

Multiple mating by females and multiple paternity in rodents: A cross-species comparative analysis

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ABSTRACT. The present review provides a compilation of the published data on the phenomena of multiple mating by females and multiple paternity in their litters in 48 rodent species with different mating systems, reproductive strategies, and social structures. Multi-male mating is common in female rodents, but this is one of the unsolved problems of behavioral ecology so far. Proposed explanations of multi-male mating assume the potential fitness benefits to females that include fertility assurance by reducing genetic incompatibility, increased genetic diversity of offspring and litter size, postcopulatory sexual selection through sperm competition, an increase in uncertainty of paternity and thus reduction in the probability of infanticide, as well as enhanced access to resources. Multiple paternity is also thought to increase offspring genetic diversity and the effective population size. Different genetic markers have been employed to document multiple paternity including DNA fingerprinting and microsatellites. The results of studies conducted on the above rodent species are discussed and analyzed to check whether the predictions of the above hypotheses about the potential benefits of fitness for females in general or in some particular cases are justified.

How to cite this article: Gromov V.S. 2024. Multiple mating by females and multiple paternity in rodents: A cross-species comparative analysis // Russian J. Theriol. Vol.23. No.1. P.57–72. doi: 10.15298/rusjtheriol.23.1.07

KEY WORDS: rodents, multiple mating, multiple paternity, mating systems, reproductive strategies.

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Множественные спаривания у самок и множественное отцовство в выводках грызунов: Сравнительный межвидовой анализ

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РЕЗЮМЕ. В статье рассматриваются результаты исследований, посвященных изучению феноменов множественного спаривания у самок и множественного отцовства в выводках у 48 видов грызунов с разными системами спаривания, репродуктивными стратегиями и социальной структурой. Феномен множественного спаривания самок описан у многих видов грызунов, но до сих пор остается загадкой поведенческой экологии. Различные гипотезы, объясняющие этот феномен, основываются на том, что самки могут получать селективные преимущества за счет повышения вероятности успешного оплодотворения, увеличения размеров выводка и генетического разнообразия потомства, снижения вероятности инфантицида со стороны половых партнеров, включения механизмов полового отбора через конкуренцию спермы, обеспечивающих получение потомства с «хорошими генами», а также за счет обеспечения свободы доступа к ресурсам, которыми обладают самцы. Полагают, что множественное отцовство также способствует увеличению генетического разнообразия потомства и эффективных размеров популяции. Для выявления множественного отцовства в выводках грызунов используются различные генетические маркеры, в особенности ДНК-дактилоскопия и микросателлиты. В статье обсуждаются результаты проведенных исследований с оценкой указанных выше гипотез: подтверждаются ли их предсказания в целом либо в каких-то частных случаях.

КЛЮЧЕВЫЕ СЛОВА: грызуны, множественные спаривания, множественное отцовство, системы спаривания, репродуктивные стратегии.

Introduction

In the course of evolution, mammals have developed a number of different mating systems, resulting from the different taxonomic and ecological conditions they are exposed to (Boonstra *et al.*, 1993; Burton, 2002). These systems may differ even within the same species, depending on factors such as habitat conditions, demography, population density, resource competition and availability, spatial distribution of individuals and the availability of a potential breeding partner (Lott, 1984). Consequently, mating strategies may differ across the geographic range of a species, especially if aforementioned factors vary (Clutton-Brock, 1989; Jones *et al.*, 2001; Waterman, 2007; Solomon & Keane, 2007).

Each individual strives to maximize reproductive success, and since each sex has different constraints on reproduction, males and females generally have evolved different strategies for mating. However, mating strategies are not the same thing as mating systems. A mating strategy is all the tactics used by an individual to maximize reproductive success, whereas a mating system is characteristic of a population or a species (Waterman, 2007). Mating systems are defined by patterns of reproductive behaviors that are influenced by spatial and temporal distributions of reproductively receptive females. The number of females with which a male mates depends not only on the spatial distribution of receptive females, but on the duration of receptivity by individual females, and the synchrony of receptivity within the population as well (Emlen & Oring, 1977). Collectively, these traits shape the operational sex ratio (OSR) of the population, which is defined as the ratio of reproductively active males to sexually receptive females (Emlen & Oring, 1977; Waterman, 2007).

