

**Do social groups of European badgers *Meles meles*
exhibit dominance hierarchies?⁷**

⁷This appendix has been published as: Hewitt S, Macdonald DW, Dugdale HL (2009). 'Context-dependent linear dominance hierarchies in social groups of European badgers *Meles meles*', *Animal Behaviour* 77(1), 161-169. doi:10.1016/j.anbehav.2008.09.022.

A2.1 Abstract

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. Here, infra-red CCTV footage, collected over three years of filming in Wytham Woods, Oxfordshire, was analyzed to test whether social groups of European badgers display linear hierarchies. Analysis of aggressive dyadic interactions between group members revealed that three out of six social-group-years were structured according to significantly linear dominance relationships. In these three groups, there was an effect of sex on dominance rank, with females gaining significantly higher rank than males in two of them. There was no effect of age on rank, however, in any of the groups, nor did social rank appear to affect the likelihood of an individual being wounded, or an individual's reproductive success. There was some evidence of a negative correlation between levels of aggression and increasing relatedness between group members. Positive correlations between levels of aggression and unreciprocated allogrooming, and aggression and sequential allomarking, were also found, but were not consistent across all groups. The European badger is thought to represent an early stage of social evolution, where social structures may not yet be well established. We further suggest that dominance structures may be situation dependent, with hierarchies arising in only those groups where (and when) competition is highest.

A2.2 Introduction

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; Koenig et al., 1992). 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, social behavior may then evolve, which further enhances these original benefits (Alexander, 1974). However, within a group certain individuals may exert disproportionate influence over others and as such egalitarian societies are thought to be rare. 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) 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.”

Societies may therefore display strong linear hierarchies, where the costs and benefits of group living are divided unequally between group members; with dominant individuals gaining the majority of the benefits (such as increased access to food or mates), while subordinate individuals suffer the majority of the costs (such as decreased access to those same resources). 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 society and have been demonstrated in, for example, brown hyenas *Hyaena brunnea* (Owens & Owens, 1996) and patas monkeys *Cercopithecus patas* (Goldman & Loy, 1997). Hierarchies may also be limited to one sex within a species, as is the case in male capybaras *Hydrochaeris hydrochaeris* (Herrera & Macdonald, 1993), female mountain goats *Oreamnos americanus* (Cote, 2000) and bighorn rams *Ovis canadensis* (Pelletier & Festa-Bianchet, 2006). Here, we investigate whether evidence can be found of dominance hierarchies within social groups of the European badger *Meles meles*.

European badgers display marked intra-specific variation in their behavioral ecology across the species' extensive geographical range (Johnson et al., 2002). In lowland Britain they live at high densities, 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, with low dispersal rates among adults (da Silva et al., 1994; 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 (Kruuk, 1989). 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, 2000). This, together with the fact that group living is rare in mustelids, has led to the suggestion that the European badger is at an early stage of social evolution (Kruuk, 1989; da Silva *et al.*, 1994).

The degree of sociality found in European badgers also varies across their geographic range, with individuals in continental Europe commonly living alone or in pairs, while

within the British Isles badgers are more typically group living (Woodroffe & Macdonald, 1993; Johnson *et al.*, 2000). Kruuk (1978b) first proposed that the Resource Dispersion Hypothesis (Macdonald, 1983) explained why badgers form groups in some areas (Woodroffe & Macdonald, 1992). The RDH 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 variability in sociality in this species has been explored (Johnson *et al.*, 2002); the effect of behavioral factors is 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. Furthermore, understanding whether badger groups exhibit dominance hierarchies is of relevance, as, firstly, it remains uncertain why badgers form groups to begin with (Woodroffe & Macdonald, 1992), and also, more widely, because it may offer important insights into the evolution of mammalian societies.

This study examines behavioral data, collected over three years of filming of badgers in Wytham Woods, Oxfordshire, to investigate: (a) through analysis of aggressive dyadic interactions between group members, whether evidence of linear hierarchies can be found in social groups in this area; (b) whether the sex and age of an individual (demonstrated to be related to dominance status in some other species) are correlated

with rank in these social groups; (c) whether high ranking individuals gain any benefit (in the form of increased reproductive success) and low ranking group members suffer a cost (in the form of increased bite wounds) due to their position in the hierarchy; (d) whether the degree of aggression displayed by badgers is correlated with relatedness between individuals; and, (e) whether patterns of aggressive behavior in these badgers are reflected in other behaviors, in order to assess wider behavioral strategies within these social groups.

A2.3 Methods

A2.3.1 Study site

This study was conducted in Wytham Woods, an area of mostly deciduous woodland 5km north-west 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; Delahay *et al.*, 2000).

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 part of Pasticks but bait marking and trapping records revealed that it had become a separate social group by 2003.

A2.3.2 Data collection

Badgers were trapped at least four times a year, generally around January, June, August and November (Macdonald & Newman, 2002). No trapping took place between February to April, to avoid disturbing the badgers during the final trimester of gestation and in the period that cubs are highly dependent on their mothers. Individuals were caught using swing-door box-traps that were baited with peanuts (Tuytens et al., 1999).

