

**Social behaviour of the European
badger *Meles meles***



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Table of contents

1	Abstract	3
2	Introduction	5
2.1	Mating system	6
2.1.1	Inbreeding	6
2.1.2	Mate choice	7
2.1.3	Mating versus mounting	8
2.2	Cooperative breeding	8
2.3	Aims	9
3	Materials and methods	10
3.1	Study site	10
3.2	Live trapping	10
3.3	Remote infrared CCTV (Closed-Circuit Television) surveillance	11
3.4	Behavioural analysis	11
3.5	Statistical analysis of the behavioural data	13
4	Results	14
4.1	Filming	14
4.2	Mounting behaviour	14
4.2.1	Mating system	14
4.2.2	Mounting duration	15
4.2.3	Mounting patterns	16
4.2.4	Mate choice	17
4.3	Parentage analysis	18
4.4	Babysitting behaviour	18
4.4.1	Breeding females	18
4.4.2	Non-breeding and yearling females	20
4.4.3	Yearling and adult males	21
4.5	Allogrooming	21
5	Discussion	22
5.1	Mounting behaviour	22
5.1.1	Mating system	22
5.1.2	Mounting duration	24
5.1.3	Mounting cycles	24
5.1.4	Length of mounting activity	25
5.1.5	Female mate choice	25
5.1.6	Male mounting activity	27
5.2	Cooperative breeding	27
5.2.1	Parental care	28
6	Acknowledgements	28
7	References	29
8	Appendix	32
8.1	P and PO Badgers	32

1 Abstract

The European badger *Meles meles* is unusual amongst social species as many of its relatives are solitary; thus, it is thought to represent sociality at a rudimentary stage of evolution. This project investigated the mating system of the European badger using infra-red CCTV equipment at two social groups in Wytham Woods, Oxford between February and May 2005, inclusive. This revealed a paradox in badger mounting behaviour, suggesting that social groups of badgers may exhibit a polygynandrous mating system, with both males and females having more than one mounting partner. This multiple mounting may be explained as a fertilisation assurance. Additionally multiple, repeated mountings may mask paternity, thereby reducing the likelihood of infanticide by males, as well as reducing competition between males for mountings. This has implications for the evolution of social behaviour in mammals in general.

Mountings were observed throughout the four-month study period, and females appeared synchronous in their mounting with clusters of activities, but this was not cyclical. Additionally, the observed mountings were of short duration and, thus, may not represent successful copulations. Females were mounted by males that sequentially allomarked and allogroomed them more than other males; however, the badgers that allogroomed a female the most were the males that mounted a female the most for only two out of 10 females, and only 30 ± 18 % of a female's total allogrooming was by males that had mounted her.

The behavioural observations also provided weak evidence for cooperative breeding. Breeding females spent significantly more time than expected by chance, with a greater number of cubs than were in their own litters. In one of the social groups, breeding females allogroomed cubs significantly more than non-breeding

females, yearling females and males. In comparison the non-breeding female in the second social group allogroomed the cubs significantly more than any of the other categories of badgers.

2 Introduction

The European badger, *Meles meles*, is unusual amongst social species as many of its relatives are solitary (Johnson et al., 2000); thus, it is thought to represent sociality at a rudimentary stage of evolution. Badgers in continental Europe live in pairs or are solitary, contrasting with the stable social groups of badgers in England and Scotland (Woodroffe & Macdonald, 1993). Badgers in England and Scotland live in multi-male, multi-female groups that maintain their numbers by the retention of young in their natal group or through immigrations (Woodroffe et al., 1993). This social organisation therefore makes the European badger an ideal species for the study of mate choice and cooperative breeding.

Badgers in Wytham Woods have been individually identified since 1987, and their nocturnal activities recorded using infra-red CCTV surveillance equipment sporadically since 1994 (Stewart et al., 1997). Every badger that has been captured in Wytham Woods has been tattooed with a unique identification number and those badgers present in filmed social groups have been clip-marked to allow recognition of individuals on camera. Furthermore, DNA samples have been collected from nearly every individual trapped producing a relatedness database stretching back for the past 18 years.

2.1 Mating system

The mating system of the European badger is largely unknown, and few studies have investigated mating behaviour within the badger social group. Mountings have been observed throughout the territory of a social group and even in neighbouring social groups (Christian, 1995; Paget & Middleton, 1974). The mating behaviour that has been observed around setts occurs throughout the year and suggests a polygynandrous mating system (Johnson, 2001); we aim to provide evidence to support this through behavioural analysis.

In Britain badgers mate throughout the year with the main mating peak in the spring (Neal & Cheeseman, 1996). Badgers exhibit delayed implantation, whereby after mating fertilised ova develop up to the blastocyst stage and then development is suspended until implantation is triggered around the winter solstice (Fischer, 1931); therefore mating and fertilisation occurring early in the year can still result in cubs being born during the birthing period between mid-January to mid-March (Neal & Cheeseman, 1996). Females can thus choose to mate with many different males, and males have time to find different females, making the polygynandrous mating system possible. This near year round availability of females as mating partners may even be the evolutionary driving force behind social living in badgers (Cresswell et al., 1992; Roper, 1994).