The mating systems described in many rodent species involve polygynandry, promiscuity, and monogamy (Xia & Millar, 1991; Boonstra *et al.*, 1993; Bryja *et al.*, 2008; Naim *et al.*, 2011; Wells *et al.*, 2017; Weber *et al.*, 2018). Polygynandry is a form of polygamy: it includes both polygyny (males having multiple female mates) and polyandry (females having multiple male mates) within the same species (Szala & Shackelford, 2019). By contrast, promiscuity is defined as a mating system in which both males and females mate nonexclusively with multiple partners in a breeding season (McEachern *et al.*, 2009). Descriptions of monogamy and polygyny assume that females mate with a single male (Waterman, 2007). The promiscuous mating system implies that during one ovulation a female mates with several males, which results in multiple paternity, that is, one litter is sired by more than one father. A priori, one can expect variance in male reproductive success to be lower under monogamy (and polyandry) than under polygyny (Nunney, 1993) since in the latter system few males typically produce most of the offspring. However, unlike males, females are not expected to increase their reproductive success by mating with multiple partners (Trivers, 1972). A mating

system is considered an indication of multi-male mating, in that females are more likely to copulate with multiple males in promiscuous or polyandrous species than in monogamous or polygynous species (Harcourt *et al.*, 1981; Kenagy & Trombulak, 1986; Møller, 1988; Stockley, 2003).

Female aggregation affects the reproductive strategies of males, and specifically their ability to acquire and monopolize mates (Bradbury & Vehrencamp, 1977; Emlen & Oring, 1977; Clutton-Brock, 1989). In polygynous mating systems, ecological factors create aggregations of reproductive females where males are likely to succeed in monopolizing mating opportunities (Emlen & Oring, 1977). However, where males are unable to monopolize mating opportunities, mating systems instead tend to be polygynandrous, where neither sex is restricted to a single mate within a breeding season (Emlen & Oring, 1977). Ostfeld (1990) argued that a promiscuous mating system has a large likelihood of occurring under the following conditions: (1) if food resources are available in abundance and distributed uniformly, (2) if population density is high enough to allow encountering of multiple mates, and (3) if the home range overlap of both sexes is extensive.

Multi-male mating (MMM) is common in female mammals including rodents, but this phenomenon is one of the unsolved problems of behavioral ecology so far (Hosken & Blankenhorn, 1999; Solomon & Keane, 2007), and evaluating the benefits of MMM is of general importance in understanding the evolution of mating behaviors (Birkhead & Møller, 1998; Hosken & Blankenhorn, 1999; Yasui, 2001; Dobson *et al.*, 2018). Proposed explanations of MMM fall into two categories (Huxley, 1938; Andersson, 1994): (1) females play a passive role, and it is the unwillingness or inability of males to monopolize access to receptive females that leads to MMM; (2) females play an active role, and female benefits are the driving force behind MMM. The first category emphasizes the role of intra-sexual selection (male-male competition) whereas the second stresses the role of inter-sexual selection (female choice).

Sexual selection theory predicts that females can maximize their reproductive success by choosing a high quality mate because females typically invest relatively more in their gametes than males and can potentially produce less offspring than males (Trivers, 1972). Choosing an attractive male may benefit the female's fitness due to the male possessing genes that increase offspring viability or mating success (Andersson, 1994). A considerable amount of data covering many species demonstrates that females are indeed choosy and benefit from doing so (Andersson, 1994). However, females of many rodent species mate with multiple males during one reproductive cycle (Birkhead & Møller, 1998), which seems contradictory to the idea of females choosing the most attractive male as a mate. Nevertheless, MMM does not necessarily exclude mate choice.

Despite the potential costs of MMM for females (they are at risk of time and energy costs, increased

disease transmission, injury caused by sexual partners, and predation; Daly, 1978; Lewis, 1987; Magnhagen, 1991; Lombardo, 1998; Yasui, 1998), females could benefit from MMM if it increases offspring fitness compared to single mating (Jennions & Petrie, 2000; Birkhead & Pizzari, 2002; Wolff & Macdonald, 2004). In many species, extra-pair males provide no parental care and their contribution to the next generation is solely genetic (Petrie & Kempenaers, 1998; Jennions & Petrie, 2000; Griffith *et al.*, 2002). In such cases, MMM could still be beneficial if females are able to select the most appropriate male's genotype to maximize indirect genetic benefits that improve the fitness of their young (Jennions & Petrie, 2000; Wolff & Macdonald, 2004; Simmons, 2005). Precopulatory mate selection processes based on phenotypic expression of genetic quality may allow females to select their optimal sexual partners for indirect benefits (Andersson, 1994). Besides, several postcopulatory selection mechanisms provide females that mated with undesirable males, an additional opportunity to bias siring success towards optimal males for their progeny (Pusey & Wolf, 1996; Neff & Pitcher, 2005).