Once caught, badgers were transferred to a holding cage and transported to a processing area. They were then sedated by an intra-muscular injection of approximately 0.2 ml Ketamine hydrochloride (Vetlar; Pharmacia and Upjohns, Crawley, UK) 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 were collected from each individual for DNA analysis.

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

In this study, we analyzed video footage from three 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 behavior 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.

A2.3.3 Behavioral analysis

We analyzed a total of 615 nights of video footage, from the period 1st February to 31st May each year. Cubs are born underground around February, and breeding females immediately enter a period of estrus post-partum (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 estrus in late summer / autumn. However, not all males remain fertile for this second period (reviewed in Appendix 1). As males may compete for access to females, while females compete for breeding status (Woodroffe & Macdonald, 1995b), dominance hierarchies may therefore be expected to be most apparent during the spring period considered in this study.

Each night's footage was analyzed according to a strict ethogram with random tape checks between observers to confirm consistency. Behavior was recorded on an ACCESS database (Microsoft Corporation, Redmond, WA), along with the identity of the badgers involved (as deduced from clip-marks). In this study we consider three behaviors; directed aggression, unreciprocated allogrooming, and sequential

allomarking. All are clear unidirectional behaviors, with one badger initiating the behavior, and the other receiving it without reciprocating.

A2.3.4 Genetic analysis

DNA was extracted 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, UK). Individuals were genotyped for 22 microsatellite loci and amplified using methods described in Chapter 2.

The Queller and Goodnight (1989) index of relatedness (R) was estimated for each badger dyad in this study using RELATEDNESS 5.0.8 (see Chapter 3 for details). R ranges from -1 (unrelated) to +1 (identical). Due to natal philopatry, group members may be closely related (Cheeseman et al., 1988). Parentage of cubs was therefore determined by assigning both or one parent through a likelihood-based approach using the program CERVUS 3.0.1.8 (Kalinowski et al., 2007) beta test version, which takes into account the presence of relatives within the group. Cubs were assigned to social groups based on the location in which they were trapped, and candidate parents selected using biological rules (Chapter 2).

The breeding status of each group member was obtained from the parentage analysis, with badgers that had bred within their own social group classed as reproductively active in that year. Although males may father cubs outside their own group, such instances were excluded from analysis, as such reproduction is outside the confines of

any dominance hierarchy. Group members were divided into three categories; breeding, non-breeding or not capable of breeding (i.e. yearlings).

A2.3.5 Statistical analysis

We constructed actor-receiver matrices (Macdonald et al., 2000) for all instances of directed aggression, unreciprocated allogrooming and sequential allomarking that were recorded within each social group, in each year of filming. All matrices were square, with an undefined diagonal. 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 is detected within a minute of the last badger leaving the screen.

Only badgers that were present, and identifiable, for the entire study period each year were included in the analyses. Any unmarked individuals (those that eluded trapping or whose clip-mark was lost through molting) 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 individuals were excluded from the matrices for P 1995 as their presence led to ‘structural zeros’ (where two individuals were never observed together and so did not have the opportunity to perform the behavior). As such values would invalidate the matrix analyses as currently performed, the decision was made to exclude these badgers.

A2.3.5.1 *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. 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 rank order for each group.

As the 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 group when using either the h or h' index (Appleby, 1983). However, it has been suggested by some authors (e.g. Isbell & Young, 2002) 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 is calculated across all dyads as: $(H-L) / (H+L)$, where H is the number of times the behavior was performed in the main direction within each dyad and L is the number of times the behavior occurred in the opposite direction. A high value therefore indicates that, for those individuals observed to interact multiple times, exchanges are highly unidirectional. The transitivity of relationships across dyads is measured as the number of circular triads observed within a social group. A circular triad occurs when, for any three individuals in a

social group, 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, with a smaller than expected number of observed triads thus indicating non-random relationships, and the strength of linearity in the group increasing 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, it should be noted that the former value can be greatly affected by dyads in which the behavior is performed frequently, suggesting caution should be used in its interpretation.

A2.3.5.2 Correlates of rank

For those social-group-years where significant linear hierarchies were found, we analyzed the relationship between dominance rank and minimum age (considered to be one 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) using Spearman's Rank correlations and unequal variance *t*-tests. Zimmerman and Zumbo (1993 – cited in Ruxton, 2006) argue 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 the program MINITAB 14 (Minitab Inc., State College, PA, USA).

A2.3.5.3 Correlates of aggression

As individuals might be expected to show lower levels of 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 a permutation procedure, in which the rows and columns were permuted simultaneously 10,000 times, was employed using MATMAN 1.1.

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 were more aggressive. 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, compared to 838 instances of unreciprocated allogrooming and 1476 of sequential allomarking.