2.1.1 Inbreeding

Within the two social groups studied in Wytham Woods for this project, males' relatedness to females ranged from 0 - 0.6 (i.e. unrelated to full sibling/mother-son, Dugdale, 2004). Inbreeding is therefore a potential problem for social badgers. Inbreeding can be avoided by males or females going to neighbouring social groups to

look for unrelated mating partners. Females in particular may be expected to avoid inbreeding because they have a greater reproductive investment in cub development and rearing (Trivers, 1972). A behavioural method that females could use to reduce inbreeding is to only engage in long matings with unrelated males. Mating may occur with any male in exchange for resource benefits such as allogrooming, and short matings may be purely rutting behaviour where penetration is not achieved (Neal & Cheeseman, 1996).

2.1.2 Mate choice

In species where females mate with more than one male, sexual selection studies have focused on the characteristics of males that obtain copulations and genetic paternity. This enables the traits that are associated with successful matings to be identified. Two traits that are potentially used by social mammals to select a mate are allogrooming and allomarking behaviours. Allomarking spreads subcaudal secretion over the recipients body and this may be a sexually selected trait that functions as an advert for individual identity, reproductive condition, and sexual attractiveness (Wiepkema, 1979). Additionally, allogrooming may be a commodity that is exchanged in a biological market for matings (Stopka et al., 2001). Males that allogroom a female more often may gain preferential copulations with her, and hence potentially higher paternity.

2.1.3 Mating versus mounting

With behavioural analysis, successful mating cannot be distinguished from mounting with any certainty, therefore henceforth we describe any mating activity as mounting behaviour.

2.2 Cooperative breeding

Cooperative breeding is the care of young by individuals other than their biological parents (Emlen, 1982). It is typically associated with those species that exhibit high reproductive skews, where only a pair or a few of the sexually mature adults actually breed (e.g. meerkats, Griffin et al., 2003), but it is also seen, although less commonly, in low skew societies (e.g. banded mongoose, Gilchrist et al., 2004). Cooperative breeding can occur when non-breeding individuals remain in a social group and help raise the offspring of others rather than breeding themselves, or migrating and breeding elsewhere. Depending on the individuals in question and whether they are non-breeding adults, juveniles or breeding adults cooperative breeding can consist of one or all of the following features: delayed dispersal from the natal group, reproductive suppression and care for others' offspring (Solomon & French, 1997). Kin selection is the most widely accepted hypothesis explaining cooperative breeding, whereby non-breeding individuals gain indirect fitness benefits through increasing the probability of survival of their relatives (Hamilton, 1964).

There is anecdotal evidence to suggest that European badgers cooperatively breed; however, one of the main difficulties is identification of individuals and establishing which adults are the breeders. A study in Wytham Woods, Oxford, proposed that alloparental care in the badger does exist (Woodroffe, 1993). It was observed that non-breeding adults babysat cubs whilst the parents were away and

protected them from attack by a fox and intruding males (Woodroffe, 1993). One of the main drawbacks of this study was the limited amount of observation time (10 hours) over a short period (15 nights) combined with individual identification being limited to a combination of natural marks, ear tags and radio-collars on adults only. Furthermore, there were no conclusive means of determining which adults were breeders or of identifying their respective cubs.

In order to determine if alloparental care does exist in socially living badgers, it is necessary to establish whether non-breeding individuals help to raise the cubs of their relatives or if breeding individuals care for more cubs than in their own litter. If cooperative breeding is not observed the alternative conclusion is that only breeding individuals help to raise their litter. Cooperative breeding can take many forms, for example; grooming of young, babysitting and bedding collection. In order to determine whether socially living badgers cooperatively breed we will investigate both the frequency with which particular adults associate with particular numbers of cubs and also the frequency with which group members allogroom cubs.

Currently it is unknown whether paternal care occurs in badgers; by investigating whether adult males undertake cub-rearing activities it should be possible to establish whether paternal care takes place.

2.3 Aims

The primary objectives of this project are: (1) to determine the mating system of the European badger *Meles meles*; and (2) to establish whether cooperative breeding occurs within social groups of badgers.

3 Materials and methods

3.1 Study site

This study was conducted in Wytham Woods, Oxfordshire UK (01°18'W, 51°46'N). The ecological characteristics of the woodland are described in Kruuk (1978) and da Silva (1993). Although mating can take place during any month of the year the main peak is in the spring. Cubs from the previous year's matings typically appear above ground mid-February (Neal & Cheeseman, 1996); therefore, in order to best describe mate choice and cooperative breeding, the filming period was from February to May 2005, inclusive.

Using bait marking techniques (Delahay et al., 2000; Kruuk, 1978) the number of social groups in 2005 was estimated to be 26. Two of these were chosen for this study: Pasticks (P) and Pasticks Outlier (PO). Both have similar adult sex ratios: 28% and 33% male respectively. The two were originally one social group with P as the main sett and PO as an outlier; however, in 2001 PO was recognised as a separate social group through the use of bait marking. These two particular setts were selected because they are easily accessible and provide good filming conditions via suitable trees on which to mount cameras, flat topography and limited plant growth in the field of view.

3.2 Live trapping

Badgers are trapped at least four times a year: January, June, July or August and November. They are caught using swing door box-traps baited with peanuts (Tuytens et al., 1999) over a period of two or three days.

The badgers are anaesthetised by an intra-muscular injection of approximately 0.2ml/kg Ketamine hydrochloride (Vetlar; Pharmacia and Upjohns, Crawley, UK). When a badger is first captured it is marked with a permanent unique identification tattoo (Cheeseman & Harris, 1982) on the inside of a hind leg. To identify individuals from CCTV footage badgers caught from P and PO are given a unique clip mark. This is done by removing the tips of guard hairs, which results in a visible white under fur pattern that contrasts with the remaining black guard hairs under infra-red light (Stewart & Macdonald, 1997). A range of measures are taken from each badger, including age and sex. DNA samples, in the form of both hair and blood, are also taken for later genotyping.

