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Polygynandrous and repeated mounting behaviour in European badgers, *Meles meles*

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Highlights

- European badgers mount polygynandrously and repeatedly, in high-density populations.

- Promiscuous and repeated mounting masks paternity, reducing male–male aggression and infanticide.

- Promiscuous mounting does not devalue the previous male’s sperm.

- Males in better condition sired more offspring; condition was not correlated with mounting frequency.

- Mounting frequency did not predict genetic paternity success.

Promiscuous and repeated mountings by females are evolutionarily intriguing as females are expected to be choosy and matings are expected to be costly. We evaluate the evolutionary basis of these behaviours in a high-density population of European badgers. We analysed postpartum mounting behaviour, in 3 years, at two neighbouring social groups each year. We demonstrate a polygynandrous social mating system, with repeated mounting. Mounting was skewed among females in four social-group-years, but overall did not differ from random, potentially because female reproductive success is context dependent, varying with local food availability and female–female competition. Some males mounted more than others; however, male mounting frequency was not related to dominance rank, self-grooming rate, or body condition index. Mounting frequency, however, did not predict paternity success; furthermore, a 16-year genetic data set showed that paternity success was positively correlated with body condition index. Females may therefore mount with males that do not father their offspring to minimize the risk of infanticide from them. Females may also trade mountings for allogrooming from males, but mounting frequency did not vary with relatedness, aggression received from males or sequential allomarking by males. We conclude that promiscuous and repeated mounting in badgers may have evolved to reduce male–male aggression around mounting and the likelihood of infanticide from males by masking paternity. Promiscuous mounting of female badgers does not devalue the previous male’s sperm, but may promote sperm competition, genetic diversity and genetic compatibility.

Keywords: body condition; extragroup mating; genetic diversity; grooming behaviour; *Meles meles*; microsatellites; multiple mating; promiscuous mating; repeated mating; reproductive success

Males should mate with as many females as possible as they produce considerably more, smaller gametes, whereas females, which produce fewer larger gametes and often invest more in parental care, should be choosier (Trivers 1972), although other factors such as sex-specific mortality rates may alter this (reviewed in Kokko & Jennions 2008). Nevertheless, female mammals are commonly mounted by multiple males (Møller & Birkhead 1989; Wolff & Macdonald 2004), and many hypotheses have been advanced to explain this (reviewed in Halliday & Arnold 1987; Birkhead & Møller 1992; Jennions & Petrie 2000; but also see Wolff & Macdonald 2004). Moreover, in some species females may be mounted repeatedly by the same male (Schwagmeyer & Parker 1994). Since mountings may be costly, given that they involve two individuals who may have conflicting optimal fitness strategies (Daly 1976), hypotheses have been developed to explain the evolution of repeated mounting behaviour (reviewed in Hunter et al. 1993).

Identifying traits that are associated with males that obtain mountings and genetic paternity enables the mechanisms through which individuals select a mate, and the evolutionary processes underlying this, to be assessed (Zeh & Zeh 2003). For example, in Columbian ground squirrels, *Urocitellus columbianus,* male age and body mass are correlated with mounting success as they determine access to females (Raveh et al. 2010). In prairie voles, *Microtus ochrogaster,* self-grooming is a sexually selected trait (Wolff et al. 2002) as it spreads scent (saliva and interdigital gland secretion), signalling individual identity, reproductive condition and sexual attractiveness (Wiepkema 1979). In the wood mouse, *Apodemus sylvaticus*, allogrooming is a commodity that is exchanged in a biological market for mountings (Stopka & Macdonald 1999).

To understand the breeding system of a species, knowledge is required of both the social and genetic mating system (Dobson et al. 2010). The European badger is group living in southern England, with up to 29 individuals resident within a social group (da Silva et al. 1994). It is a good species in which to study social behaviour as, although badgers may live in groups, there is little evidence that they gain cooperative benefits from this (Woodroffe & Macdonald 2000; Johnson et al. 2004; Dugdale et al. 2010). Dispersal is restricted (Pope et al. 2006), and groups are maintained by natal philopatry of both sexes (although males may perform more temporary group movements than females, Macdonald et al. 2008). Badger groups therefore contain relatives (mean pairwise R ± 95% confidence interval = 0.20 ± 0.04, Dugdale et al. 2008). In high-density populations the genetic mating system is polygynandrous, with multiple-male paternity in 16–31% of litters (Carpenter et al. 2005; Dugdale et al. 2007). In our study population, reproduction is skewed within groups (i.e. slightly fewer individuals breed than random expectation, Dugdale et al. 2008); up to seven males and seven females breed within a group and approximately half of the paternities were assigned to extragroup males, primarily from neighbouring groups (Dugdale et al. 2007). There is therefore moderate relatedness (mean pairwise R = 0.09 ± 0.03) between neighbouring groups (Dugdale et al. 2008). Despite the large number of studies on the European badger, very few published studies have investigated its behavioural mating system. This is primarily because badgers are nocturnal, living underground during the day, with the main mating period occurring in the colder months. Additionally, badgers can live in large groups but are not individually identifiable from natural markings, and although they socialize around sett entrances, they forage solitarily. Opportunities to observe mounting behaviour are therefore limited without infrared illumination and marking of individuals.

Nevertheless, a few studies have shown that mountings vary greatly in duration lasting from less than a minute to several hours (Neal & Harrison 1958; Paget & Middleton 1974; Christian 1995). Males have been observed mounting repeatedly with a female from their social group, and with limited aggression from within-group males (Johnson 2001). Additionally, observations have been made of extragroup mountings (Paget & Middleton 1974; Christian 1994, 1995), aggression between neighbouring and resident badgers (Kruuk 1978; Roper et al. 1986), and resident males chasing away extragroup males (Christian 1994, 1995). Furthermore, females have been observed mounting promiscuously over a few days (Christian 1995), and within the same night (Neal & Harrison 1958; Paget & Middleton 1974; Johnson 2001).

Johnson (2001) reviewed 14 hypotheses that may explain promiscuous and/or repeated mountings of female badgers. Johnson (2001) surmised that four of these hypotheses are more likely to apply to badgers: devaluing the previous male’s sperm (Walker 1980; McKinney et al. 1983), promoting sperm competition (Møller & Birkhead 1989), reducing socially disruptive male–male competition and the risk of infanticide from males (Bertram 1975; Hrdy 1979; Ebensperger 1998; Wolff & Macdonald 2004) and promoting genetic diversity (Williams 1975). We discuss evidence for these hypotheses and for the genetic incompatibility hypothesis (Zeh & Zeh 1996).

Females that are mounted multiply may also be mounted repeatedly by the most recent male in order to devalue the previous male’s sperm (Walker 1980; McKinney et al. 1983). This hypothesis predicts that when copulation is not forced females should not allow the first male to mount again, after the female has been mounted by a second male, and that copulations should not occur outside of the oestrous period (Hunter et al. 1993).