A2.4 Results

A2.4.1 Analysis of dominance

Of the six social-group-years investigated, three showed a significant degree of linearity (SH 1995: $h' = 0.393$, $df = 13$, $P_{\text{right}} < 0.05$; P 2004: $h = 0.929$, $df = 6$, $P_{\text{right}} < 0.05$; P 2005: $h' = 0.683$, $df = 8$, $P_{\text{right}} < 0.05$). Two groups displayed no significant hierarchy (P 1995: $h' = 0.286$, $df = 7$, $P_{\text{right}} = 0.635$, PO 2004 - $h' = 0.607$, $df = 6$, $P_{\text{right}} = 0.201$), while one further group (PO 2005) contained too few individuals for testing using this method.

DC indices for the six groups studied here were high (ranging from 0.7 to 1), with a DC index of 0.84 for PO in 2005 suggesting a high degree of unidirectionality within dyads. The number of circular triads observed were also lower than expected in all groups except P 1995, although not greatly so in PO 2005 (observed = 1.75, expected = 2.5). This suggests that members of this social group year have asymmetric relationships, although the degree of linearity within the group may be low.

A2.4.2 Correlates of rank

Females had significantly higher dominance ranks than males in two of the three social-group-years for which hierarchies were detected (unequal variance t -tests: SH 1995: $t' = 5.02$, $N_1 = 10$, $N_2 = 4$, $df = 10$, $P = 0.001$; P 2004: $t' = 4.04$, $N_1 = 3$, $N_2 = 4$, $df = 4$, $P = 0.016$; Figure A2.1). While there was no significant difference between male and female rank in P 2005 ($t' = 1.56$, $N_1 = 2$, $N_2 = 7$, $df = 6$, $P = 0.170$), sexually mature females did occupy the top ranks in this group, although the sexually

immature female yearlings were ranked bottom (Figure A2.1b). Age, however, was not related to rank in any of the three social-group-years (Spearman's Rank correlations: SH 1995: $r_s = 0.336$, $N = 14$, $P = 0.240$; P 2004: $r_s = -0.222$, $N = 7$, $P = 0.632$; P 2005: $r_s = 0.630$, $N = 9$, $P = 0.069$).

A significant relationship between rank and breeding status was seen in one social group year (unequal variance *t*-tests: SH 1995: $t' = -0.28$, $N_1 = 3$, $N_2 = 5$, $df = 2$, $P = 0.803$; P 2004: $t' = -4.04$, $N_1 = 2$, $N_2 = 5$, $df = 4$, $P = 0.016$; P 2005: $t' = -2.94$, $N_1 = 4$, $N_2 = 2$, $df = 1$, $P = 0.209$). However, the small sample sizes, and the low rank of the sole breeding male in SH, were likely to have been influential. There would appear to be non-orthogonality between sex and breeding status in these social groups, with only one male seen to reproduce within his own group (in SH 1995). Thus any apparent relationship between rank and breeding status may well be artificial, instead reflecting the difference in rankings between males and females (Figure A2.1).

Small sample size was also a problem for these analyses when testing the relationship between rank and wounding status, with no badgers documented as carrying wounds during the period of this study in P 2005. No significant relationship was found between the two variables in the remaining two social-group-years (unequal variance *t*-tests: SH 1995: $t' = -0.25$, $N_1 = 6$, $N_2 = 8$, $df = 11$, $P = 0.806$; P 2004: $t' = 1.83$, $N_1 = 2$, $N_2 = 5$, $df = 4$, $P = 0.140$).