3.3 Remote infrared CCTV (Closed-Circuit Television) surveillance

Four CCTV surveillance systems were set-up under the recommendations of Stewart et al. (1997). PO had one camera in operation, whereas P had three cameras focussing on three different sett entrances. The systems operated using infrared technology to observe the nocturnal activities of the badgers.

3.4 Behavioural analysis

Behaviours observed were scored from a strict set of definitions, (as defined below), and the badger identified by its individual clip mark. Data were entered into an ACCESS database. Unidentifiable badgers and badgers without clip marks (from not having been caught at recent trapping events) were excluded from the analyses.

Behaviours of particular importance were allogrooming, sequential allomarking, mounting and babysitting. For allogrooming and sequential allomarking, every event between two badgers (either adult or yearling) was recorded,

along with their identity. The identity of badgers involved in mounting and the length of the mount were recorded. A mount was classified as ‘failed’ and hence excluded from analysis if the male badger was not directly aligned with the female (therefore genital contact was not possible) or if a cub was being mounted (as they are not sexually mature until they are on average, 13-14 months old in females and between 12-15 months in males. Mounting started with the male biting the female’s neck and ended with the release of this neck grab.

‘Babysitters’ were defined as adults or yearlings that were on screen and interacting positively with cubs, whilst no other adults or yearlings were present. The frequency with which group members babysat was recorded by the number of babysitting bouts that they undertook. A babysitting bout commenced when an adult or yearling badger appeared on screen with cubs and terminated when either there were no cubs on the screen for five seconds, or when the last adult or yearling left the screen. The maximum number of cubs seen on screen with an adult during each babysitting bout was also recorded. If the cubs were groomed by another badger this was recorded once per babysitting bout for each adult or yearling badger that groomed them. Unfortunately cubs could not be individually identified as it is not ethical to trap them until they are independent from their mothers at around 12 weeks of age.

Badger activity bouts were also recorded, to control for the amount of time that a badger was seen on screen. A badger activity bout commenced when a badger appeared on screen and terminated when there were no badgers on screen for over a minute.

The tattoo number of each badger in the filmed social groups, along with their sex and reproductive status, are detailed in Appendix 8.1.

3.5 Statistical analysis of the behavioural data

Data on mounting partners, duration of mounting and peaks in mounting activity were displayed graphically. The social interactions, allogrooming and sequential allomarking, were correlated with mounting frequency. We employed the Kr test (Kendal's partial row-wise matrix correlation; (De Vries, 1993)) with 2000 permutations to test for significant correlations using the software MATMAN v.1.1 (De Vries et al., 1993). A matrix stating the number of camera nights any two badgers were seen on the same camera was used to control for the greater number of cameras at Pasticks and to control for the reduced likelihood of interactions between badgers from different social groups.

The total number of bouts of badger activity was calculated and for each individual the proportion of babysitting bouts it undertook with different numbers of cubs was also recorded. This was displayed along with the expected frequency that the individual would be seen on screen with those numbers of cubs based on the overall number of bouts cubs were seen on screen. For each individual the differences between the observed and expected values for all numbers of cubs were clumped and tested using a Wilcoxon signed-ranks test.

4 Results

4.1 Filming

CCTV footage was successfully filmed from 01/02/2005 - 28/05/2005. This resulted in an average of 114 nights of footage from each of the cameras and a total of 5,400 hours of footage, from which 41 mounts and 57 hours of footage of cub behaviour were analysed.

4.2 Mounting behaviour

4.2.1 Mating system

From Table 1 it can be seen that females were mounted by one or two males from their social group, whereas males mounted two or more females from their social group. The younger males from both social groups mounted more females than the older males. No mountings were seen between individuals from the two different social groups as indicated by the white areas in Table 1. Such mountings may occur, but there were no cameras set up between setts to monitor for this.

		Males				Total
		660	968	491	917	
Females	B	1	18	0	0	19
	816	0	2	0	0	2
	507F	0	3	0	0	3
	819	0	2	0	0	2
	713	0	0	0	0	0
	972	0	2	0	0	2
	979	2	2	0	0	4
	323	0	0	2	1	3
	65W	0	0	0	2	2
	765	0	0	0	1	1
	959	0	0	2	1	3
	Total	3	29	4	5	41

Table 1: Frequency of mounting events at the two studied social groups (dark grey = Pasticks, light grey = Pasticks Outlier), from February to May 2005, inclusive.

There was only one incidence of a female being mounted by two different males on the same night. This occurred on the 21/04/2005 at Pasticks with B being mounted by both 660 and 968.

4.2.2 Mounting duration

Mounting duration ranged from 2 – 468 seconds with the average being 40 seconds. Longer mountings may be more likely to be successful than the shorter mounts. Only 10 mounting events were longer than 60 seconds; nine of these were by younger males and only one by the older male at Pasticks Outlier. All potentially sexually receptive groups of badgers (breeding females, non-breeding females and yearlings) were involved in mounting behaviour (Figure 1). Younger males spent longer, in total, mounting than the older male in each social group (Figure 1).

