



Oestrous females investigate the unfamiliar male more than the familiar male in both commensal and non-commensal populations of house mice

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ABSTRACT

We studied female preferences for familiar and unfamiliar males. The subjects were laboratory-born house mice: (1) non-commensal *Mus musculus domesticus* from the eastern part of Syria along the Euphrates River; and (2) commensal *M. m. musculus* from the Czech Republic. Pair-choice preference tests have revealed that oestrous females of both populations sniffed towards unfamiliar males more than familiar males. In the case of females exhibiting postpartum oestrus, this preference was less pronounced and statistically not significant. Thus, our mice clearly exhibited the behavioural pattern known from commensal populations of polygynous and/or promiscuous *M. m. domesticus*. We found no inverse tendency to seek proximity to the familiar male that has been previously reported from closely related and presumably monogamous aboriginal mouse *Mus spicilegus*. We conclude that neither commensal *M. m. musculus*, nor non-commensal *M. m. domesticus*, are likely to share a monogamous mating system with mound-building mice.

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1. Introduction

Monogamy is a derived social and/or mating system that has been extensively studied in terrestrial vertebrates (Gowaty, 1996; Reichard and Boesch, 2003). Monogamy is most frequent in birds (e.g., Ligon, 1999; Bennett and Owens, 2002), only exceptional in reptiles (Bull et al., 1998), and regular but uncommon in mammals. It occurs in less than 5% of mammalian species (Kleiman, 1977), e.g., some small rodents (Waterman, 2007), ungulates (Komers, 1996), carnivores (MacDonald and Sillero-Zubiri, 2004) and primates (Hrdy, 1981), including humans (Murdock, 1967). Most studies of monogamy have been performed in birds and small rodents. While the ecological determinants of mate choice and mate fidelity in the wild have been predominantly examined in birds (cf. Ens et al., 1996), the physiological mechanisms underlying monogamy have been studied in the latter model group (see below). In comparison, the effect of familiarity on pair-bonding has received less attention in both groups.

In small muroid rodents, the most popular mammalian model for behavioural studies, true social monogamy, including pair-bonding, is fairly rare. It has been described in some species of voles (*Microtus ochrogaster*: Getz and Carter, 1980; Getz et al., 1980, 1990,

1993; *Microtus pinetorum*: Fitzgerald and Madison, 1983), deer-mice (*Peromyscus californicus*: Ribble and Salvioni, 1990), gerbils (*Meriones unguiculatus*: Hendrie and Starkey, 1998), and hamsters (*Phodopus campbelli*: Jones and Wynne-Edwards, 2001). Hormone levels have been proposed as a physiological mechanism promoting pair-bond formation (e.g., vasopressin, Winslow et al., 1993). The occurrence of monogamy may be successfully predicted from behavioural data (Dewsbury, 1981) and it is closely associated with paternal care: *M. ochrogaster* and *M. pinetorum* (Wilson, 1982; Oliveras and Novak, 1986), *P. californicus* (Gubernick and Alberts, 1987), *M. unguiculatus* (Clark and Galef, 1999), *P. campbelli* (Wynne-Edwards and Lisk, 1987, 1988; Jones and Wynne-Edwards, 2001), which may have important fitness consequences suspected to be an ultimate cause of this social system (Cantoni and Brown, 1997). Monogamous species usually exhibit typical patterns of affiliative behaviour (e.g., allogrooming, body contact) and vaginal cytology (e.g., Shapiro and Dewsbury, 1990).

The most documented feature of monogamous rodents is, however, sexual preference in favour of their familiar partner. These preferences were repeatedly found in, e.g., *M. ochrogaster* (Shapiro et al., 1986; DeVries et al., 1997; DeVries and Carter, 1999) and *P. californicus* (Gubernick and Nordby, 1993). In the case of the latter species, however, social preferences have not perfectly matched the mating patterns in laboratory tests (Gubernick and Addington, 1994), but in natural conditions paternity analyses have revealed that pairs have remained faithful (Ribble, 1991). Nonetheless,

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female preference for familiar males was also found in rodent species that are strongly polygynous or show a marked flexibility in their social and mating system (Huck and Banks, 1979; Thomson et al., 1995; Parker et al., 2001; Randall et al., 2002). These cases may be explained by a female strategy to avoid the risk of aggressive interactions with an unfamiliar male or to reduce time budgets spent by familiarisation.

The first experimental studies suggesting monogamy within the otherwise polygynous/promiscuous genus *Mus* have appeared only recently in mound-building mice (*Mus spicilegus* Petényi, 1882). It was reported that females of mound-building mice consistently preferred a familiar over an unfamiliar male when given a choice. Moreover, they refused to copulate with unfamiliar males (Patris and Baudoin, 1998). The presence of the male partner is required for maintenance of proper oestrus cycling (Feron and Gheusi, 2003) and females kept in polygynous groups reproduce less successfully (Gouat and Feron, 2005). *M. spicilegus* males also contributed significantly to covering the young, retrieving stray pups, and other parental care (Patris and Baudoin, 2000) that reduced inter-litter intervals (Feron and Gouat, 2007). Formations of stable male-female associations within enclosures as well as physiological data clearly suggest formation of social pair-bonding in this species (Baudoin et al., 2005, but see Bardet et al., 2007). It is important to note that these animals are capable of efficient individual and kin recognition (Busquet and Baudoin, 2005; Colombelli-Negrel and Gouat, 2006). While the inhabitants of a single mound are not descendants of a single pair as previously believed (Garza et al., 1997) and while polygynous mating occurs occasionally in the natural populations (Gouat et al., 2003), monogamy is consistent with the results obtained in semi-natural conditions and may be accepted as a typical social/mating system in the mound-building mouse (Dobson and Baudoin, 2002; Patris et al., 2002; Poteaux et al., 2008).