The potential fitness benefits to females mating with multiple males include fertility assurance by reducing genetic incompatibility (Birkhead *et al.*, 1993; Hunter *et al.*, 1993; Sheldon, 1994; Zeh & Zeh, 1996, 1997, 2001; Hoogland, 1998; Jennions & Petrie, 2000; Colegrave *et al.*, 2002; Mays & Hill, 2004), an increase in genetic diversity of offspring (Loman *et al.*, 1988; Watson, 1991; Madsen *et al.*, 1992; Jennions & Petrie, 2000; Zeh & Zeh, 2001; Tregenza & Wedell, 2002; Head *et al.*, 2005), an increase in uncertainty of paternity and thus a decrease in the probability of infanticide, i.e. killing their own offspring (Hrdy, 1977; Agrell *et al.*, 1998; Wolff & Macdonald, 2004), promotion of parental care on the part of males (Davies *et al.*, 1996), as well as enhanced access to resources (Gray, 1997). Female multiple mating is thought to increase the effective population size of a species relative to monogamous and polygynous mating systems, since more alleles will be represented in the next generation (Sugg & Chesser, 1994). Besides, MMM may increase litter size in species with induced ovulation (Dewsbury, 1984; Ågren, 1990). Female multiple mating is also considered to act as a genetic bet-hedging mechanism, by which females can reduce the assessment error in regard to mates' genetic quality when only uncertain information is available (Yasui, 2001; Fox & Rauter, 2003). Furthermore, postcopulatory sexual selection may occur through sperm competition (Parker, 1970; Gomendio & Roldan, 1993; Yasui, 1997) or cryptic female choice (Møller & Birkhead, 1989), whereby the fitness of the female's offspring is enhanced by virtue of the good genes contributed by the victorious spermatozoans (Yasui, 1997; Evans & Magurran, 2000). Recent studies are suggestive that selection for inbreeding avoidance is also possible (Firman & Simmons, 2008a; Musolf *et al.*, 2010).

In rodents, MMM is common and potentially influenced by population demographics and environmental

factors (Schulte-Hostedde *et al.*, 2004; Cohas *et al.*, 2007; Bergeron *et al.*, 2011). The number of males in the vicinity of females is known to correlate with the probability of MMM (Klemme *et al.*, 2007a; Lane *et al.*, 2008); besides, MMM is likely to be affected by annual variation in food abundance, which has important effects on rodent population dynamics (Pedersen & Greives, 2008).

In mammals, there is variation in fertilization probability associated with mating order (Ginsberg & Huck, 1989). As for rodents, first-mated males are reported to hold an advantage in several species. For example, the proportion of offspring sired by first males is 91% for the Arctic ground squirrel, *Spermophilus parryii plesius* (see Lacey *et al.*, 1997), 58% for the Columbian ground squirrel, *Spermophilus columbianus* [syn. *Urocitellus columbianus*] (Raveh *et al.*, 2010), and 81% for the sandy inland mouse, *Pseudomys hermannsburgensis* (see Firman, 2014). However, in the bank vole, *Clethrionomys glareolus* (syn. *Myodes glareolus*), the number of offspring sired by first- or second-mated males do not significantly differ (Ratkiewicz & Borkowska, 2000).

Multiple paternity (MP) is a result of insemination of a female by at least two males to produce a single litter or brood. Multiple paternity has the potential to shape the strength of sexual selection. The opportunity for sexual selection is determined by intra-sexual variation in the number of offspring produced. The strength of sexual selection is often defined as the slope of the linear relationship between offspring produced and number of mates obtained, known as Bateman's gradient (Bateman, 1948; Jones *et al.*, 2002). The relationship can be estimated by calculating the slope of a regression line relating fecundity (number of offspring produced) to mating success (number of mates). A non-zero Bateman's gradient supports that sexual selection is operating in the precopulatory phase of sexual selection (Jones 2009). These gradients can also be compared between the sexes within a species to assess the opportunity for sexual selection and determine the mating system. For example, if males have a steep Bateman's gradient and females have a shallow gradient, then sexual selection will be stronger in males, and the mating system is likely to be polygynous. If females have a steep Bateman's gradient and males a shallow gradient, then sexual selection tends to be stronger in females, and the mating system is predicted to be polyandrous. If both sexes have Bateman's gradients close to zero, the mating system may be monogamous. If both sexes have steep Bateman's gradients, they may both compete for mates, and the mating system may be polygynandrous (Munroe & Koprowski, 2011). In many species, variance in reproductive success is expected to be greater in males than females (Bateman, 1948) since enhanced competition for access to partners results in a greater range of reproductive outcomes for members of this sex (Hauber & Lacey, 2005).