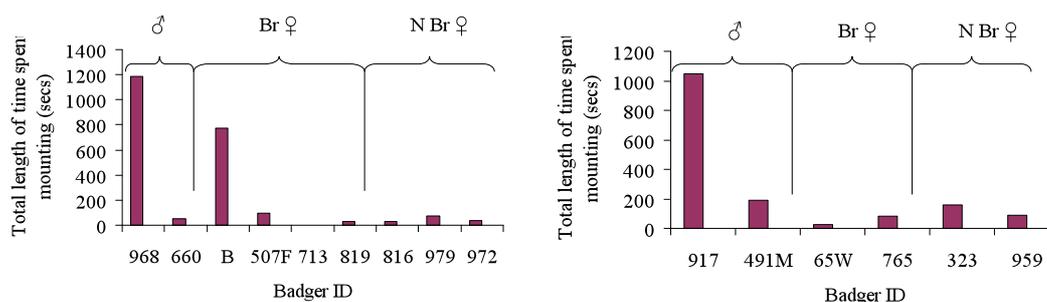


Figure 1: Total time each badger at Pasticks (left) and Pasticks Outlier (right) engaged in potentially successful mounting, during the February to May filming period (Br = Breeding; N Br = Non-breeding).

4.2.3 Mounting patterns

Females seemed to show mounting synchrony within each social group as shown by clusters of mounting peaks throughout the filming period (Figure 2 and Figure 3). These mounting peaks do not seem to exhibit a cyclic pattern. Females at Pasticks (Figure 2) showed greater mounting activity earlier on in the filming period than females at Pasticks Outlier (Figure 3). This corresponds to cubs being seen on camera earlier at Pasticks than at Pasticks Outlier; thus, the post-partum mounting at Pasticks will have occurred earlier. More mounting activity was filmed overall at Pasticks compared to Pasticks Outlier due to the combination of both a greater female and a greater camera presence at Pasticks.

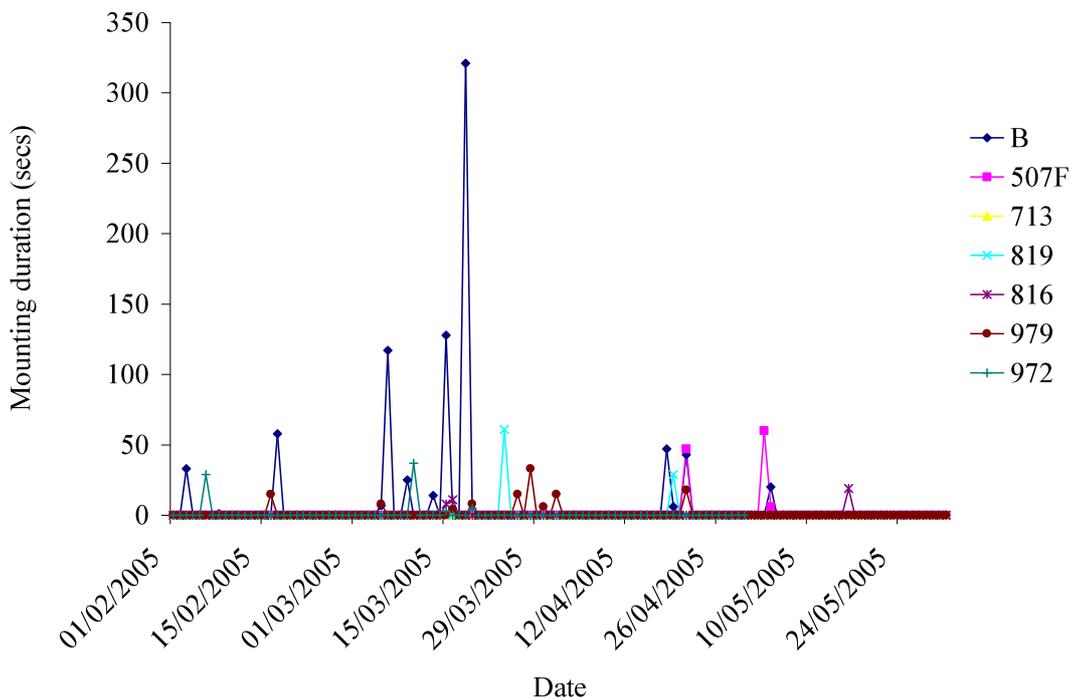


Figure 2: Mounting activity for each female badger at Pasticks throughout the February to May filming period.

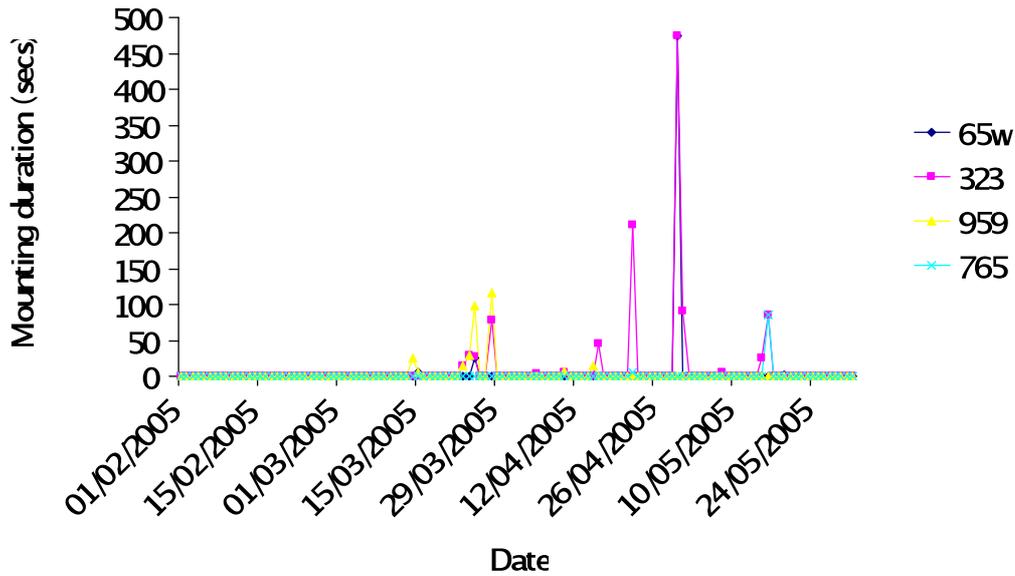


Figure 3: Mounting activity for each female badger at Pasticks Outlier throughout the February to May filming period.