Sperm competition theory predicts that the highest-quality males should gain paternity, with females then gaining genetic benefits from sons that can bias paternity, if male ability to bias paternity after copulation is heritable (Birkhead & Møller 1992). To incite postcopulatory sperm competition, females may signal their reproductive status to attract mates (O'Connell & Cowlishaw 1994; but see Maestripieri et al., 2005). Female badgers may signal their reproductive status by vocalizing during mounting (Paget & Middleton 1974; Wong et al. 1999), allomarking (Buesching et al. 2003) and object marking (Buesching & Macdonald 2004). Additionally, their vulva may swell and turn pink (Neal & Cheeseman 1996), although whether these changes can be detected by males is unproven. Scent marking at latrines (Kruuk 1978; Roper et al. 1986; Pigozzi 1990; Roper et al. 1993; Revilla & Palomares 2002), sett entrances (Buesching & Macdonald 2004) and through allomarks (Buesching et al. 2003) increases around the postpartum mating season. We suggest that female scent-marking behaviour may therefore attract mates, thereby promoting promiscuity and sperm competition. Sperm competition theory, however, predicts that copulations should not occur outside of the oestrous period (Hunter et al. 1993).

The genetic diversity hypothesis proposes that promiscuous mating should increase genetic diversity at the level of the litter (Williams 1975), whereas the genetic incompatibility hypothesis proposes an increase at the level of the individual (Zeh & Zeh 1996; Jennions 1997; Jennions & Petrie 2000). Half of the badger cubs in the study population are sired by extragroup males, primarily neighbouring males (Dugdale et al. 2007), and neighbouring badgers are less related than within-group badgers (Dugdale et al. 2008), so promiscuous mounting with extragroup mates may increase genetic diversity and reduce genetic incompatibility. Relatedness analyses of mother–offspring and mother–litter are required to test these hypotheses. These hypotheses, however, do not explain repeated mountings or mountings outside of the oestrous period.

Finally, it has been hypothesized that promiscuous mounting reduces the level of male–male aggression around mounting, and in return paternity confusion reduces the risk of infanticide from males (Bertram 1975; Hrdy 1979; Wolff & Macdonald 2004). Bite wounds are more commonly seen in male than female badgers (Macdonald et al. 2004; Delahay et al. 2006). Bite wounding generally peaks around the postpartum mating period (Cresswell et al. 1992; Delahay et al. 2006), although one study found no seasonal trend (Macdonald et al. 2004). Additionally, circumstantial infanticide has been reported in badgers (Kruuk 1989; Lüps & Roper 1990; Cresswell et al. 1992; Woodroffe & Macdonald 1995a; Dugdale et al. 2003). Infanticide may be a form of predation; however, although Lüps & Roper (1990) reported a cub in the stomach of a road kill badger, the road kill was female. If males commit infanticide, which is feasible given the altricial state of cubs at birth, infanticide is not an attempt to reduce paternal care, as this does not occur in badgers (Dugdale et al. 2010). Infanticide is unlikely to reduce the interbirth interval in badgers, as females only give birth once a year (Neal & Cheeseman 1996). In years of low food availability, however, infanticide may decrease competition for food resources. If males commit infanticide, females that are mounted promiscuously will obscure the paternity of their litters and may reduce the risk of infanticide from males (Bertram 1975; Wolff & Macdonald 2004). This hypothesis is compatible with repeated mountings and mountings outside of the oestrous period.

We present the most detailed study of the pattern of badger mounting behaviour to date. In combination with genetic parentage data, we then ask four questions. (1) Is the evolution of promiscuous and repeated mounting behaviour best explained by devaluing the previous male’s sperm (Walker 1980; McKinney et al. 1983), promoting sperm competition (Møller & Birkhead 1989) or reducing socially disruptive male–male competition around mounting and the risk of infanticide from males (Bertram 1975; Hrdy 1979; Ebensperger 1998; Wolff & Macdonald 2004)? (2) Is mounting frequency skewed among badgers, and, if so, which traits are associated with mounting frequency? (3) Does mounting success correlate with parentage success? (4) Do females trade mountings for social services, such as allogrooming?

METHODS

Study Site and Population

We filmed at two neighbouring groups in Wytham Woods, Oxfordshire, U.K. (01° 19’W, 51° 46’N). The primarily deciduous woodlands are enclosed by a deer fence that contains most of the badger setts (dens) and encompasses 4 km^2. Badger social groups consist of a main sett and several smaller setts throughout the territory, and territory borders in the study area are mapped every 2 years by bait marking (Delahay et al. 2000). There were 20 active social groups in 1995, 27 in 2004 and 26 in 2005; the mean (1987–2005) was 19 ± 2 (means are provided ± their 95% confidence intervals, unless otherwise stated). These groups (1987–2005) contained a mean of 5.6 ± 0.4 candidate mothers and 5.8 ± 0.4 candidate fathers, of which 1.9 ± 0.1 were assigned as mothers or fathers (Dugdale et al. 2010). The adult (Macdonald & Newman 2002) and cub (Dugdale et al. 2003) population sex ratios do not differ from 50%.

Sample Collection and Genetic Analyses

Fieldwork was carried out under Home Office and English Nature licences. Badgers were usually trapped four times a year, for 1 week in January and 2 weeks in each of June, August and November (Macdonald & Newman 2002). Badgers were trapped in box traps baited with peanuts, sedated by an intramuscular injection of approximately 0.2 ml/kg ketamine hydrochloride (Vetlar; Pharmacia and Upjohns, Crawley, U.K.), sexed, and identified through a unique tattoo on the inguinal area (Hewitt et al. 2009). Tooth wear was graded on a scale of 1 to 5 (Dugdale et al. 2007). Badgers were aged as cub or adult, based on size; badgers first caught as an adult with tooth wear of 4–5 were judged to be at least 2 years old, otherwise they were judged to be at least 1 year old (da Silva & Macdonald 1989). We estimated an index of body condition that we calculated as observed body weight divided by expected weight, obtained from a regression of weight and head–body length (Dugdale et al. 2003). Head-body length data were only collected from 1990 onwards. Body condition index was taken as the mean over the period May–August after the observed mating period. Blood (ca. 3 ml from the jugular vein) or guard hair (ca. 100) samples were collected for genetic analyses.

We used previously published parentage (Dugdale et al. 2007) and relatedness (Dugdale et al. 2008) data from 915 badgers that were genotyped for 16–22 microsatellite loci. These studies assigned parentage through a likelihood-based approach in CERVUS 3.0.1.8 (Kalinowski et al. 2007) and COLONY 1.2 (Wang 2004) and estimated the Queller & Goodnight index of pairwise relatedness (R) using RELATEDNESS 5.0.8 (Queller & Goodnight 1989). In addition, we assigned parentage to a further four cubs , using the methods described previously by Dugdale et al. (2007). Overall, paternity was assigned for 611 of 630 cubs conceived in 1987–

2004 (Dugdale et al. 2007) and three of four cubs conceived in 2005 with 80% confidence. Owing to delayed implantation, females give birth in the year following conception (reviewed in Yamaguchi et al. 2006). Parent pairs were assigned to all 17 genotyped cubs that resulted from the mountings in the filmed social groups; one of the cubs conceived in 2005 was not genotyped (Table 1).

Behavioural Analyses

Filming took place at two neighbouring social groups between 1 February and 31 May in 1995, 2004 and 2005. We define this as the postpartum mating season based on the following physiological and behavioural evidence. Plasma testosterone (Maurel et al. 1977) and spermatozoa levels (Page et al. 1994) peak in males in February, declining to a minimum in October or November, when testes may ascend into the body cavity. The proportion of females carrying large follicles also peaks in February, and again in August (Cresswell et al. 1992). Owing to delayed implantation, females do not implant ova until triggered by a change in the photoperiod around December (Canivenc et al. 1985), and in lowland U.K. they give birth once a year around February. Anecdotal observations of mountings (Neal & Cheeseman 1996) show they may occur throughout the year, with one postpartum peak in early spring and a smaller peak from July to September. The main peak in mounting behaviour is around February (Neal & Cheeseman 1996) and blastocysts from this period represent the majority of those present preimplantation (Cresswell et al. 1992), suggesting that this is the most important mating period.