Another apparent peculiarity of the social behaviour in *M. spicilegus* (and its sister species *M. macedonicus* Petrov and Ruzic, 1983) is an elevated level of aggression (Frynta and Čiháková, 1996; Suchomelová et al., 1998; Patris et al., 2002). Surprisingly, not only males but also females of these species are highly agonistic towards each other. In contrast, female house mice *Mus musculus* Linnaeus, 1758, are generally fairly tolerant to each other, notably in neutral cage tests (e.g., Munclinger and Frynta, 2000; Patris et al., 2002), and they became aggressive only under particular circumstances, e.g., when in competition for reproductive status or in the presence of juvenile offspring (Parmigiani et al., 1989; Parmigiani and Palanza, 1994; Palanza et al., 1996).

Recently, we demonstrated that non-commensal house mice populations in the Near East (e.g., Auffray et al., 1990) belonging to *M. m. domesticus*, in a sharp contrast to their commensal conspecifics, exhibited patterns of aggressive behaviour resembling that of *M. spicilegus* (Frynta et al., 2005). Dyadic interactions in adults of either sex were usually highly agonistic. Reduced aggression in commensal populations may be explained by a surplus and/or high aggregation of food resources in stores and other typical habitats of commensal house mice. In contrast to seeds hoarded in caches by non-commensal mice, such artificial resources are extensive and hardly defensible. Moreover, high local densities typical for commensal populations may further reduce the defensibility of resources. For females, the sex competing primarily for food resources rather than for sexual partners, aggressive strategies thus become less advantageous. Not only aggression, but also other behavioural (e.g., reduction of food hoarding; Frynta, unpublished results) and physiological traits (e.g., elevated corticoid levels Ganem et al., 1989; Ganem, 1991) may be affected by commensal living.

The above results raised the question which type of social and mating system is typical for non-commensal populations of

house mice. In general, house mice are considered to be polygamous/polygynous (e.g., Crowcroft and Rowe, 1963; Wolff, 1985), however, this conclusion is based almost exclusively on data collected in commensal populations or those in recently colonised areas such as the isles around the United Kingdom, America, or Australia, which passed through the commensal stage and are usually reported as feral. In contrast, the Near East is probably the source area of the *M. m. domesticus* expansion (Prager et al., 1998; Rajabi-Maham et al., 2008), and the non-commensal way of life may be the primary stage in at least some house mouse populations of this region. Although the link between female aggression and monogamy is not necessarily straightforward, it is reasonable to test whether mice from the Near East exhibit the same sexual preferences as their presumably monogamous close relatives, *M. spicilegus* (for phylogenetic relationships within the genus *Mus* e.g., Guénet and Bonhomme, 2003; Suzuki et al., 2004; Gucchi et al., 2006; Macholán et al., 2007). A recent finding that both commensal and non-commensal populations of *M. musculus* possess much smaller testes than *M. spicilegus* (Frynta et al., 2009) is challenging and emphasises the urgent need to examine female mating preferences in these animals.

The aim of this study was to assess female sexual preferences in highly aggressive non-commensal mice from the Near East and in a commensal population of another subspecies exhibiting low aggression (*M. m. musculus*). To enable a comparison with published results, we followed almost the same procedure as Patris and Baudoin (1998). We formulated the following two alternative predictions and corresponding underlying hypotheses: (1) Females of non-commensal *M. m. domesticus* populations differ from conspecific females from commensal populations and exhibit the same unusual sexual preferences as those previously reported in *M. spicilegus*. This similarity should be due to shared social organisation resulting from a non-commensal way of life and associated factors such as scarcity of food resources, the necessity to hoard and elevated aggression. Preferences for familiar males may be explained by formation of pair-bonds or alternatively as a female strategy to avoid the risk of possibly harmful social interactions with unfamiliar conspecifics; (2) Females of non-commensal *M. m. domesticus* as well as commensal populations belonging to the other subspecies *M. m. musculus* exhibit similar behavioural patterns as those previously reported in a commensal *M. m. domesticus* population. This expected similarity of populations belonging to distinct subspecies and currently exhibiting contrasting ecological strategies (across these subspecies) should be attributed to the shared evolutionary history of the species.

2. Materials and methods

The stocks were derived from following wild populations: (1) *M. m. domesticus*—environs of villages Halabiyah, Doura Europos and Tell Shaikh Hammad, Euphrates river valley, district Deir az-Zor, Eastern Syria. The mice were captured in fields and along the Euphrates River, without any obvious association with human settlements. Consequently, they are referred to as non-commensal; (2) *M. m. musculus*—Ruzyně village, district Praha, Bohemia, Czech Republic. The population is consistently found in buildings, especially grain stores, and was thus considered commensal.

Experimental animals were adult (at least three months old), socially experienced, wild-derived captive bred mice of the first, second or third outbred generation in captivity (40 males and 20 females of each population).

All animals were kept under an artificial 12L:12D light cycle and housed in plastic cages 30 cm × 15 cm × 15 cm in size. Water and food (VELAZ ST1 mouse and rat breeder diet, wheat etc.) were provided *ad libitum*. Each cage contained sawdust bedding, nesting

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