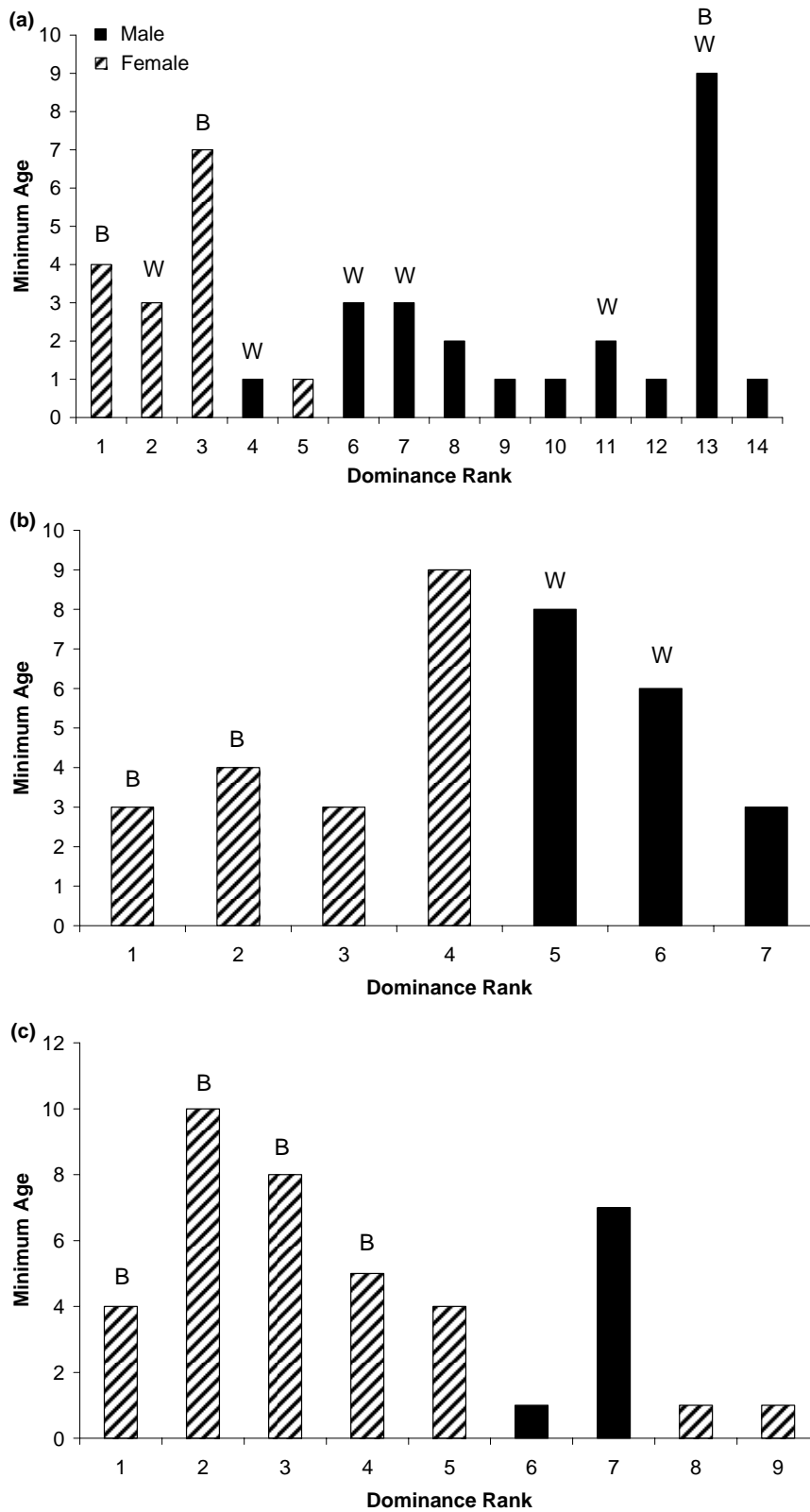


Figure A2.1 The age (years), sex, breeding status and wounding status of badgers of each dominance rank in: (a) SH 1995; (b) P 2004; and (c) P 2005. A rank of 1 is the highest rank. Individuals that successfully bred in each social group year are indicated by a B, wounded individuals by a W.

A2.4.3 Correlates of aggression

There was a negative correlation between levels of directed aggression and relatedness in the three social-group-years that were structured according to linear dominance hierarchies, although this was significant for only P 2005 (SH 1995: $K_r = -93$, $P_{\text{left}} = 0.070$; P 2004: $K_r = -19$, $P_{\text{left}} = 0.111$; P 2005: $K_r = -37$, $P_{\text{left}} < 0.05$). The remaining three social-group-years showed no evidence of this relationship (P 1995: $K_r = 1$, $P_{\text{left}} = 0.616$; PO 2004: $K_r = 17$, $P_{\text{left}} = 0.917$; PO 2005: $K_r = 3$, $P_{\text{left}} = 0.652$).

There was some evidence that badgers were more likely to receive unreciprocated allogrooming from those individuals to which they were more aggressive. Positive correlations between the two behaviors were seen in four social group years, although these were significant for only P 1995 and PO 2004 (SH 1995: $K_r = 23$, $P_{\text{right}} = 0.2988$; P 1995: $K_r = 22$, $P_{\text{right}} < 0.01$; PO 2004: $K_r = 27$, $P_{\text{right}} < 0.05$; P 2004: $K_r = -22$, $P_{\text{right}} = 0.923$; PO 2005: $K_r = 12$, $P_{\text{right}} = 0.072$; P 2005: $K_r = 0$, $P_{\text{right}} = 0.5116$). Similarly, four of the six social-group-years showed evidence of a positive correlation between levels of directed aggression and sequential allomarking, suggesting that badgers more frequently allomark individuals towards which they are more aggressive. However, this relationship was significant for only one group; P 2005 (SH 1995: $K_r = -3$, $P_{\text{right}} = 0.527$; P 1995: $K_r = 7$, $P_{\text{right}} = 0.219$; PO 2004: $K_r = 25$, $P_{\text{right}} = 0.076$; P 2004: $K_r = 20$, $P_{\text{right}} = 0.178$; PO 2005: $K_r = -2$, $P_{\text{right}} = 0.649$; P 2005: $K_r = 55$, $P_{\text{right}} < 0.01$).

A2.5 Discussion

Although dominance hierarchies are often alluded to in studies of the European badger (Kruuk, 1989; Woodroffe & Macdonald, 1995b; Revilla & Palomares, 2002), empirical evidence of such hierarchies has to date proved elusive (Macdonald et al., 2002). European badgers do not seem to gain from many of the benefits often suggested to arise from group living, such as greater hunting efficiency or cooperative defense (Kruuk, 1989), although benefits from allogrooming have been established (Johnson et al., 2004). This lack of cooperation and competition between group members may explain the apparent lack of dominance hierarchies previously found in social groups. Here we present evidence of significant linear hierarchies in social groups from southern England, as determined from analysis of aggressive interactions in the vicinity of sett entrances. The hierarchies were detected during the mating and cub rearing season, suggesting that dominance structures may be situation dependant, with hierarchies arising where (and when) competition is highest.