4.2.4 Mate choice

Females were mounted significantly more by males that allogroomed ($Kr = 0.509$, $p = 0.0400$) and sequentially allomarked ($Kr = 0.717$, $p = 0.0005$) them more often. Females are potentially, therefore, (1) selecting their mounting partners on the basis of the frequency with which males allomark them, and, (2) exchanging mountings as a commodity in a biological market for allogrooming. However, one of the 10 mounted females was not marked by the male that mounted her and only two of the 10 mounted females were allogroomed the most by the males that mounted them more often. Of the total number of times a female was allogroomed, only an average of $30 \pm 18\%$ of the allogrooming was by males that mounted them (range 0 – 66%).

4.3 Parentage analysis

In June 2005, 10 cubs were caught at the filmed social groups: five at P and five at PO. Three of the five from both P and PO were male, giving overall cub sex ratios of 60% male. One further cub was trapped at P during the August trapping. All of the cubs caught during the June trapping were genotyped. The additional cub trapped in August was not genotyped by the time of this write-up. All of the genotyped cubs were assigned a mother at $\geq 80\%$ confidence. B, 819, 713 and 507F were assigned maternity at Pasticks, and 65W and 765 were assigned maternity at Pasticks Outlier. Seven of the 10 cubs were also allocated fathers at $\geq 80\%$ confidence. None of the allocated fathers were resident in the cub's social group.

4.4 Babysitting behaviour

4.4.1 Breeding females

In total, four breeding females were identified at P and three at PO. Breeding females at P were seen to spend significantly more time than expected with cubs ($T = 236$, $n = 24$, $p = 0.015$) whereas females at PO spent significantly less time than expected ($T = 6$, $n = 12$, $p = 0.011$).

To test for cooperative breeding only the differences for cub numbers greater than the mother's litter size were tested (Figure 4). At PO breeding females spent significantly less time than expected with cub numbers greater than their own litter size ($T = 0$, $n = 8$, $p = 0.014$). Breeding females at P were seen to spend significantly more time with cub numbers greater than their own litter size ($T = 153$, $n = 19$, $p = 0.021$). To account for the extra cub a further test was performed where one was added to the P breeding female's litter size. Even under this condition the females

spent more time than expected with the cubs; however, this was not significant ($T = 92, n = 15, p = 0.074$).