The significance of MP is that, relative to single paternity, it increases offspring genetic diversity (Wolff & Macdonald, 2004; Reynolds, 1996) and the effective

population size (Sugg & Chesser, 1994; Chesser & Baker, 1996; Karl, 2008), which may subsequently enhance survival of offspring (Yasui, 1998). At a proximate level, the extent of MP in a population is influenced by the ability of males to protect their paternity, by the ability of males to gain access to already mated females, and by the extent to which females seek copulation with several males (Berteaux *et al.*, 1999). There are several predictions in the hypotheses posed to explain variation in MP. According to Emlen and Oring (1977), and Shuster and Wade (2003), increased spatial clustering of females will decrease MP, but increased breeding synchrony will increase MP. Kokko and Rankin (2006) also predicted that increased male density or male-bias in operational sex ratio would increase MP. Male-bias in operational sex ratio is also expected to increase MP by increasing the rate at which females encounter male mates (Kokko *et al.*, 2006). According to Cotton *et al.* (2006) and Daly (1978), females in poor condition, as well as young females, will decrease MP.

Different genetic markers have been employed to document MP. These include chromosomal markers, allozymes, DNA fingerprinting, and microsatellites (Sugg *et al.*, 1996; Travis *et al.*, 1996). Microsatellites may be the preferred marker (Jarne & Lagoda, 1996; Burton, 2002). Determining MP is an important aspect of studies on multiple mating by females in rodents, because MMM is often difficult to observe in the wild due to cryptic mating behavior of rodents.

The purpose of this review is to present and discuss the results of studies of the phenomena of MMM and MP in different rodent species with various social structures, and to check whether the predictions of the aforementioned hypotheses about the potential fitness benefits to females mating with several males are justified in general or in some particular cases. The social structure and mating systems of rodents are diverse and intriguing: some species are essentially solitary, whereas others are gregarious and form relatively stable multi-male–multi-female associations (called breeding colonies; Bujalska & Saitho, 2000); for a number of species, a family-group lifestyle is characteristic (Gromov, 2017). Solitary and gregarious species exhibit primarily polygynandrous and promiscuous mating system, whereas monogamy or polygyny is typical of species with a family-group lifestyle. Therefore, MMM and MP would be much more expected in solitary and gregarious rodent species than among species living in family groups. Accordingly, the studies of phenomena of MMM and MP in different rodent species are considered separately in this review, regarding their different social structures and predominant mating systems.

Solitary and gregarious species

In this category of rodent species, breeding females tend to occupy exclusive home ranges that may overlap with those of multiple males; many males usually congregate on estrus females' home range to mate (Gromov, 2008, 2017). Such a spatial population structure

suggests promiscuity rather than monogamy or polygyny as a predominant mating system, so MMM and, as a result, MP may frequently occur, like in many sciurid and muroid rodents. In many species, female behavior clearly promotes MP, and their role is an active one (Solomon & Keane, 2007; Waterman, 2007).

Data collected from the literature on sexual behavior of tree squirrels show that MMM is typical of *Sciurus aberti*, *Sciurus vulgaris*, *Tamiasciurus hudsonicus*, and *Tamias striatus* (Farentinos, 1980; Wauters *et al.*, 1990; Lane *et al.*, 2008; Bergeron *et al.*, 2011). Specifically, *T. hudsonicus* females copulated with an average of 5.8 ± 0.3 males. The majority of the polytocous litters (82.5%) were multiply sired, with a mean number of sires represented in litters as 2.3 ± 0.1 . The results of this study (Lane *et al.*, 2008) did not support hypotheses of cryptic direct benefit (fertility assurance and infanticide avoidance) because MMM did not influence neither pregnancy rate nor litter size. There was no correlation between MMM and offspring quality, MP or litter allelic diversity, and therefore, no support for hypotheses of genetic benefit. In addition, females did not incur a detectable cost. Thus, female mating behavior in *T. hudsonicus* appears to be a passive response to selection on multi-female mating in males (Lane *et al.*, 2008).