Of the six social-group-years studied, half exhibited significant linear hierarchies. Another (PO 2005) showed evidence of asymmetric relationships, with a high degree of unidirectionality in aggressive behavior within dyads, but, due to small group size, it was not possible to test for linearity within this group. Of the three groups found to display significant linearity, the h' value for SH 1995 was somewhat low. This may be due to the number of individuals in this group, as models predict that linearity will decrease with group size. Furthermore, obtaining high values of linearity is problematic in groups of more than around nine individuals (Mesterton-Gibbons & Dugatkin, 1995). However, there was no evidence of linear dominance hierarchies in two of the social-group-years studied here. This may suggest that different groups

display different social structures. Of the groups studied, PO contained the fewest individuals (in both years); thus, competition in this social group may be lower, with less opportunity for individuals to assert dominance. This social group was also only identified as a separate group from P in 2003 and so social dynamics may not yet have been well established. For P 1995, however, it seems likely that the relatively low frequency of interactions between group members had an effect, with a high proportion of unknown relationships, and the further exclusion of two individuals due to structural zeros, making it difficult to detect any evidence of a hierarchy. In addition, an unusually high number of unmarked individuals were observed within this social group, with a maximum of five unmarked badgers seen on screen together. As unmarked individuals could not be included in the analysis, important interactions with additional group members were potentially missed, decreasing the likelihood of detecting any hierarchy even further.

A2.5.1 Correlates of rank

For those social-group-years in which linear hierarchies were seen, a further particularly striking finding of this study was the clear difference in dominance rankings between males and females. 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 all social groups found to have hierarchies (although the same did not hold for immature female yearlings; see Figure A2.1). Macdonald et al. (2002) suggest that the high competitive ability of female European badgers may result from the high energetic costs of raising young (resulting in a payoff asymmetry), or from their potential to withhold mating

opportunities from males. Additionally, intra-sexual competition for breeding opportunities may limit competitive asymmetries in this species. Competition for breeding status appears to be high in female badgers within social groups, with da Silva et al. (1994) finding that at least 48% of females of reproductive age failed to breed within Wytham Woods, while the number was estimated to be as high as 69% in Chapter 2. Additionally there is significant reproductive skew within badger social groups (Chapter 3).

One resource for which females may compete is breeding dens (Kruuk, 1989; Stewart et al., 1999) and it has been suggested that females may monopolize such areas during cub rearing (Cresswell et al., 1992). Females may therefore display territorial behavior around sett entrances, providing an explanation for the high dominance rankings of females of reproductive age seen here. The increased aggression observed in these females may be explained both by competition for the resource in question, and due to the risk of infanticide by other group members. Females that have bred successfully will fight to maintain their hold on breeding space and to protect their cubs, while those females who have not bred successfully in the current year will compete to obtain breeding space for future seasons.

Overall there appears to be no relationship between female dominance rank and reproductive status in this study. Although only the two highest ranking females reproduced in P 2004, suggesting that social rank may be linked to reproductive success in this group, only one reproductively active female (out of five) failed to breed in P 2005. Similarly, the top and third ranking of three sexually mature females in SH 1995 successfully raised cubs; again suggesting no relationship. Previous

studies of this population have indicated that the females that breed (or fail to breed) in one year will not necessarily do the same the next year (da Silva *et al.*, 1994; Woodroffe & Macdonald, 1995b), although they do have a greater probability of breeding in the following year (Chapter 4). It is thought that resource availability plays a key role, with da Silva *et al.* (1994) observing that in areas of high food availability several females may raise cubs within a group, and that there was a trend for the proportion of females that breed to decline with increased group size. It is likely that it is the availability of food in autumn that is important, with females that are heavier at this time more likely to successfully raise cubs the next year, due to their reliance on fat reserves during gestation and early lactation (Cheeseman *et al.*, 1987; Woodroffe & Macdonald, 1995a; Dugdale *et al.*, 2003).

Where though, do males fit in? Males may be expected to compete for access to females, with dominant males securing more mating opportunities, as seen in capybara (Herrera & Macdonald, 1993), and the brown lemming *Lemmus trimucronatus* (Huck & Banks, 1982). However, females have been observed to mate with multiple males during a single estrus (Johnson, 2001), and extra-group paternity is common (Carpenter *et al.*, 2005), with approximately 50% of cubs in Wytham sired by extra-group males (Chapter 2). Three of the identifiable males included in this study sired cubs outside of their own group (in SH 1995; rank 6 / 14, P 2004; rank 7 / 7, and in P 1995; unranked), and four males sired a cub within their own social group (two in P 1995; unranked, one in SH 1995; rank 13 / 14 and one in PO 2004; unranked). The SH male was the oldest male in this group (9 years) but the second lowest ranking (rank 13), suggesting that for this individual at least, dominance rank had little effect on reproductive success. Although we observed some instances of

fighting breaking out over females on the video footage, and males were sometimes seen to harass mounted males (presumably in an attempt to break up the mating pair and gain access to the female themselves), competition between males may be relatively low in this context.