We used infrared-sensitive remote video surveillance systems (Stewart et al. 1997) at one focal social group (Pasticks) in all 3 years, and at one neighbouring group (Pasticks Outlier in 2004 and 2005; Sunday's Hill in 1995). Filming equipment was installed and checked during daylight hours to minimize disturbance to the nocturnal badgers. Data were collected continuously, throughout the night, with cameras focused around active sett entrances covering a field of view of ca. 13 m^2. We could not film all mountings given that the fixed field of views limited the observation area. Our behavioural data therefore provide a snapshot view of above-ground mounting behaviour, around sett entrances, during the postpartum mating period. We analysed 960 videotapes, corresponding to 319 calendar nights (totalling 11 230 h; Table 1). Adult and yearling badgers were identified through clip marks, where the tips of guard hairs are removed, resulting in a visible white under fur pattern that contrasts with the remaining black guard hairs under infrared light (Stewart & Macdonald 1997). We also recorded unmarked badgers, unmarked cubs and the occasional unidentifiable clip-marked badger. The yearly social-group compositions are detailed in Table 1, and interobserver reliability is given in Dugdale et al. (2010).

We recorded each incidence of mounting behaviour (ejaculation cannot be detected through observation) and the duration of each incidence. Mounting events commenced when the mounting badger grabbed the mounted badger by the scruff of the neck and finished when the neck hold was released, after which the badger dismounted. Occasionally the neck hold was released during the mounting event in which case the end time was when the male dismounted. If the male dismounted only briefly this was still classified as a separate mounting event. We recorded failed mounting events when: (1) the male was not directly aligned with the female (and thus genital contact was not possible); (2) the mounting badger was female or a cub; or (3) the mounted badger was male or a cub (cubs are not sexually mature generally until they are yearlings, Neal & Harrison 1958; Ahnlund 1980). We also recorded the identity of badgers that were present during mounting events and whether they interacted with the mounting badgers.

Although badgers may be induced ovulators and exhibit superfetation (conception during pregnancy; reviewed in Yamaguchi et al. 2006), they do have ovarian cycles that last 28 days, in which an oestrous period lasts 3–12 days (Service et al. 2002). We therefore defined the day on which a female was first observed mounting as day 1, and noted further mountings, up to and including day 28, to see whether mountings within this period spanned more than 3 or 12 days.

We recorded each incidence of directed aggression and sequential allomarking (defined by Hewitt et al. 2009). We also recorded escalated aggression events (whereby both badgers initiated and received aggression in the same incident) and the number of bouts of activity in which males were observed self-grooming (activity bouts began when the first badger was seen on screen and ended when there was 1 min without a badger on screen). Finally, we recorded dyadic allogrooming events, in which a male badger groomed a female badger (whether or not the female reciprocated); allogrooming events terminated when the dyad physically moved apart.

Statistical Analyses

We used SAS 9.2 (SAS Institute, Cary, NC, U.S.A.) for our statistical analyses, unless otherwise stated, and we ran generalized linear models (GLMs) using a maximum likelihood method or generalized linear mixed models (GLMMs) using a Laplace method in the GLIMMIX procedure (Littell et al. 2006).

Skew in mounting and parentage

We quantified skew in within-group mounting events, for both males and females separately, by calculating the binomial skew index (β) using SKEW CALCULATOR 2003 1.2 (Nonacs 2000). One-tailed *P* values and two-tailed 95% confidence intervals of β were calculated over 10 000 simulations. We tested whether we had power to detect skew based on mean values (pooled over years: group size = 8, 34 mounts, two nonmounters and equal distribution of mounts across other group members) and 10 000 simulations. This suggested one group would be sufficient. The mean β across all groups was therefore tested by pooling data over years for the same social group, and its one-tailed *P* value was also calculated. β is the observed variance in skew minus the expected variance if all individuals had equal chance of being observed mounting/mounted, adjusted for group size, number of within-group mounting events and the observation probability of each individual. β can range from –1 to +2; it is positive when skew is greater than expected, zero when randomly distributed and negative when more evenly distributed than expected. The minimum β is calculated through equal sharing of mounting among group members, and the maximum β is calculated through monopolization of mounting by the individual observed mounting the most. The one extragroup male that was observed mounting once, in one social group, was excluded from the skew analyses.

We calculated β in within-group parentage, for each sex separately. Only groups with at least two cubs assigned a parent in the same year were analysed, as SKEW CALCULATOR 2003 cannot detect significant reproductive skew in groups with just one cub, unless there is a large discrepancy in residency times. Residency was set to one, as all individuals were seen on screen during the postpartum mating season (except for one unclipped female, who was later trapped in the group and assigned as a mother; she was included with a residency of one). We excluded one group, in 1 year, when one cub was not genotyped and therefore not assigned parentage (Table 1).

Parentage success of mounting badgers

We ran a GLMM with Poisson error structure and log link. The response was the number of within-group cubs a badger (*N* = 48) was assigned parentage of the following year. Categorical fixed effects were social group, year and sex. Continuous fixed effects were total number of activity bouts in that social group that year and the number of mounts observed. Social group and year both had three classes, which is too few to estimate variance through inclusion as random effects (Bolker et al. 2009). Badger identity was entered as a random effect to control for 12 badgers present in more than 1 year. Fixed fields of view are problematic as some badgers may be rarely seen, although they are close by; hence, there is a greater chance of observing behaviours by those individuals that are on screen for longer. The number of bouts of activity in which a badger was observed was included as a continuous fixed effect to control for the likelihood of observing the male.

Correlates of male mounting frequency and paternity success

We ran a GLM with Poisson error structure and log link (Littell et al. 2006), for 15 males (with no repeated measures). We entered the number of mountings by males that we observed as the response, and the predictors were body condition index, dominance rank (Hewitt et al. 2009) and the number of times that the male was observed self-grooming. Social group was fitted as a fixed categorical effect, (few levels prevented inclusion as a random effect). Year and the number of bouts of activity in which the male was observed were included as continuous fixed effects.

We ran a GLMM with Poisson error structure and log link, including year, badger identity and social group as random effects. The response was the number of cubs that males were assigned parentage of in the following year (1991–2005). Fixed effects were age, age^2 and body condition index (N = 833 records for 289 males). We included age, as this has a concave-down relationship with the number of cubs sired (Dugdale et al. 2011), and re-ran the analysis on a restricted data set containing only the 188 males of known age (i.e. first caught as a cub) to confirm that the result held.