In a wild population of *T. striatus*, the proportion of litters with MP varied from 25% to 100% (Bergeron *et al.*, 2011). Genetically related parents were found to be common in this population and produced less heterozygous offspring. Furthermore, litters with multiple sires showed a higher average relatedness among partners than litters with only a single sire. In multiply sired litters, however, males that were more closely related to their partners sired fewer offspring. The results of this study suggest that MMM could act as a bet-hedging strategy that may effectively provide indirect genetic benefits for females by reducing the risk of inbreeding in this species where mating among close relatives is common (Bergeron *et al.*, 2011).

Multiple mating by females occurs in many ground squirrels, including *Spermophilus beldingi* (syn. *Urocitellus beldingi*), *Spermophilus richardsonii*, *Spermophilus tridecemlineatus*, *Spermophilus beecheyi*, *Spermophilus lateralis* (syn. *Callospermophilus lateralis*), and *Xerus inauris* (Hanken & Sherman, 1981; Michener, 1983; Schwagmeyer & Woontner, 1985; Boellstorff *et al.*, 1994; Waterman, 1998; Wells *et al.*, 2017). Accordingly, MP has been also detected in many ground squirrels, including *Spermophilus brunneus*, *Spermophilus tereticaudus* (syn. *Xerospermophilus tereticaudus*), *S. lateralis*, *S. beldingi*, *S. tridecemlineatus*, *S. beecheyi*, *S. richardsonii*, and *Ictidomys parvidens* (Hanken & Sherman, 1981; Foltz & Schwagmeyer, 1989; Sherman, 1989; Boellstorff *et al.*, 1994; Hare *et al.*, 2004; Munroe & Koprowski, 2011; Schwanz *et al.*, 2016; Wells *et al.*, 2017). The frequency of MP varied from 50% in *S. tridecemlineatus* (see Foltz & Schwagmeyer, 1989) to 89% in *S. beecheyi* (see Boellstorff *et al.*, 1994).

The study in a population of *S. tereticaudus* (see Munroe & Koprowski, 2011) has shown that polygyny was evident in all years when the population size was

reduced. Multiple mating occurred in both sexes, and females had sired multiple litters in all years. Multiple paternity occurred in the majority of litters (55%) with 2.5 ± 0.26 sires/litter, and litter size was positively correlated with the number of sires. Bateman's gradient was greater in males than females; therefore, males had a greater opportunity for sexual selection than females. Besides, the mating system in *S. tereticaudus* defined through genetic analyses and Bateman's gradients was found to be polygynandrous compared to the previously suggested polygynous mating system as established by behavioral observations.

In *Ictidomys parvidens*, MP was detected in 62% of litters, and up to five fathers were assigned to juveniles within the same litter (Schwanz *et al.*, 2016). In *S. tridecemlineatus*, the direction of the paternity bias suggests that sperm competition operates to reinforce precopulatory mechanisms of intra-sexual selection (Foltz & Schwagmeyer, 1989). However, MMM had no effect on conception in this species (Schwagmeyer, 1986). Therefore, the data obtained do not support the hypothesis of cryptic direct benefit (fertility assurance) in *S. tridecemlineatus*.

The detailed study in a population of *S. lateralis* (Wells *et al.*, 2017) has shown that MP did not affect litter size, and male density did not affect the likelihood of MP. Operational sex ratio also did not affect MP. Breeding asynchrony had no effect on MP as well. Variation in the rate of MP was determined by density and the active strategies of males and females: high female density decreased the likelihood of MP when males were relatively scarce, but increased the likelihood of MP when males were abundant. From Bateman's gradients, there was found no direct fitness benefit of MP for females of this species (Wells *et al.*, 2017).

The relationship between OSR and MP in ground squirrels was found to be not clear. Male-biased OSR was associated with increased multiple mating by *S. tridecemlineatus* females (Schwagmeyer & Brown, 1983). In *S. richardsonii* see (Michener & McLean, 1996) and *Xerus inauris* (see Waterman, 1998), however, female rate of multiple mating was independent of changes in OSR: females mated with multiple males when the OSR was strongly male-biased and when it was less so. In *S. lateralis*, OSR also did not affect rates of MP (Wells *et al.*, 2017).