The effect of dominance ranking on reproductive status therefore remains uncertain in this study. There would also appear to be no relationship between dominance rank and the likelihood of receiving bite wounds in these social groups, although few wounds were recorded overall, again hindering any firm conclusion. However, the patterns of wounding seem to provide support for the findings of Macdonald *et al.* (2004) that bite wounds are more likely for males and that wounds are more common in larger groups (see Figure A2.1). Dominance rank would seem to be inconsistent between years for those individuals that were present at P in both 2004 and 2005, although the introduction and loss of several individuals in the second year may have affected social dynamics. Age does not appear to be related to dominance rank, either within groups as a whole (as shown by the Spearman's rank correlations for each social group) or within the sexes (not tested for statistical significance due to small sample sizes but see Figure A2.1). The influence on dominance status of size / weight (McElligott *et al.*, 2001; Holand *et al.*, 2004) could not be tested in this study because badgers undergo marked weight changes over the seasons (Kruuk & Parish, 1983); so the weights of badgers caught at one trapping event cannot be justifiably compared with the weights of those caught at another. This factor therefore remains to be considered.

A2.5.2 Correlates of aggression

There would appear to be some evidence that individuals are less aggressive towards closer relatives, with negative correlations between levels of aggression and relatedness values found within those social groups which displayed linear hierarchies. Belisle and Chapais (2001) found that female Japanese macaques *Macaca fuscata* were more tolerant of co-feeding by close relatives, with the aggression levels of dominant females towards subordinate females decreasing with increasing degree of kinship. Due to natal philopatry and restricted dispersal, however, relatedness levels between group members in these badger social groups are high and one third of group members are parent–offspring or full-siblings (Chapter 3). Any potential fitness benefit badgers derive from reducing aggression to closer kin may therefore be negligible.

Positive correlations between aggression and unreciprocated allogrooming were seen for four of the six groups, although only significantly so in two. This suggests that badgers in these groups are more likely to be groomed by individuals to which they direct greater aggression, a result that has also been observed in meerkats *Suricata suricatta* (Kutsukake & Clutton-Brock, 2006). Unreciprocated allogrooming may be considered costly to the actor (Johnson et al., 2004) and so may reflect a form of tolerance payment, with individuals attempting to appease dominants. However, if this is the case in badger social groups, it might be expected that the relationship between aggression and unreciprocated allogrooming should be strongest in those groups for which hierarchies were found, and weak or non-existent in those groups without hierarchies. Such a pattern was observed in female chacma baboons *Papio cynocephalus ursinus* (Barrett et al., 2002). In a period where aggression was lower in

the troop and the dominance gradient appeared to be shallower, dominants no longer appeared to attract grooming from subordinates, and instead reciprocal exchange of grooming increased. This was not reflected in the badger social groups studied here. Although reciprocated allogrooming between badgers has not been considered in this study, it would seem that the motivation behind unreciprocated grooming behavior in these social groups is unclear.

The relationship between aggression and sequential allomarking also seems to vary between groups. However a positive correlation was again seen in four groups (significantly so in P 2005), suggesting that these badgers more frequently allomark individuals to which they are more aggressive. Buesching et al. (2003) found that sequential allomarking in badgers was related to sex and age, with males marking more than females and yearlings and sub-adults marking the most frequently. They therefore suggest that, in addition to distributing a “group-smell”, which helps individuals to distinguish between group members and outsiders, this type of allomarking also advertises individual-specific information. It is possible that sequential allomarking may serve as a means of ‘reinforcing’ aggression, with individuals following aggressive acts with sequential allomarking and perhaps also conveying information on social status in the process. However, the results seen here again do not allow any broad conclusions about motivational strategies associated with this behavior.

The European badger is thought to represent an early stage of social evolution and a full understanding of the social system of this species remains incomplete. In this study we have presented evidence of female led dominance in the vicinity of sett

entrances within badger social groups during the mating and cub rearing season. However, it remains unclear what factors may promote dominance, or what benefits / costs individuals may receive because of their dominance status. Further research on the social structure of European badgers is needed, both because it may add to our understanding of how sociality in badgers develops and is maintained, and because it may offer insights into the evolution of mammalian societies generally.