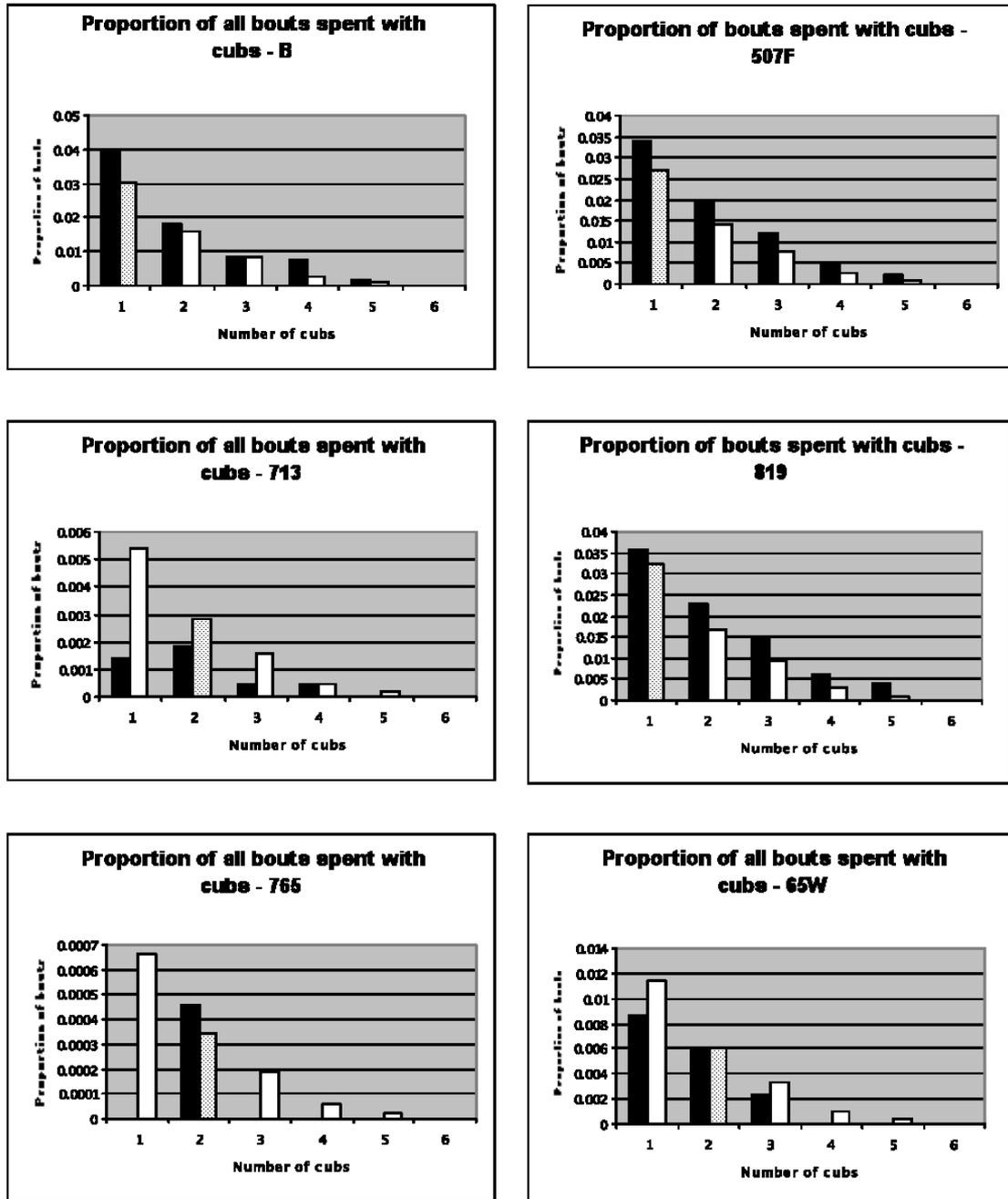


Figure 4: Expected and observed frequencies for breeding females with different numbers of cubs. Data is adjusted for individual appearance on screen. Black bars = observed frequency; white bars = expected frequency; shaded bar = litter. One of the females at P (B, 507F, 713 and 819) may have another cub.

4.4.2 Non-breeding and yearling females

The non-breeding female at PO, 323, spent the expected amount of time with cubs (Figure 5). The non-breeding at P female, 816, spent less time with cubs, but not significantly so ($T = 2, n = 6, p = 0.093$). Yearling females at PO spent significantly less time than expected with cubs ($T=0, n=6, p = 0.036$) and those at P also spent less time with cubs, but not significantly less ($T = 14, n=6, p = 0.055$).

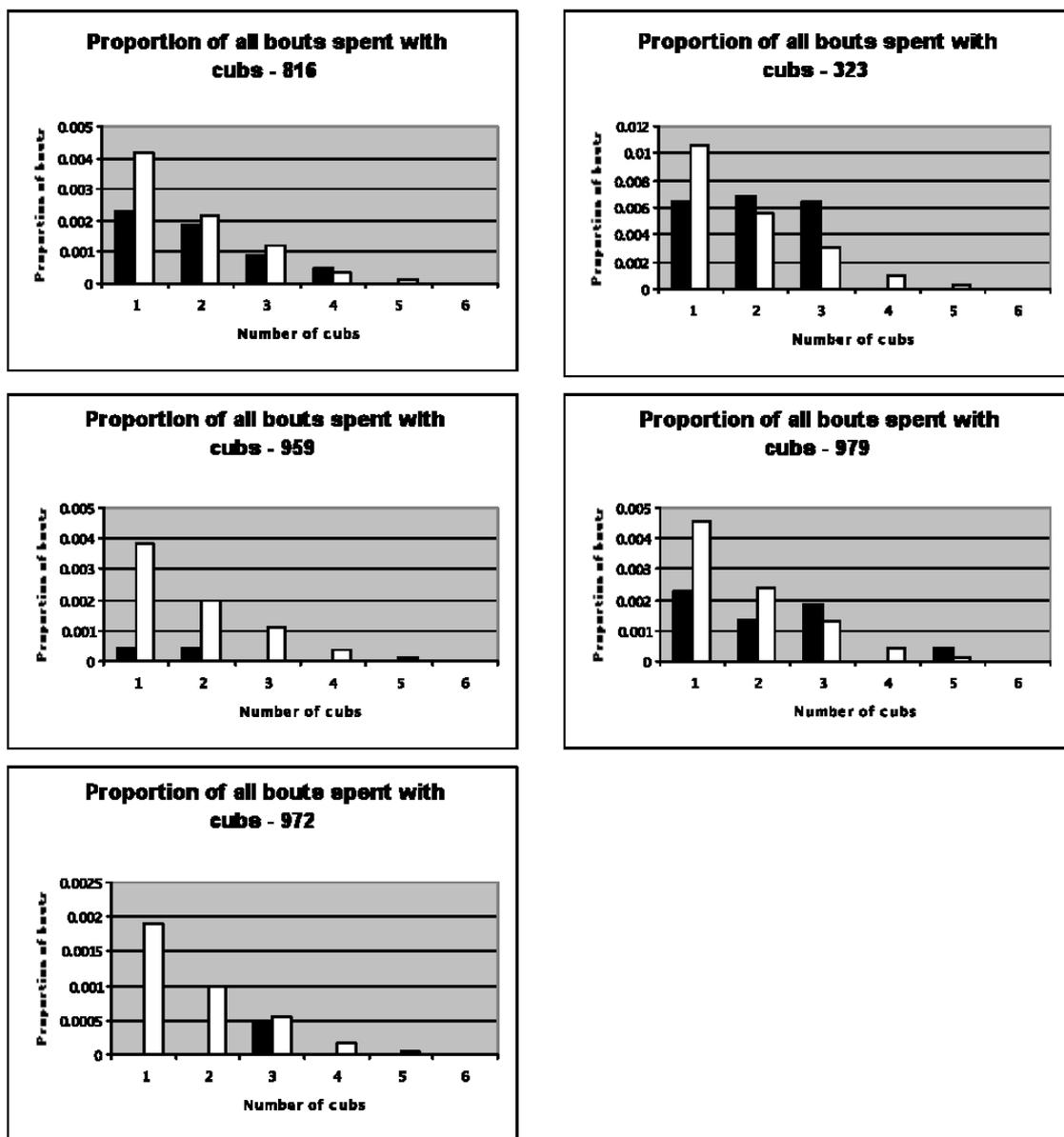


Figure 5: Expected and observed frequencies for non-breeding and yearling females with different numbers of cubs. Data is adjusted for individual appearance on screen. Black bars = observed frequency; white bars = expected frequency.

