, hierarchies were significantly steeper than random in five of six social-group-years. The hierarchies were detected during the mating and cub-rearing season, and further work is required to assess whether dominance structures occur at other times and what factors, such as competition over access to breeding sites, determine where (and when) hierarchies arise.

Table 4

Results of the Kendall's (K_r) row-wise correlations between directed aggression and relatedness, unreciprocated allogrooming, and sequential allomarking

		1995		2004		2005	
		P	SH	P	PO	P	PO
Relatedness	K_r	3	−93	−19	17	−37	3
	P_{left}	0.69	0.07	0.11	0.92	0.039	0.65
Unreciprocated allogrooming	K_r	21	88	−22	27	0	12
	N	26	125	164	103	332	81
	P_{right}	0.010	0.054	0.92	0.046	0.51	0.07
Sequential allomarking	K_r	7	57	20	25	55	−2
	N	44	367	292	207	401	142
	P_{right}	0.25	0.12	0.18	0.08	0.044	0.65

Significant results ($P_{left} < 0.05$; $P_{right} < 0.05$) determined by permutation tests are shown in bold. N indicates the number of behavioural events observed.

Three of the six social-group-years showed significant linear hierarchies. The index h' varied from 0.39 to 0.93, which is slightly higher than in bighorn sheep (0.33–0.57, Pelletier & Festa-Bianchet 2006). Variation in h' may be caused by differences in the number of individuals on which they are based (Mesterton-Gibbons & Dugatkin 1995), or differences in sampling effort (i.e. total observation time; Table 2) and the number of unknown relationships (Galimberti et al. 2003).

Steepness values also varied between social-group-years, ranging from 0.05 to 0.63. The shallowest hierarchy (P 1995) was not significantly steeper than random, and was not linear, possibly suggesting egalitarianism. It seems more likely, however, that the low frequency of aggressive interactions had an effect (Galimberti et al. 2003), with a high proportion of unknown relationships, and the exclusion of at least five unmarked individuals and two marked individuals (owing to structural zeros) further decreasing the likelihood of detecting a hierarchy. Although the degree of linearity was not significant in PO 2004 and could not be tested in PO 2005, both had significant mid-range steepness values, similar to those seen in female bonobos, *Pan paniscus* (Stevens et al. 2007), and so could be described as weakly or semidespotic. PO was only identified as a separate group from P in 2003 and so social dynamics might not have been well established. The lower steepness and directional consistency and higher frequency of aggression in PO 2004 may suggest that group members showed less acceptance of the hierarchy in this year than in 2005, supporting this idea.

Overall the small number of social-group-years analysed, the nonindependence of some social-group-years, and the small number of individuals in some of these social-group-years limited this study. Future analyses are required on a larger sample size to gain a more detailed picture of sociality within badger groups.

Traits Correlated with Rank

The ranks of individuals were not consistent between years (e.g. Fig. 1b, c). For those social-group-years with linear hierarchies, there was a striking difference in dominance rankings between the sexes. Females generally had a high dominance rank indicating that they initiated the most and received the least aggression, whereas males generally had a low dominance rank indicating the reverse. Species in which females are dominant or equal in status to males are generally rare in mammals (Kappeler 2000) yet the older, sexually mature female badgers were consistently ranked above males in these three social-group-years (although immature female yearlings were not; see Fig. 1). Macdonald et al. (2002) suggested that the high competitive ability of female European badgers may result from the high energetic costs of raising young (resulting in a payoff asymmetry). Competition for breeding status appears to be high in female badgers within social groups; the percentage of females of reproductive age that fail to breed is estimated at 48–70% (da Silva et al.

1994; Carpenter et al. 2005; Dugdale et al. 2007). Furthermore, there is significant reproductive skew within badger social groups (Dugdale et al. 2008), with female–female competition likely to be higher than that between males because of the high level of extragroup paternity, which was not considered in these skew calculations.