As for muroid rodents (Myomorpha), MMM as well as MP are well documented for *Peromyscus maniculatus* (see Birdsall & Nash, 1973), *Peromyscus leucopus* (see Xia & Millar, 1991), *Peromyscus crinitus* (see Shurtliff *et al.*, 2005), *Mesocricetus auratus* (see Huck *et al.*, 1989), *Apodemus agrarius*, *Apodemus sylvaticus*, *Apodemus speciosus* and *Apodemus uralensis* [syn. *Apodemus microps*] (Baker *et al.*, 1999; Bartmann & Gerlach, 2001; Polechova *et al.*, 2004; Booth *et al.*, 2007; Bryja & Stopka, 2005; Bryja *et al.*, 2008; Wakabayashi *et al.*, 2017), *Clethrionomys glareolus* (syn. *Myodes glareolus*) and *Clethrionomys rufocanus* [syn. *Craseomys rufocanus*] (Ratkiewicz & Borkows-

ka, 2000; Klemme *et al.*, 2006, 2007b; Wakabayashi & Saitoh, 2019), *Microtus oeconomus* and *Microtus pennsylvanicus* (Boonstra *et al.*, 1993; Berteaux *et al.*, 1999; Borkowska *et al.*, 2009), *Neotoma micropus* (see Baxter *et al.*, 2009), *Muscardinus avellanarius* (see Naim *et al.*, 2011), *Calomys musculinus* (see Sommaro *et al.*, 2015), and *Glis glis* (Morris & Morris, 2010; Weber *et al.*, 2018; Moska *et al.*, 2021).

Among aforementioned species, the frequency of occurrence of insemination by more than one male can be estimated as being between 19% (in *P. maniculatus*; see Birdsall & Nash, 1973) and 100% (in *A. sylvaticus*; Polechova *et al.*, 2004). In litters with MP, offspring were found to be sired by two to four males.

In the bank vole, *C. glareolus*, no difference in males' mating success with respect to the mating order was found, and MP probably evolved as a mechanism to prevent inbreeding (Ratkiewicz & Borkowska, 2000). According to Klemme *et al.* (2006), however, dominant males sired significantly more offspring than subordinate males. This varied according to mating order: dominant males sired more offspring when they were second than when they were first. Moreover, litter sizes were significantly smaller when the dominant male was first compared to litter sizes when mating order was reversed or both males were equal in status. The results of another study (Klemme *et al.*, 2007b) have shown a significant reduction in pregnancy rate of females that mated only once compared to females that mated twice. This direct benefit is most likely explained by an increased stimulus gained from multiple mating. However, no difference in reproductive success of females mated twice with the same male or once with each of two males has been found. Thus, no fitness benefits of polyandry have been found in this species.

A decreased probability in conceiving following MMM has been detected in two promiscuous species (*P. maniculatus*; Dewsbury, 1982) and *Phodopus sungorus* (see Wynne-Edwards & Lisk, 1984). Such a decrease may be the result of a strange-male-induced pregnancy block.

In the studies on *N. micropus* (Baxter *et al.*, 2009) and *C. musculinus* (Sommaro *et al.*, 2015), no association between MP, litter size, and genetic variability has been found. In addition, MP did not vary in relation to their population density. Based on the absence of infanticide by siring males, and the low offspring survival in the presence of non-siring males, Coda *et al.* (2011) proposed that *C. musculinus* females would mate with multiple males as a counter-strategy against infanticide by males.

The results of the studies in populations of *G. glis* and *M. avellanarius* (Morris & Morris, 2010; Naim *et al.*, 2011; Weber *et al.*, 2018; Moska *et al.*, 2021) suggest that MMM may be a strategy to avoid excessive male harassment. Direct benefits to females of both species were found to be not obvious. However, small isolated populations of *G. glis* are at risk of losing their genetic variation (Pilastro, 1992; Pilastro *et al.*, 1994; Moska *et al.*, 2021), so MP and promiscuity observed in this species can help to maintain its genetic diversity.