4.4.3 Yearling and adult males

None of the resident males fathered cubs in the filmed social groups. There was only one yearling male, 968 at P, and he spent the expected amount of time with cubs. Adult males at both social groups spent significantly less time than expected with cubs (P: $T = 9$, $n = 12$, $p = 0.021$; PO: $T = 0$, $n = 12$, $p = 0.003$).

4.5 Allogrooming

At P, breeding females allogroomed cubs significantly more than non-breeding females ($W = 26095$, $p = 0.015$), yearling females ($W = 25656$, $p = 0.003$) and adult males ($W = 29146$, $p = 0.004$). At PO, the non-breeding female allogroomed significantly more than breeding females ($W = 2202$, $p = 0.002$) and adult males ($W = 3293$, $p = 0.000$). There was no significant difference in the frequency of allogrooming between the remaining categories.

5 Discussion

5.1 Mounting behaviour

5.1.1 Mating system

Our data revealed a paradox in badger mounting behaviour. The results from this study suggest that the European badger exhibits a polygynandrous mating system, with both males and females having more than one mounting partner. Females have been recorded mounting frequently with one or two partners while males are even more promiscuous with two or three mounting partners. Parental investment theory predicts that males should mate with as many females as possible, whereas females should be more selective in their mate choice due to their greater reproductive investment in offspring (Trivers, 1972). Additionally, sperm competition acts on males to mate as often as possible (Birkhead, 1998). Therefore theory predicts that males should favour frequent multiple matings, whereas females should favour a more monogamous mating system.

Female badgers were observed engaging in both repeated mounting (many times with one male) and multiple mounting (mounting with more than one male). All the females found at PO engaged in mounting behaviour, while all bar one of the females (breeding female 713) at P were involved in mounting events. In comparison, but as expected, males too engaged in repeated and multiple mounting events and, similar to those patterns observed with the females, only one male did not participate in mounting activity. Although there is no explanation for the lack of mounting by 713, the lack of mounting activity by 533 can be attributed to the fact that he was rarely seen on camera and when he was he was very lethargic. He was found dead just outside the field of view at P2 on 19/04/2005.

Howard (see Neal & Cheeseman, 1996) observed two males mounting with the same female on two consecutive nights; such multiple mounting was also reported by another study (Paget & Middleton, 1974). This was also true of this study's findings when B was recorded being mounted by both 660 and 968 on 21st April 2005; all of the males apart from 917 were seen mounting more than one female within the same night.

There have been numerous hypothesis put forward to try to explain why female badgers mount repeatedly and with multiple males. Fertilisation assurance along with reduction of competition between males and avoidance of infanticide are two of the hypothesis that best support the promiscuous and repeated mounting activity of the observed badgers.

Fertilisation assurance is a plausible explanation for the repeated mountings that were observed. Although sperm from a single mating can in theory fertilise all of a female's gametes, not all sperm are viable. In badgers, less than 30% of potential fertilisations are successful (Cresswell et al., 1992). Thus, frequent copulation might serve to help guarantee fertilisation.

Reduction of competition between males and avoidance of infanticide also adds weight to the explanation of why repeated mountings occur and explains why promiscuous mounting occurs. By preventing males from mounting her, a female may encounter harassment from the male, which may be harmful to her and her offspring yet alleviated by promiscuity. Indeed, the most convincing explanation for multiple mating is that it masks paternity, reducing the risk of infanticide from males (Wolff & Macdonald, 2004). Some females may not experience infanticide and in this case it has been hypothesised that multiple and repeated copulations are a result of harassment (Wolff & Macdonald, 2004). This is because multiple and repeated

copulation increases the probability that all males will eventually gain some copulations and therefore each single copulation is less worth fighting over.

5.1.2 Mounting duration

The duration of mounting behaviour is highly variable. Many incidences previously reported in the field lasted in the field lasted two minutes but usually ranged from 10-90 minutes (Neal & Cheeseman, 1996). The mounting activity witnessed at the two social groups in this study varied from between just two seconds and 468 seconds. The high level of mounting behaviour carried out by young, inexperienced males coupled with very short mounting time could in fact indicate rutting behaviour where penetration was not achieved (Neal & Cheeseman, 1996). However, it may also be that prolonged mountings constitute post-ejaculatory mate guarding (Alcock, 1994), but it was not possible to test this.

5.1.3 Mounting cycles

Females in the two studies social groups showed some degree of mounting synchrony in that there were clusters of mounting activity, in between periods with no mounting activity. It has been suggested, based on hormone levels found in urine samples from two unmated females monitored daily for a year, that up to five oestrous cycles may occur in late winter/spring and autumn with an average interval of 28 days (Service et al., 2002). The data from this study does not support this; however, it does not refute it, as not all mountings can be observed using the CCTV techniques employed. Additionally, it may be that the longer duration mountings correspond to

actual oestrus periods, but unfortunately there were not enough long duration mounting observed to investigate this.