Mounting partner choice

We calculated Kendall's partial row-wise matrix correlation ($\tau_{rw;XY.Z,}$ de Vries, 1993). We ran 10 000 permutations, permuting rows and columns independently, to assess the significance of $\tau_{rw;XY.Z}$ using the software MATMAN 1.1 (de Vries et al. 1993). We created matrices with females in the rows and males in the columns for each social group, in each year, including the one extragroup male who was observed mounting. We tested the row-wise conjecture that the number of times each female was mounted by each male was correlated with their pairwise Queller & Goodnight (1989) index of relatedness (R) or the number of times each male initiated aggression at, sequentially allomarked or allogroomed each female. A matrix of the number of bouts of activity in which each pair were present controlled for individual variation in on-screen presence. We accounted for multiple tests through false discovery rate (FDR) control (Benjamini & Hochberg 1995). We assessed overall significance, across social groups, using Fisher's method of combining probabilities (Sokal &

Rohlf 1994); as some badgers were present in Pasticks in both 2004 and 2005 and Pasticks Outlier in 2004 and 2005, we deleted the lowest *P* value from each of these pairs and tested across four social-group-years.

RESULTS

Patterns of Mounting Behaviour

We observed 198 mounting events on 90 calendar nights (Table 1); in 89 of these events (on 50 calendar nights) both mounting partners were identified, with a peak in February and March (Fig. 1). We also observed 59 failed mountings of females, by males, in which genital contact was not made. We observed one mounting between an extragroup male and a resident female; no other male was present on screen. All other mountings were between members of the same group.

Mean mount duration was 230 ± 95 s (median = 34 s, $N = 198$; Fig. 2). Mountings were classified into short (< 1 min: range 1–58 s, mean = 20 ± 3 s, $N = 127$), medium ($1 \leq t < 5$ min: mean = 141 ± 21 s, $N = 43$) and long duration (≥ 5 min: maximum = 82 min, mean = 23 ± 9 min, $N = 28$). Mean mount duration, of identifiable badgers only was 235 ± 191 s ($N = 89$; Fig. 2). Sixty-two of these mounts were short (mean = 22 ± 4 s), 16 medium (mean = 130 ± 28 s) and 11 long duration (mean = 27 ± 17 min). In the long-duration mountings, females were observed mounting 0–2 nights previously, and males 0–15 nights previously. Three females were mounted for long durations by two different males, with a mounting interval of 6 s – 2 days. The mean time between two males mounting the same female on the same night was 14 ± 28 min (range 0–53 min, median = 3 min, $N = 5$).

Mounting Outside of the Oestrous Period

Of 16 females that were observed mounting, 12 were observed mounting more than once. Seven were mounted in more than one 4-week period in the same year. Seven females were observed mounting with an interval of between 4 and 25 days; five of these females had intervals of more than 12 days.

Polygynandrous and Repeated Mounting

For the 89 mounting events for which both individuals were identified, males, females and mounting pairs were observed repeatedly mounting, both throughout the season (Fig. 3a) and on the same night (Fig. 3c, e). Males and females were also observed mounting promiscuously within a season (Fig. 3b) and within a night (Fig. 3d, f).

Skew in Mounting and Parentage

Across groups, pooled over years, there was significant skew in male mounting behaviour (simulation: mean $\beta = 0.06$, range = 0.01–0.12, $N = 3$, $P = 0.003$), but not for females (simulation: mean $\beta = 0.18$, range = 0.07–0.37, $N = 3$, $P = 0.052$), although P was low. The positive β indicated that some males were observed mounting more than would be expected with random distribution of mounting events among within-group males (controlling for the number of activity bouts in which individuals were observed on screen, group size and overall levels of group activity). One-tailed tests showed that some males mounted, or some females were mounted, more than expected at random in two (Fig. 4a) and four (Fig. 4b) social-group-years, respectively. Equal sharing of mounting among group members, however, could not be ruled out for males in five social-group-years and females in three social-group-years, as the lower 95% CI equalled the minimum possible β (Fig. 4a, b).

Across groups, there was no skew in maternity (simulation: mean $\beta = 0.11$, range = -0.06–0.44, $N = 3$, $P = 0.10$), and the one group with more than one cub assigned a within-group father did not show skewed paternity (Fig. 4c). Power to detect skewed parentage, however, was low as the 95% confidence intervals covered most of the region from the lowest to highest possible β (Fig. 4c).

Parentage Success of Mounting Badgers

The number of mounting events did not correlate with the number of offspring an individual was assigned parentage of the following year (GLMM: estimate = -0.09 ± 0.06, $F_{1,8} = 2.3$, $P = 0.17$). We did not observe any of the 15 assigned parent pairs (of the cubs born the following year) mounting together.

Correlates of Male Mounting Frequency and Paternity Success

Males that were observed mounting the least had a higher body condition index (between May and August) than those that were observed mounting most, but mounting frequency was not correlated with rank or self-grooming frequency (Table 2). Six males, however, had no dominance rank as their groups showed no linear hierarchy; when this variable was omitted body condition index was not related to mounting frequency (GLM: estimate = 4.57 ± 2.13, $F_{1,13} = 1.1$, $P = 0.31$). In contrast, males that were assigned more cubs in a year had a higher index of body condition (between May and August) in the previous postpartum mating season than males that were assigned fewer cubs, controlling for age, social group, year and repeated measures on an individual (Table 3). The relationship held when restricting the data set to 188 badgers of known age (GLMM: estimate = 2.97 ± 0.83, $F_{1,357} = 12.8$, $P = 0.0004$).

Mounting Partner Choice

Females were observed mounted more often by males that allogroomed them more often in two social-group-years (Table 4), with an overall significant effect (Fisher's method of combining probabilities: $\chi^2_8 = 25.7$, $P < 0.01$). On average, females within a social-group-year were allogroomed 44 ± 18% of the time by males.

There was no relationship between the number of times that females were observed mounted by males and the number of times that males directed aggression at them (Fisher's method of combining probabilities: $\chi^2_8 = 12.3$, $P > 0.05$) or allomarked them ($\chi^2_8 = 13.1$, $P > 0.05$; Table 4). There was also no relationship between mounting frequency and relatedness of mounting pairs ($\chi^2_8 = 9.4$, $P > 0.05$; Table 4).

Male–Male Behaviour around Mounting

On 29 mounting events, in 11 bouts of activity, a second male was observed. Aggression was observed between the mounted and second male in eight (73%) bouts: unreciprocated aggression (mounted male to second male) in four (37%) bouts, unreciprocated aggression (vice versa) in four (37%) bouts, and escalated aggression (the receiver reciprocated) in six (55%) bouts. Allogrooming was observed between these males, however, in six of the eight bouts in which aggression was observed.

On two of the three occasions when females mated promiscuously on the same night, the first male remained on screen when the second male mounted, but was never observed interacting with the mounting badgers.

DISCUSSION

Polygynandrous and Repeated Mounting

Males mounted more than one female and females were mounted by more than one male during the postpartum mating period, and on the same night. Furthermore, on approximately a quarter of the nights when females were observed mounted, females were mounted repeatedly by the same male. We discuss whether these findings are explained by three hypotheses, which are not mutually exclusive.

Devaluing the previous male's sperm

Although females successfully prevented males from mounting them, females were mounted by more than one male and were mounted repeatedly by some males. We also observed for the first time, however, female badgers being mounted twice by a male, and by a different male in between these mounts. As mounting duration varies, the later mounting by the first male may have occurred outside of the oestrous period or may not represent a successful mounting. One female, however, was mounted, for a long duration, by two males on the same night and then by the first male on the next night, again for a long duration; thus, females are not devaluing the previous male's sperm.