Among gregarious species, commensal rodents (*Mus domesticus*, *Mus musculus*, *Rattus rattus*, *Rattus norvegicus*) deserve special consideration. House mice (*M. domesticus* and *M. musculus*) are known to exhibit significant population structuring, meaning limited dispersal results in genetic differences among distant populations (Sage, 1981). Local social structure usually consists of a dominant male, as males fight aggressively until a single dominant emerges (Brown, 1953; Sage, 1981). Once established, the boundaries of the territories of dominant males are substantially stable (Mackintosh, 1970). Female mice and juveniles move freely between territories of dominant males (Mackintosh, 1970; Potts *et al.*, 1991). Females often mate non-randomly with dominant males (Dean *et al.*, 2006). Given this type of social hierarchy, it has been suggested that dominant males are the only effectively breeding males in the population (Bronson, 1979). However, while sexual development of subordinate males is suppressed, they regularly achieve fertilizations (DeFries & McClearn, 1970; Oakeshott, 1974).

Both field and experimental studies provide evidence that MMM is a common feature of natural populations of house mice (Egid & Brown, 1989; Oakeshott, 1974; Carroll *et al.*, 2004; Ehman & Scott, 2004). The rate of MP was found to range from 6% to 46% of litters, and MP was found to be significantly more frequent in relatively high-density vs. low-density populations (Dean *et al.*, 2006; Firman & Simmons, 2008a, b; Thonhauser *et al.*, 2013, 2014a, b). Within multiply sired litters, a maximum of two sires was detected. Paternity skews suggested that one male sired most of the offspring. Although females mated with just two males, the actual number of mates, and thus the intensity of sperm competition, is likely to be higher (Firman & Simmons, 2008b). Multiple paternity was found to be significantly greater when the males were virgins. Since virgin male mice are highly infanticidal, this finding is consistent with the infanticide avoidance hypothesis (Thonhauser *et al.*, 2013). Besides, MP was associated with increased litter size but only in the intrusion treatment (when scent-marked objects from the neighboring males were introduced into the males' territories), which suggests that the effect of MP on offspring number is dependent on male–male interactions. Thonhauser *et al.* (2014a) have found no evidence that MP enhanced females' litter size. Multiple paternity was associated with reduced mean and variance in offspring body mass, which suggests that females allocate fewer resources or that there is increased intrauterine conflict in multiple- vs. single-sired litters. This finding suggests that MP may have negative fitness effects for females and their offspring. Additionally, these authors have found increased allelic diversity in multiple-sired litters, as predicted by the genetic diversity hypothesis. In another study, however, Thonhauser *et al.* (2014b) have found no evidence that genetic similarity of females' potential mates (MHC-identical siblings vs. MHC-dissimilar non-siblings) influenced the rate of MP (MHC — the major histocompatibility complex).

The results of this study do not support the idea that female mice increase MP when they have the opportunity to increase the genetic diversity of their offspring, as expected from the genetic diversity hypothesis. No support has been also found for the hypothesis that females are more likely to mate with multiple males when they have the opportunity to increase the genetic diversity of their progeny. Although previous work (Thonhauser *et al.*, 2013) showed higher levels of genetic diversity within multiple- than in single-sired litters, female mice did not have more multiple-sired litters when they had the opportunity to increase the genetic diversity of their progeny. Moreover, no evidence was found that inbred females were more likely to give birth to multiple-sired litters than outbred females, regardless of the genetic diversity of the available males.

As for *R. norvegicus*, the mating behavior of this species varies according to population density. At low densities, males hold territories and guard groups of females for exclusive mating (Calhoun, 1963; Waterman, 2007). At high densities, the social structure shifts to a despotic system where territories are ill-defined and males rank themselves in dominance, generally according to age (Barnett, 1958; Lott, 1984; Waterman, 2007). In this situation, males are unable to defend females for exclusive mating, and roving bands of males attempt to mate with any female that comes into estrus, resulting in multiple mating (Calhoun, 1963; Robitaille & Bovet, 1976). Ewer (1971) and Corbet & Southern (1977) described similar density-dependent behavior to *R. norvegicus* among *R. rattus* populations that were commensal with humans. However, Hooker & Innes (1995) found that wild *R. rattus* in New Zealand that were non-commensal with humans tended to prefer solitude. Males did not maintain groups of females in their territories, even when population density was low. Nevertheless, multiple paternity was found to be common in wild populations of both *R. norvegicus* and *R. rattus* (Miller *et al.*, 2010; King *et al.*, 2014): genetic contributions from two or more (up to four) males were identified in multiply sired litters. The potential fitness benefits to females mating with multiple male are associated with increased genetic diversity in their offspring (Miller *et al.*, 2010).

