



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

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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 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.

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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,

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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 $R \pm 95\%$ 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 $R = 0.09 \pm 0.03$) 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 & Cowlshaw 1994; but see Maestriperi 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 1995; 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

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