Promoting sperm competition

We recorded females vocalizing during mounting and we observed males sniffing the genital area of females before mounting and also while another male was mounting. Sperm competition may therefore play a role in female promiscuity in badgers, but it does not explain why mountings occur outside of the oestrous period.

Reducing male–male aggression and the risk of infanticide from males

This hypothesis best explains the paradoxical promiscuous and repeated mountings of female badgers, and both the cooperative allogrooming behaviour observed between males and the levels of male–male aggression. When a second male was present during mounting events, male–male aggression was commonly observed, but this did not always escalate. Additionally, males allogroomed each other in many of these bouts. Males did not appear to mate-guard females from within-group males; on three occasions when a within-group male mounted a female for a long duration, the male did not interact with a second within-group male when the second male mounted the same female on the same night, although interactions may have occurred outside of the field of view. Males, however, may continue mounting well after ejaculation, as a form of mate guarding, in an attempt to maximize their likelihood of paternity. As ejaculation could not be detected, and mating order effects are unknown in badgers, this cannot be ruled out. As the majority of males were observed mounting, female promiscuity may reduce the level of male–male aggression around mounting. Additionally, the high relatedness of within-group males (Dugdale et al. 2008) may further reduce the level of within-group male–male competition over access to mates.

Promiscuous mounting of females may therefore reduce within-group male–male competition around mounting; however, it is likely that competition occurs between within-group and extragroup males. Resident males were not present during the only extragroup mounting that we observed. Christian (1995) reported a resident male chasing an extragroup male from his territory, after which the resident male object-marked around his territory border. Object marking (Buesching & Macdonald 2004), sequential allomarking (Buesching et al. 2003) and the use of boundary latrines by males (Roper et al. 1993) increase around the postpartum mating season, which may be subtle mate guarding of within-group females from extragroup males. Additionally, extraterritorial ranging (Roper & Lüps 1993) and expansion of a neighbouring male's territory (Revilla & Palomares 1999) upon the deaths of resident males have been inferred as attempts to gain access to females for mating. Overall, promiscuous mounting of females may reduce male–male aggression around mounting, although subtle forms of mate guarding, especially from extragroup males may occur.

Urine oestradiol levels, which may be elevated in females for 3–12 days (Service et al. 2002), and our observation of long-duration mountings clustered within a 3-day period suggest that female badgers may have an oestrous period. By being mounted by males outside of this period (if males are unable to detect correctly the oestrous period and if sperm viability is short) or being mounted by males for a short duration within this period (if short-duration mountings are less likely to be successful), females may reduce the risk of infanticide from males, while masking paternity.

These three hypotheses are not mutually exclusive and it is likely that more than one may play a role in the promiscuous and repeated mounting of female badgers. Promiscuous and repeated mounting of female badgers is likely to have evolved originally as a strategy to reduce male–male aggression around mounting and infanticide from males. Once this strategy evolved, sperm competition and benefits from increased genetic diversity or genetic compatibility may be a factor in the occurrence of promiscuous mounting of females; further studies are required to test this.

Skew in Mounting and Correlated Traits

At least 10 of 11 yearling females were mounted, and each season 70% of the filmed females were observed being mounted, which corresponds to post mortem studies in which the majority of yearling and adult females conceive (reviewed in Yamaguchi et al. 2006). Females varied in their mounting behaviour between the 2 years for which repeated observations were made, with some mounted in 1 year but not in the next, although mountings may have occurred away from filming. There was no significant skew, however, in the distribution of mounting events among within-group females over groups and years, although skew did occur in four social-group-years. This vriability may be linked to the fact that reproduction in female badgers may be controlled by both individual adaptation to local food availability and female–female competition (Dugdale et al. 2008). Filming was restricted to the areas around active sett entrances and it is probable that individuals also mounted later in the year or elsewhere as mounting has been heard underground (Paget & Middleton 1974), heard (Neal & Harrison 1958) and observed (Neal & Cheeseman 1996) in the territory away from the main sett, and observed outside of resident territories (Paget & Middleton 1974; Christian 1995; this study).

All males were observed mounting, except in one group where only two mounting events were observed (by one male). Although only two social-group-years showed skewed mounting, overall there was significant skew in mounting frequency among within-group males. We did not detect skew in maternity or paternity, but we had low power to detect this, and a larger data set has shown skewed parentage among within-group candidate mothers and fathers (Dugdale et al. 2008).

The number of mounts by a male was not correlated with their dominance rank or the number of times the male was observed self-grooming. This is consistent with a previous study that found no effect of rank on male reproductive success; however, power to detect this was low (Hewitt et al. 2009). Males with a lower body condition index were observed mounting more often; however, the sample size was small and this relationship was not found when six badgers from groups without linear dominance hierarchies were included in a model without rank as a predictor.. A previous study found no difference in the body condition of male badgers that were sexually mature but were either sexually active or not active (Woodroffe & Macdonald 1995b). In contrast, paternity success was positively correlated with body condition, such that fatter males gained more paternity than thinner males, as reported in other mammals (Raveh et al. 2010). Body condition may therefore be a phenotypic predictor of male fitness, but females could allow males that do not father their offspring to to minimize the risk of infanticide.

Mounting Partner Choice

Female badgers may impose a degree of overt mate choice. Females have been observed to refuse mountings by flattening their body on the ground (Neal & Harrison 1958) or, as we observed, by turning on their side or backing into sett entrances. Additionally, females may choose to mate with extragroup over within-group males; however, it is not known which sex solicits extragroup matings or where they occur. Extragroup males have been observed mounting resident females (Paget & Middleton 1974; Christian 1994, 1995) but both males and females have been seen in neighbouring territories (Christian 1994). Our observation of one extragroup male mounting a resident female adds to the anecdotal evidence that males solicit extragroup matings. Furthermore, in our population males make more temporary moves between groups than females (from trapping data, Macdonald et al. 2008), but detailed tracking is required to confirm this. Males may therefore solicit mountings in extragroup female territories, but females are able to refuse mountings in addition to the opportunities that they have for cryptic female choice during delayed implantation and potential superfetation, and by reabsorption of implanted embryos (Yamaguchi et al. 2006).

Females may trade mountings for a social service (Stopka et al. 2001); females were groomed half of the time by males, and overall were observed mounted more often by males that allogroomed them more often, suggesting a biological market. The relationship was not significant in four social-group-years, however, suggesting variation according to context. There was no relationship between the amount of aggression that a male directed at a female, or the number of times that they allomarked a female, and the number of mountings observed between them.

In conclusion, promiscuous and repeated mountings may reduce male–male aggression around mounting and the risk of infanticide from males. Additionally, promiscuous mounting of female badgers does not devalue the previous male’s sperm, but may promote sperm competition, and may increase genetic diversity and compatibility. Mounting frequency did not correlate with parentage success. Mounting durations were very variable and ejaculation may potentially occur only in the long-duration mountings, but none of the long-duration mountings were between males and females that sired offspring together, reinforcing the findings that mounting observations do not always correlate with genetic success (Hughes 1998; Coltman et al. 1999).

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FIGURE LEGENDS

Figure 1. Histogram of the number of mountings observed, by all (including unmarked) and by marked badger pairs, per month. The number of mountings, per hour of footage observed, is shown as a line.

Figure 2. Duration of observed mounting events (s), log transformed, against the number of observed mounting events. Grey bars include unmarked or unidentifiable individuals. Black bars represent identified badgers only. d = log duration.