Overall, there was no significant relationship between rank and breeding status; however, a general pattern that rank may be linked to female breeding status was apparent (Fig. 1 and breeding females had the highest DS rank in both years in PO). Given the small numbers of nonbreeding but sexually mature females in these groups, a larger sample size is required to investigate whether this relationship exists. Male–male competition for breeding opportunities may be relatively low because of the promiscuous mounting system (Johnson 2001; Dugdale 2007), with 50% of cubs sired by extragroup males (Carpenter et al. 2005; Dugdale et al. 2007). This contrasts with polygynous, more sexually dimorphic species, such as ungulates, where there is intense competition between males, with high-ranking individuals securing more matings than males of a lower rank (e.g. reindeer, *Rangifer tarandus*: Hirotoni 1994; mountain goats: Mainguy et al. 2008; bighorn rams: Pelletier & Festa-Bianchet 2006).

There was no relationship between dominance rank and the likelihood of receiving bite wounds, although few wounds were recorded overall, hindering any firm conclusion. Overall, age was not related to dominance rank, either within groups (Spearman rank correlations) or within the sexes (small samples hindered statistical testing, but see Fig. 1). The influence on dominance status of size and weight (McElligott et al. 2001; Holand et al. 2004) could not be tested because of limited data.

Relatedness and Directed Aggression

Negative K_r statistics for levels of directed aggression and relatedness values, found within social-group-years with linear hierarchies, suggested that individuals direct less aggression towards closer relatives; however, this was significant in only one social-group-year. Belisle & Chapais (2001) found that female Japanese macaques were more tolerant of co-feeding by close relatives. Owing to natal philopatry and restricted dispersal, however, relatedness levels between badger group members are high (Dugdale et al. 2008). Any potential fitness benefit that badgers derive from reducing aggression to closer kin may therefore be negligible.

Behaviours Correlated with Directed Aggression

Positive K_r statistics for directed aggression and unreciprocated allogrooming were seen in four social-group-years, although significantly so only in two. Badgers were, therefore, more likely to be allogroomed by individuals to which they directed greater aggression, as seen in meerkats (Kutsukake & Clutton-Brock 2006). Unreciprocated allogrooming appears to follow a Tit-for-Tat strategy in badgers, with events usually terminating within 1.2 s (Macdonald et al. 2000). Recording the duration of unreciprocated allogrooming events may strengthen the relationship that we observed. When unreciprocated allogrooming is not quickly terminated, it may reflect a form of tolerance payment, with individuals attempting to appease dominants. In a period where aggression was lower and the dominance gradient shallower in a troop of female chacma baboons, *Papio cynocephalus ursinus*, dominants no longer appeared to attract grooming from subordinates, and instead reciprocal exchange of grooming increased (Barrett et al. 2002). Comparing reciprocated and unreciprocated allogrooming during periods when dominance hierarchies may and may not be well established would enable a test of this.

The relationship between directed aggression and sequential allomarking was less variable between groups: a positive K_r statistic

was seen in five social-group-years (significantly so in P 2005), suggesting that these badgers more frequently allomark individuals to whom they direct more aggression. Buesching et al. (2003) suggested that, in addition to distributing a 'group smell', sequential allomarking advertises individual-specific information, such as social status. Further analyses are required, however, before any broad conclusions may be reached about the motivational strategies associated with sequential allomarking.

A full understanding of the social system of the European badger remains incomplete. In this study we have presented evidence of breeding female-led dominance in the vicinity of sett entrances within badger social groups during the mating and cub-rearing season. It is possible that these hierarchies are context dependent and are not always present. It remains unclear what factors may promote dominance, or what benefits/costs individuals may receive because of their dominance status. The variation in patterns of social interactions observed between social groups suggests that dynamic approaches to future studies will be required.

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APPENDIX

The following behaviours, along with the identity of each actor and receiver, were recorded.