A2.6 References

- Alexander RD (1974) The evolution of social behaviour. *Annual Review of Ecology and Systematics*, **5**, 325–383.
- Appleby MC (1983) The probability of linearity in hierarchies. *Animal Behaviour*, **31**, 600–608.
- Archie EA, Morrison TA, Foley CAH, Moss CJ, Alberts SC (2006) Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*, **71**, 117–127.
- Barrett L, Gaynor D, Henzi SP (2002) A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Animal Behaviour*, **63**, 1047–1053.
- Belisle P, Chapais B (2001) Tolerated co-feeding in relation to degree of kinship in Japanese macaques. *Behaviour*, **138**, 487–509.
- Berdoy M, Smith P, Macdonald DW (1995) Stability of social status in wild rats: age and the role of settled dominance. *Behaviour*, **132**, 193–212.
- Buesching CD, Stopka P, Macdonald DW (2003) The social function of allo-marking in the European badger (*Meles meles*). *Behaviour*, **140**, 965–980.
- Carpenter PJ, Pope LC, Greig C *et al.* (2005) Mating system of the Eurasian badger, *Meles meles*, in a high density population. *Molecular Ecology*, **14**, 273–284.
- Cheeseman CL, Cresswell WJ, Harris S, Mallinson PJ (1988) Comparison of dispersal and other movements in 2 badger (*Meles meles*) populations. *Mammal Review*, **18**, 51–59.
- Cheeseman CL, Wilesmith JW, Ryan J, Mallinson PJ (1987) Badger population dynamics in a high-density area. In: *Mammal Population Studies: Proceedings*

- of a Symposium at the Zoological Society of London (ed. Harris S), p. 279–294. Clarendon Press, Oxford.
- Cote SD (2000) Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour*, **137**, 1541–1566.
- Creel S, Macdonald D (1995) Sociality, group-size, and reproductive suppression among carnivores. In: *Advances in the Study of Behavior, Volume 24* (eds. Slater PJB, Rosenblatt JS, Snowdon CT, Milinski M), p. 203–257. Academic Press Inc., San Diego.
- Cresswell WJ, Harris S, Cheeseman CL, Mallinson PJ (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 B*, **338**, 393–407.
- da Silva J, Macdonald DW, Evans PGH (1994) Net costs of group living in a solitary forager, the Eurasian badger (*Meles meles*). *Behavioral Ecology*, **5**, 151–158.
- de Vries H (1993) The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika*, **58**, 53–69.
- de Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, **50**, 1375–1389.
- de Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, **55**, 827–843.
- de Vries H, Netto WJ, Hanegraaf PLH (1993) MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157–175.
- Delahay RJ, Brown JA, Mallinson PJ *et al.* (2000) The use of marked bait in studies of the territorial organization of the European Badger (*Meles meles*). *Mammal Review*, **30**, 73–87.
- Drews C (1993) The concept and definition of dominance in animal behavior. *Behaviour*, **125**, 283–313.
- Dugdale HL, Macdonald DW, Newman C (2003) Offspring sex ratio variation in the European badger, *Meles meles*. *Ecology*, **84**, 40–45.
- Goldman EN, Loy J (1997) Longitudinal study of dominance relations among captive Patas monkeys. *American Journal of Primatology*, **42**, 41–51.
- Herrera EA, Macdonald DW (1993) Aggression, dominance, and mating success among capybara males (*Hydrochaeris hydrochaeris*). *Behavioral Ecology*, **4**, 114–119.
- Holand O, Gjostein H, Losvar A *et al.* (2004) Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *Journal of Zoology*, **263**, 365–372.

- Huck UW, Banks EM (1982) Male dominance status, female choice and mating success in the Brown Lemming, *Lemmus trimucronatus*. *Animal Behaviour*, **30**, 665–675.
- Isbell LA, Young TP (2002) Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour*, **139**, 177–202.
- Johnson DDP (2001) *Models of Coexistence, Conflict and Cooperation* D.Phil. thesis, University of Oxford.
- Johnson DDP, Jetz W, Macdonald DW (2002) Environmental correlates of badger social spacing across Europe. *Journal of Biogeography*, **29**, 411–425.
- Johnson DDP, Macdonald DW, Dickman AJ (2000) An analysis and review of models of the sociobiology of the Mustelidae. *Mammal Review*, **30**, 171–196.
- Johnson DDP, Stopka P, Macdonald DW (2004) Ideal flea constraints on group living: unwanted public goods and the emergence of cooperation. *Behavioral Ecology*, **15**, 181–186.
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1106.
- Kappeler P (2000) Female dominance in primates and other mammals. In: *Perspectives in Ethology* (eds. Bateson PPG, Klofer PH, Thompson NS), p. 143–115. Plenum, New York.
- Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology*, **67**, 111–150.
- Kruuk H (1978a) Foraging and spatial organisation of the European badger, *Meles meles* L. *Behavioral Ecology and Sociobiology*, **4**, 75–89.
- Kruuk H (1978b) Spatial organisation and territorial behaviour of the European badger *Meles meles*. *Journal of Zoology*, **184**, 1–19.
- Kruuk H (1989) *The Social Badger: Ecology and Behaviour of a Group Living Carnivore (Meles meles)* Oxford University Press, Oxford.
- Kruuk H, Parish T (1983) Seasonal and local differences in the weight of European badgers (*Meles meles* L.) in relation to food supply. *Zeitschrift für Säugetierkunde - International Journal of Mammalian Biology*, **48**, 45–50.
- Kutsukake N, Clutton-Brock TH (2006) Social functions of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, **72**, 1059–1068.
- Macdonald DW (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379–384.