Figure 3. Mean number of times that focal units (mounting males, mounted females and mounting pairs) were observed mounting (a, c, e), and mean number of partners that focal units (mounting males and mounted females) were observed mounting with (b, d, f) per season (a, b), per night that the focal unit was observed mounting at least once (c, d), and per night that the focal unit was seen mounting more than once (e, f). Error bars represent the 95% confidence intervals. Solid black dashes indicate the minimum and maximum values; numbers above graphs are the number of observations per focal unit.

Figure 4. Binomial skew index (β) of mounting behaviour among within-group (a) males and (b) females, and of (c) parentage. β is positive when mounting/parentage is distributed among fewer individuals than expected at random. Error bars display the two-tailed 95% confidence intervals. * indicates that β is significantly greater than zero (one-tailed test; horizontal line indicates β = 0). Data were collected in two neighbouring groups each year: P = Pasticks; PO = Pasticks Outlier; SH= Sunday's Hill. Solid black dashes indicate the minimum (equal sharing) and maximum (monopolization by one individual) possible values of β within each group.

Table 1 The composition of each of the six filmed social-group-years, along with the number of hours of footage analysed, the number of mountings observed and the number of parents assigned to the cubs from these mating seasons

	1995		2004		2005	
	P	SH	P	PO	P	PO
Adult & yearling females	8	4*	4†	4	7	4
Adult & yearling males	6*	10	3†	3†	2†	2
Unmarked[‡]	5	4	2	1	2	3
Badgers known to be unmarked[§]	5[a]	4[b]	1[c]	1[d]	0	3[e]
Group size (excluding cubs & including known unmarked badgers)	19	18	8	8	9	9
Total observation time (h)	1383	1242	2444	798	3872	1491
Total number of mountings	72	13	49	15	34	15
Mountings of identifiable pairs	7	2	24	12	34	10
Resulting cubs	2	1	6	5	3	1
No. of assigned mothers	1	1	4	3	2**	1
No. of within-group fathers	0	1	1	1	0**	1
No. of extragroup fathers	1	0	3	2	2**	0

P = Pasticks, PO = Pasticks Outlier, SH= Sunday's Hill.

Additional badgers were present in this category, but were not seen on screen (1 adult male in P 1995 and two adult females in SH 1995), so they were excluded from the analyses and the group size estimate.

† Additional badgers were not present for all of the study period, either because they were found dead (one adult male in P 2004 and in P 2005) or presumed dead as they were only seen for a maximum of 3 days and then were not seen again (two adult females in P 2004, and one adult male in PO 2004). As we did not observe any of these individuals mounting, they were excluded from the analyses and the group size estimates.

[‡] 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 the majority (two males and one female at P and SH in 1995 were not clipped until May) of the study, from trapping records are: [a] five females; [b] three males and one female; [c] one female; [d] one male; [e] two males and one female.

**One cub conceived by a P female in 2005 was not genotyped.

Table 2 Factors influencing the number of mounting events by 15 males.

Fixed effect		Estimate	SE	*df*	*F*	*P*
Intercept		4187.03	754.94			
Social group	P	21.67	3.43	2,7	67.8	**< 0.0001**
	PO	23.26	3.85			
	SH	0.00				
Year		-2.10	0.38	1,7	13.6	**0.008**
Bout		$1.9\text{x}10^{-3}$	$9.1\text{x}10^{-4}$	1,7	27.8	**0.001**
Body condition index		-6.03	1.99	1,7	19.0	**0.003**
Rank		0.44	0.61	1,7	0.4	0.533
Self-groom		-0.01	0.01	1,7	0.9	0.373

P = Pasticks, PO = Pasticks Outlier, SH= Sunday’s Hill.

Table 3 Estimates from a GLMM predicting the number of cubs a male (*N* = 289) was assigned paternity of the following year

Fixed effect	Estimate	SE	*df*	*F*	*P*
Intercept	-6.51	0.92			
Age	0.89	0.18	1, 506	0.3	0.592
Age^2	-0.06	0.01	1, 506	25.8	< **0.0001**
Body condition index	2.07	0.72	1, 506	8.3	**0.004**
Random effect					
Year	0.47	0.23			
Individual	0.99	0.24			
Social group	0.02	0.07			

Table 4 Partial Kendall row-wise correlation ($\tau_{rw;XY.Z}$) of the number of times that females, in each social group and year, were observed mounted by within-group or extragroup males and the number of times that the males allogroomed, initiated aggression at or sequentially allomarked the females, or their pairwise relatedness

	P 1995		SH 1995*		P 2004		PO 2004		P 2005		PO 2005	
	$\tau_{rw;XY.Z}$	*P*	$\tau_{rw;XY.Z}$	*P*	$\tau_{rw;XY.Z}$	*P*	$\tau_{rw;XY.Z}$	*P*	$\tau_{rw;XY.Z}$	*P*	$\tau_{rw;XY.Z}$	*P*
Allogrooming	0.46	**0.013**	0.29	**0.001**	0.37	0.085	-0.18	0.235	-0.17	0.500	-0.33	0.505
Aggression	0.40	0.039	-0.01	0.579	-0.13	0.366	-0.09	0.359	0.17	0.287	1.00	0.133
Allomarking	0.07	0.375	0.28	**0.034**	0.00	0.509	-0.15	0.250	Undefined†		-0.52	< **0.0001**
Relatedness	-0.16	0.223	0.05	0.399	-0.55	0.044	-0.39	0.070	0.35	0.207	-0.33	0.491

Analyses controlled for the number of bouts of activity in which pairs of badgers were observed on screen together. P = Pasticks, PO = Pasticks Outlier, SH = Sunday's Hill. *P* values in bold represent significant results after false discovery control for multiple tests ($m = 6$, $\alpha = 0.05$, adjusted $P = 0.050–0.008$).

* Only one female was observed mounted in this group.

† Six females were mounted by two males and the male that mounted them the most was the male that allomarked each female the most and was observed the most with each female. $\tau_{rw;XZ} = 1$ and therefore the partial correlation was undefined, as it resulted in division by zero.

Figure 1

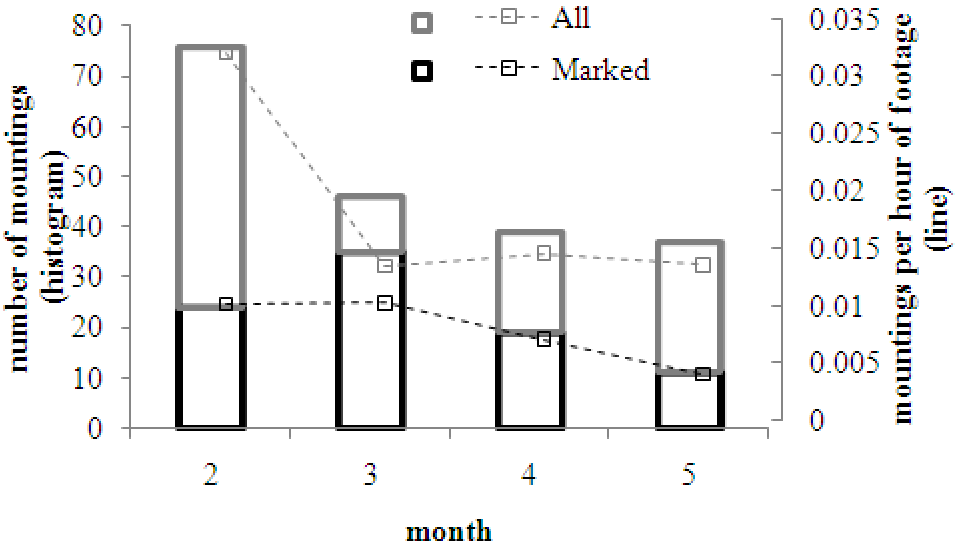

All
Marked
number of mountings (histogram)
mountings per hour of footage (line)
80
70
60
50
40
30
20
10
0
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
2
3
4
5
month