Directed Aggression

This dyadic interaction occurs when an actor initiates aggression at a receiver. Aggression (bite, nip or charge) is only shown by the actor; the receiver does not reciprocate the aggression. Directed aggression ends when the dyad move at least two body lengths apart for at least 20 s.

Unreciprocated Allogrooming

Allogrooming events are described by Macdonald et al. (2000). Unreciprocated allogrooming occurs when one group member allogrooms another, without the receiver reciprocating. The dyadic interaction terminates when the initiator stops allogrooming and the dyad physically move apart.

Sequential Allomarking

Sequential allomarking occurs when the actor lifts its tail and presses its anal region onto the body of the receiver (Buesching et al. 2003).

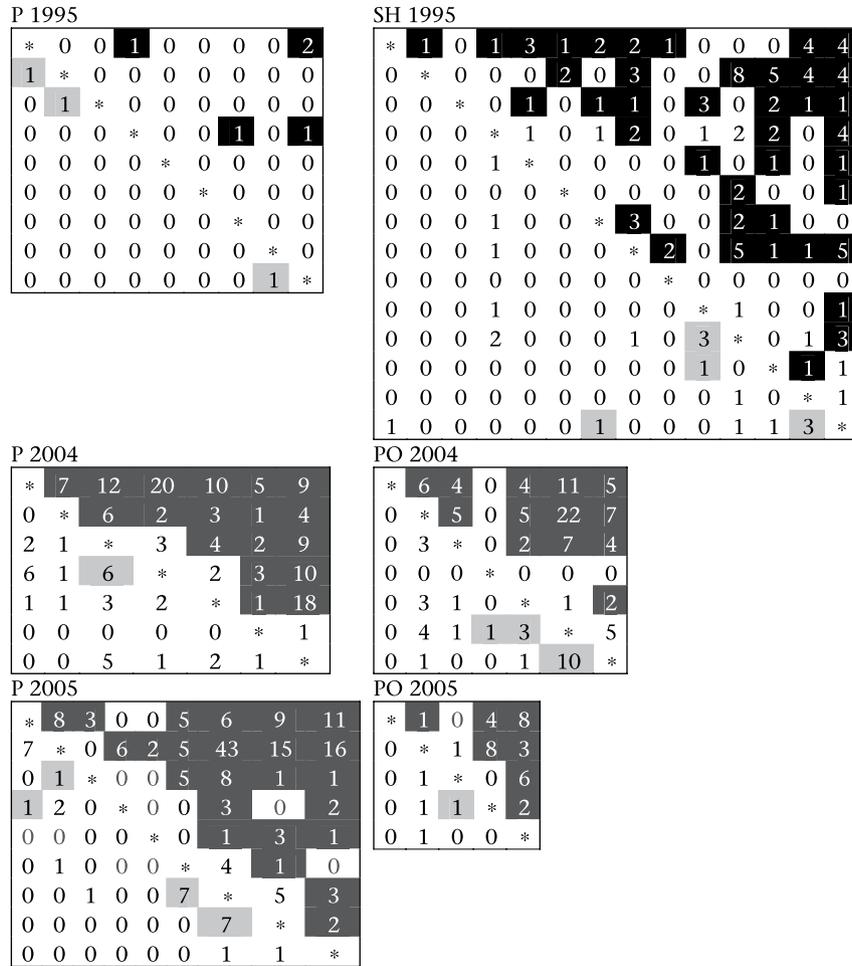


Figure A1. Matrices of the number of directed aggression events observed between dyads in each of the six social-group-years. Rows show individuals that received directed aggression and columns individuals that initiated the directed aggression. Cells in each matrix are colour coded to show individuals in each dyad that directed the most aggression in that dyad and had the highest (black cells) or lowest (grey cells) DS rank. White cells indicate dyads in which no directed aggression or an equal number of directed aggression events were observed, or they indicate an individual in a dyad that directed the least aggression.