- Macdonald DW, Harmsen BJ, Johnson PJ, Newman C (2004) Increasing frequency of bite wounds with increasing population density in Eurasian badgers, *Meles meles*. *Animal Behaviour*, **67**, 745–751.
- Macdonald DW, Newman C (2002) Population dynamics of badgers (*Meles meles*) in Oxfordshire, UK: numbers, density and cohort life histories, and a possible role of climate change in population growth. *Journal of Zoology*, **256**, 121–138.
- Macdonald DW, Stewart PD, Johnson PJ, Porkert J, Buesching CD (2002) No evidence of social hierarchy amongst feeding badgers, *Meles meles*. *Ethology*, **108**, 613–628.
- Macdonald DW, Stewart PD, Stopka P, Yamaguchi N (2000) Measuring the dynamics of mammalian societies: an ecologists guide to ethological methods. In: *Research Techniques in Animal Ecology: Controversies and Consequences* (eds. Boitani L, Fuller TK), p. 332–388. Columbia University Press, New York.
- McElligott AG, Gammell MP, Harty HC *et al.* (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behavioral Ecology and Sociobiology*, **49**, 266–272.
- Mesterton-Gibbons M, Dugatkin LA (1995) Toward a theory of dominance hierarchies: effects of assessment, group size, and variation in fighting ability. *Behavioral Ecology*, **6**, 416–423.
- Owens D, Owens M (1996) Social dominance and reproductive patterns in brown hyaenas *Hyaena brunnea*, of the central Kalahari desert. *Animal Behaviour*, **51**, 535–551.
- Pelletier F, Festa-Bianchet M (2006) Sexual selection and social rank in bighorn rams. *Animal Behaviour*, **71**, 649–655.
- Pope LC, Domingo-Roura X, Erven K, Burke T (2006) Isolation by distance and gene flow in the Eurasian badger (*Meles meles*) at both a local and broad scale. *Molecular Ecology*, **15**, 371–386.
- Queller DC, Goodnight KF (1989) Estimating relatedness using genetic-markers. *Evolution*, **43**, 258–275.
- Rasa OAE (1986) Coordinated vigilance in dwarf mongoose family groups: the "watch-man's song" hypothesis and the costs of guarding. *Ethology*, **71**, 340–344.
- 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.
- Ruxton GD (2006) The unequal variance t-test is an underused alternative to Student's t-test and the Mann-Whitney U test. *Behavioral Ecology*, **17**, 688–690.

- Stewart PD, Bonesi L, Macdonald DW (1999) Individual differences in den maintenance effort in a communally dwelling mammal: the Eurasian badger. *Animal Behaviour*, **57**, 153–161.
- Stewart PD, Ellwood SA, Macdonald DW (1997) Remote video-surveillance of wildlife - an introduction from experience with the European badger *Meles meles*. *Mammal Review*, **27**, 185–204.
- Tuytens FAM, Macdonald DW, Delahay R *et al.* (1999) Differences in trappability of European badgers *Meles meles* in three populations in England. *Journal of Applied Ecology*, **36**, 1051–1062.
- van Hooff JARAM, Wensing JAB (1987) Dominance and its behavioral measures in a captive wolf pack. In: *Man and Wolf* (ed. Frank H), p. 219–252. W. Junk, Dordrecht.
- Walsh PS, Metzger DA, Higuchi R (1991) Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques*, **10**, 506–513.
- Woodroffe R, Macdonald DW (1992) Badger clans - demographic groups in an antisocial species. *Journal of Zoology*, **227**, 696–698.
- Woodroffe R, Macdonald DW (1993) Badger sociality - models of spatial grouping. In: *Mammals as Predators: Proceedings of a Symposium at the Zoological Society of London* (eds. Dunstone N, Gorman ML), p. 145–169. Clarendon Press, Oxford.
- Woodroffe R, Macdonald DW (1995a) Costs of breeding status in the European badger, *Meles meles*. *Journal of Zoology*, **235**, 237–245.
- Woodroffe R, Macdonald DW (1995b) Female/female competition in European badgers *Meles meles*: effects on breeding success. *Journal of Animal Ecology*, **64**, 12–20.
- Woodroffe R, Macdonald DW (2000) Helpers provide no detectable benefits in the European badger (*Meles meles*). *Journal of Zoology*, **250**, 113–119.

A2.7 Acknowledgements

Stacey Hewitt was supported by a Mammals Trust UK (MTUK) internship. The core Wytham badger project is generously supported by the Peoples Trust for Endangered Species, who also support Hannah Dugdale. Laboratory work was carried out at the Sheffield Molecular Genetics Facility by Hannah Dugdale, and was funded by the Natural Environment Research Council. We would like to thank Lisa Pope and Terry Burke for their invaluable advice on the genetic work. We are extremely grateful to Stephen Ellwood for his advice on CCTV set-ups and to all of the volunteers, and especially MTUK field assistants Amy Isherwood and Becky Dean, who contributed to the video analysis. Paul Johnson provided invaluable statistical advice. We are grateful to Sandra Baker and Karen de Vries for helpful comments on our paper. Fieldwork was carried out under Home Office License PPL 30 / 1216 and English Nature License 20001537.