Figure 2

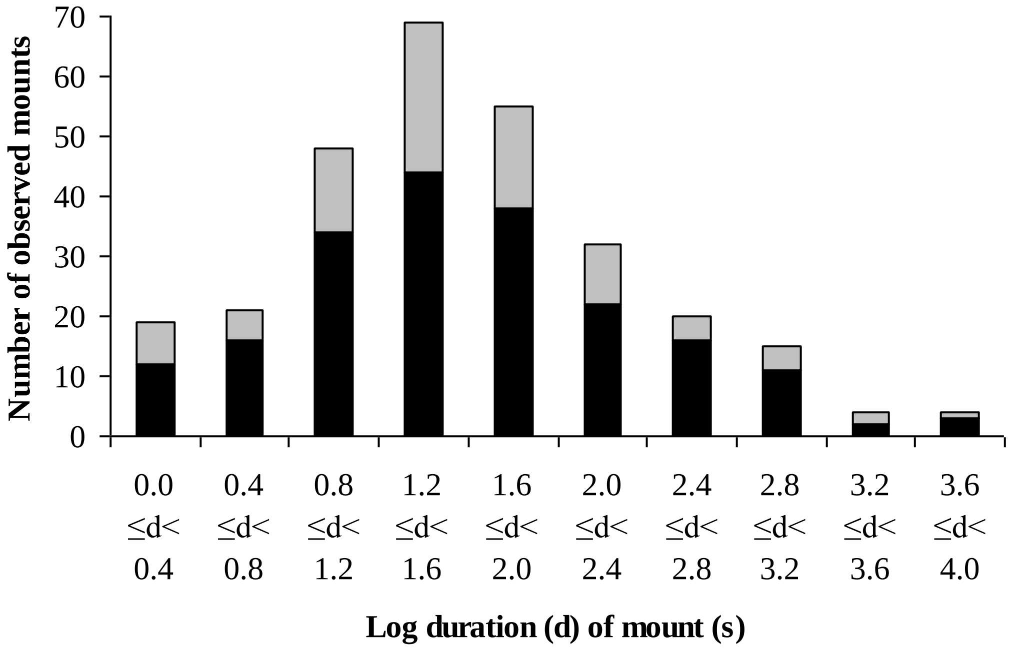
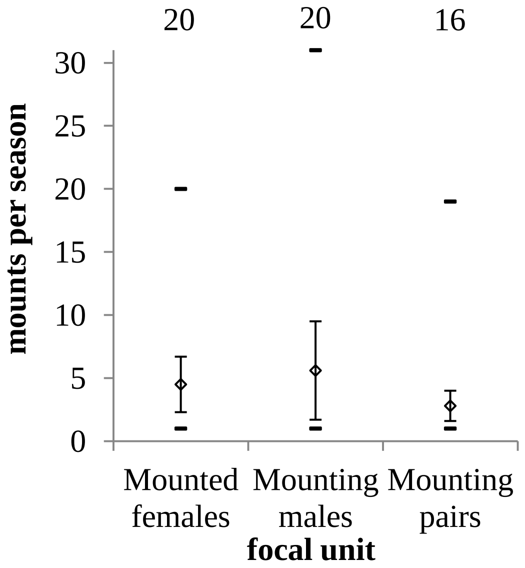
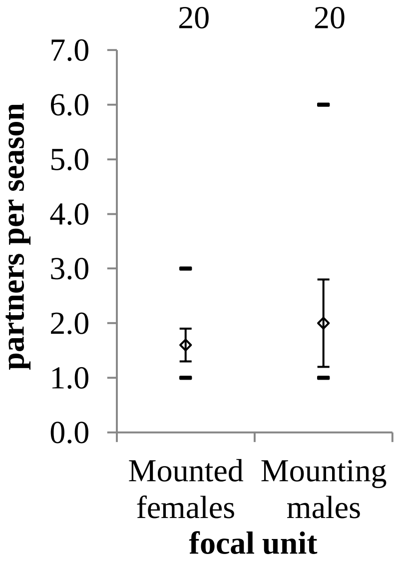

Number of observed mounts
70
60
50
40
30
20
10
0
0.0 ≤d< 0.4
0.4 ≤d< 0.8
0.8 ≤d< 1.2
1.2 ≤d< 1.6
1.6 ≤d< 2.0
2.0 ≤d< 2.4
2.4 ≤d< 2.8
2.8 ≤d< 3.2
3.2 ≤d< 3.6
3.6 ≤d< 4.0
Log duration (d) of mount (s)

Figure 3

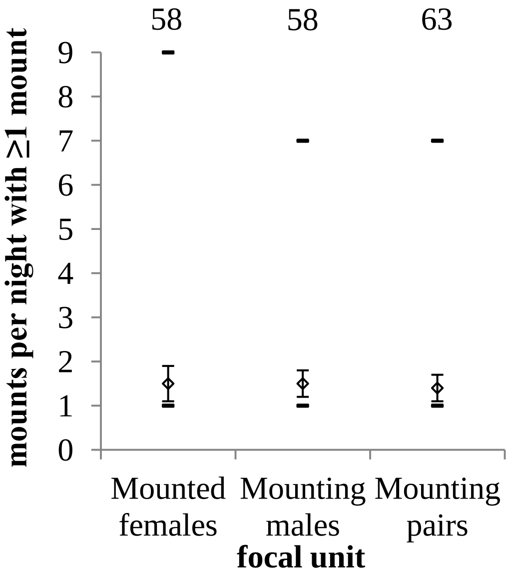
(a)



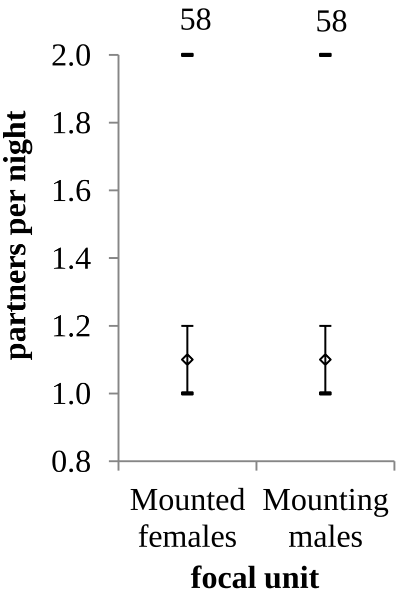
(b)



(c)