5.1.4 Length of mounting activity

Mounting activity was observed throughout the four month study period. This study period was purposely chosen to cover the main peak of mounting activity in early spring. Post-mortem studies have previously suggested that there are two peaks in mating activity, one post-partum and one in late-autumn (Cresswell et al., 1992; Page et al., 1994). The occurrence of mounting behaviour throughout the four month study period supports this and also suggests that mounting can occur over a long time scale, but a longer study is required to confirm whether this does occur year-round.

5.1.5 Female mate choice

There was a significant correlation between the allogrooming partners and mounting partners, and between the sequential allomarking partners and mounting partners. Thus, females were more likely to be mounted by those males that allogroomed and sequentially allomarked them the most.

Sequential allomarking places the scent of one badger, onto another. This scent is a unique secretion from the sub-caudal gland that is located between the anus and the base of the tail. Gas-chromatographic analyses of subcaudal secretion indicates that it contains information on group membership and sex and that it was influenced by age, body condition, and reproductive status (Buesching et al., 2002). It has previously been suggested that sequential allomarking may function to advertise individual-specific, fitness-related information (Buesching et al., 2003). This

secretion may therefore contain information that is useful for females when selecting a mate.

As well as being mounted more by males than sequentially allomarked females the most, these males also allogroomed the females the most. A consequence of badgers living in highly dense populations in Great Britain is that they suffer from intense ectoparasite infestation, a result of a combination of two factors; direct contact with each other and commonly used sett sites (Roper et al., 2001). These ectoparasites can carry lethal disease therefore it is vital for the badgers to somehow minimise these parasite loads and hence reduce the risk of unnecessary ill health. It is known that badgers can reduce these loads by both selfgrooming and allogrooming (Stewart & Macdonald, 2003). Preliminary observations suggest that allogrooming followed a tit-for tat (TFT) like rule (Stewart & Macdonald, submitted) whereby each grooming bout was reciprocated by the partner. The TFT strategy hinted at a classic Prisoners Dilemma (Johnson et al., submitted) in which A needs to get rid of fleas but cannot do it without cooperation from B (because they cannot groom their backs themselves). Therefore, this mutual cooperation that is observed suggests an alternative and compelling explanation for sociality in badgers. Investigating the allogrooming partners of females suggested that females may be exchanging mountings as a commodity in a biological market for allogrooming. However, allogrooming by mounting partners only represented an average of 30% of the total allogrooming partnerships; thus, it does not necessarily follow that females are exchanging mountings for allogrooming.

5.1.6 Male mounting activity

The observations obtained from this study show that by far, 968, the yearling male, carried out the majority of mounting behaviour and thus spent the greatest length of time engaged in mounting activity. Additionally, 968 sequentially allomarked females most frequently and was sequentially allomarked and allogroomed by females more than any other male present. .

The high incidence of mounting behaviour that was seen with the majority of females in his social group may be attributed to the fact that this individual has just reached sexual maturity and as such could be experiencing an increased libido. In contrast, the low mounting activity observed amongst the adult males could be a result of them visiting neighbouring social groups to obtain extra-group paternity. This could also help to explain why none of the adult males were assigned parentage to any of this year's cubs in their own social groups.

5.2 Cooperative breeding

The results from this study suggest that European badgers may display some degree of cooperative breeding when living in social groups. Results from the babysitting data show that breeding females spend a significant amount of time with numbers of cubs greater than their own litter size's pointing to cooperative care. However, although non-breeding females and males did babysit cubs, this was not more than was expected by chance. Non-breeding individuals did allogroom cubs, but only the non-breeding female at PO did this significantly more than any other badger category. This does weakly hint at cooperative breeding, especially given that the benefits to the actor seem minimal, considering that there is no known dominance hierarchy in badgers (Macdonald et al., 2002). However, it is certainly not conclusive

evidence as it was only seen at one social group, but due to the genetic analysis we can be confident that this non-breeding female is not the mother of these cubs. Therefore, any cub rearing behaviour performed by 323 may suggest cooperative breeding.

As individual cubs were not identifiable this prevented testing of the hypothesis of whether individuals are more likely to perform alloparental care to close relatives rather than unrelated individuals

5.2.1 Parental care

One of the aims of this study was to determine if European badgers displayed any form of paternal care. None of the filmed males were allocated paternity to the cubs, which excluded the possibility of testing this hypothesis. A point of note is that none of the allocated fathers were ever seen on screen at their cub's social group.

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8 Appendix

8.1 P and PO Badgers

The tattoo number of each badger observed in the two filmed social group is listed in Table 2. This also details their sex and categorisation according to their age and breeding status.

Social Group	Tattoo	Sex	Category
Pasticks	533	M	Adult males
	660	M	
	713	F	Breeding females
	819	F	
	507F	F	
	B	F	
	816	F	Non-breeding females
	H	F	
	968	M	Yearling male
	972	F	Yearling females
	979	F	
	1001	M	Cubs
	1010	F	
	1019	M	
	1020	M	
1036	F		
Pasticks Outlier	491M	M	Adult males
	917	M	
	765	F	Breeding females
	65W	F	
	323	F	Non-breeding female
	959	F	Yearling female
	999	M	Cubs
	1005	F	
	1012	M	
	1013	F	
1021	M		

Table 2: The tattoo number, sex and categorisation of all badgers observed at the two filmed social groups, between February and May 2005, inclusive.