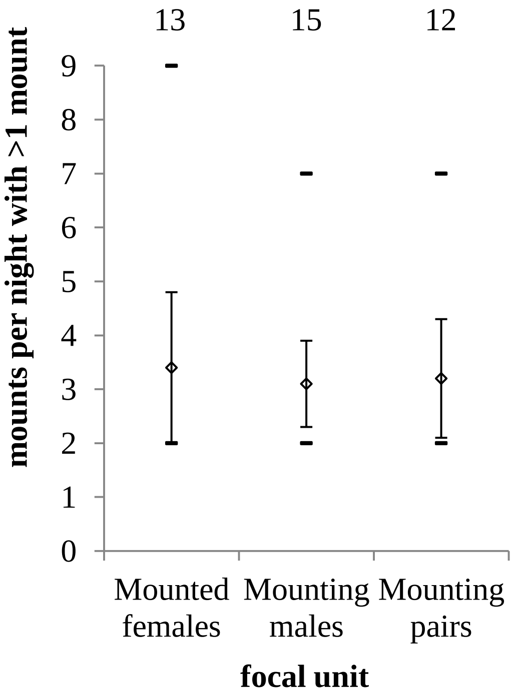


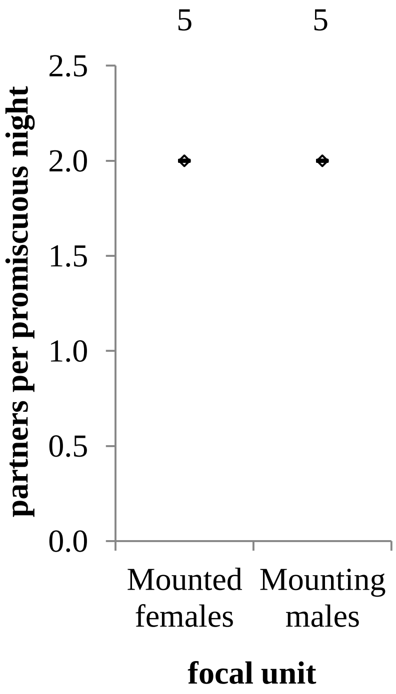
(d)



(e)

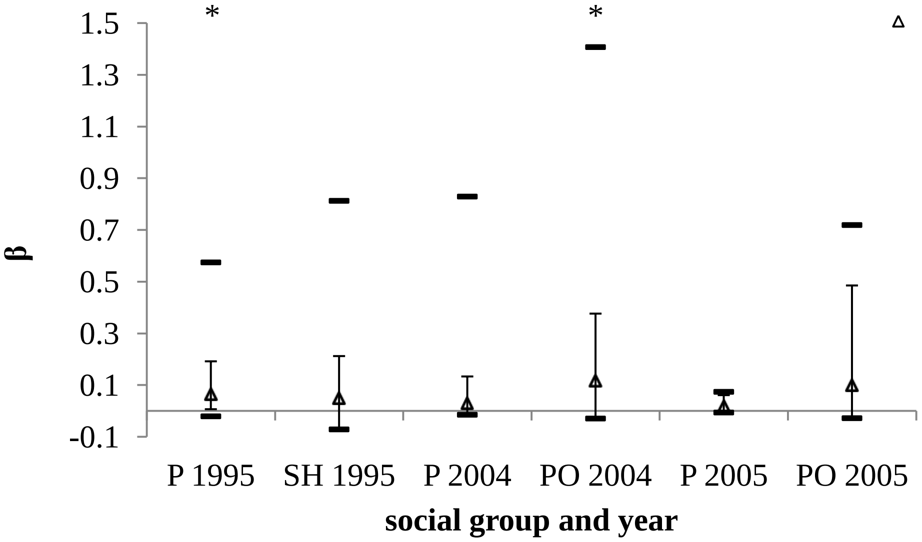
(f)


13
15
12
mounts per night with >1 mount
9
8
7
6
5
4
3
2
1
0
Mounted females
Mounting males
Mounting pairs
focal unit

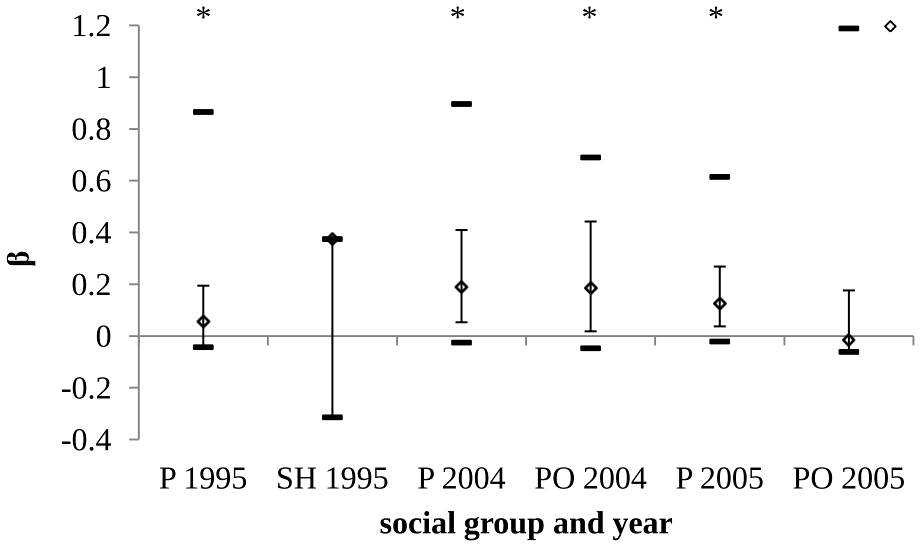

5
5
partners per promiscuous night
2.5
2.0
1.5
1.0
0.5
0.0
Mounted females
Mounting males
focal unit

1 **Figure 4**

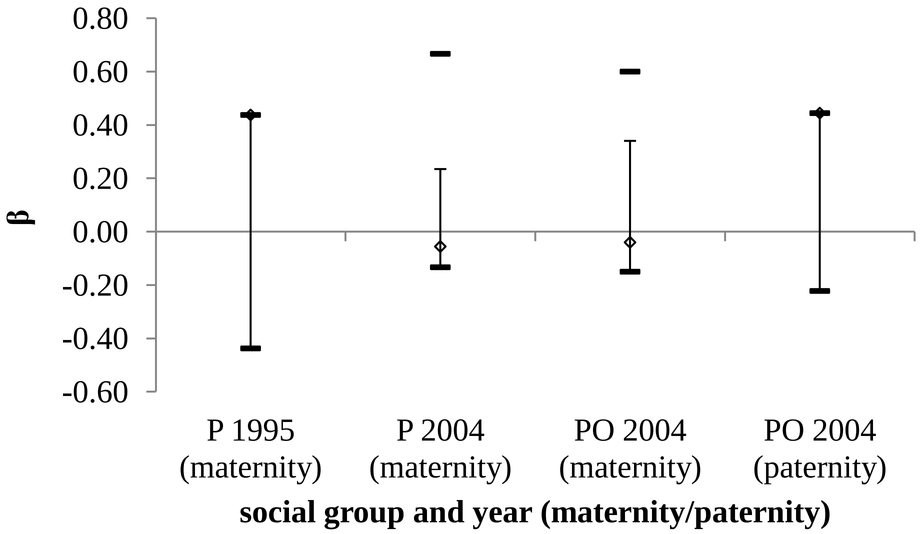
(a)



(b)



(c)


0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
-0.60
β
P 1995 (maternity)
P 2004 (maternity)
PO 2004 (maternity)
PO 2004 (paternity)
social group and year (maternity/paternity)