Species with a family-group lifestyle

A family-group lifestyle means, first of all, that breeding partners share their home ranges (territories) and maintain long-term pair bonds, as in beavers, prairie dogs, marmots, some voles and gerbils. Members of a family group exhibit considerable overlap, including sharing a nest burrow or other shelter. Interactions within family groups markedly differ from those between groups with the former being to include affiliative, cooperative, and nepotistic social acts, while the latter are mostly aggressive. Relationships between neighboring family groups are based on territoriality: all members of a family group, especially adult ones, defend their territories from both neighbors and stragg-

ers. Socially monogamous family groups consist of a breeding pair and their offspring. In extended family groups, more than one adult individual of either one sex or both sexes can breed. In extended polygynous family groups (i.e., harems consisting of one adult male and two or more adult females), breeding females can occupy separated home ranges or share the same nest burrow. The composition of family groups, usually consisting of a breeding pair and their offspring, suggests monogamy and, therefore, a lack of MMM. However, field data as well as laboratory studies suggest multiple paternity in some of the species in question.

Among ground squirrels, some kind of polygynous family groups (harems) is documented in *Spermophilus columbianus* (Michener, 1973). Despite the harem structure of the social units, females of this species were found to mate with more than one male, and 16% of 165 sampled litters were multiply sired (Murie, 1995). Litter size did not vary with the number of mates a female had. However, numbers and proportion of juveniles surviving to yearling age tended to increase with the number of mates for mothers. Murie (1995) suggested that mate choice for “good genes” via sperm competition was the most plausible benefit of MMM in *S. columbianus*. Concerning the relationship between OSR and MP, it was found that male-biased OSR was associated with reduced multiple mating by females. Besides, MMM had no effect on conception (Murie, 1995), and this finding does not support the hypothesis of cryptic direct benefit (fertility assurance).

As for other ground-dwelling sciurids, a family-group lifestyle is especially typical of prairie dogs (*Cynomys gunnisoni*, *Cynomys leucurus*, *Cynomys ludovicianus*, *Cynomys parvidens*) and most marmots (*Marmota* spp.). Specifically, a harem-based mating system is documented for *Marmota flaviventris* (Armitage, 1962; Barash, 1973). Nevertheless, multiple mating by *M. flaviventris* females, evidenced by genetic studies, results in MP detected in 18% (28/153) of the litters (Martin *et al.*, 2014). For all 28 multiply sired litters, at least one male originated from another colony than the mother. The occurrence of MP was influenced by the OSR: when the OSR was large, heavier females were more likely to produce litters with multiple sires. The results of this study suggest that MP is mainly limited by the opportunity to have access to multiple mates and is influenced by costs or mate choice because heavier females are more likely to have litters with multiple sires than smaller ones. Thus, despite the fact that the reproductive strategy of *M. flaviventris* is generally described as female-defense polygyny (Armitage, 1986) an essential proportion of the litters was sired by multiple fathers, a finding that suggests a polygynandrous mating system (Martin *et al.*, 2014). The results of these studies appear to support the hypothesis of genetic benefit of MMM (i.e. an increase in genetic diversity of offspring).

Multiple mating by females has been documented in other marmot species, such as *Marmota caligata* (see Kyle *et al.*, 2007) and *Marmota marmota* (see Goossens *et al.*, 1998). The results of the study in the popula-

tion of *M. marmota* (Goossens *et al.*, 1998) have shown that the genetic mating system of this species was quite different from a strictly monogamous breeding system: extra-pair paternity (EPP) occurred in 11 of 35 litters examined (31.4 %). The authors of this study proposed several explanations why the proportion of EG-EPC (extra-group, extra-pair copulations) is so high in the population of *M. marmota*. First, the resident males do not control the reproductive functions of extra-group males. Second, resident males may be unsuccessful in guarding their mate from EPC. Third, mate guarding may be unsuccessful because the resident female actively solicited EPC and escaped from the resident male. Benefits for resident females of this species engaging in EPC may be of two types. First, resident females may solicit EPC to avoid infanticide because male takeover of a family group is generally followed by the killing of juveniles by the incoming male (Perrin *et al.*, 1994; Coulon *et al.*, 1995). Second, females may copulate with a male whose genetic quality is superior to that of their partner. According to Goossens *et al.* (1998), genetic benefits are the most likely reason for resident females engaging in EPC. Similar results were obtained in the study conducted by Cohas *et al.* (2006).

As for prairie dogs, they are known to live in monogamous or extended (harem-polygynous) family groups called clans (e.g., in *C. gunnisoni*; Rayor, 1988; Travis & Slobodchikoff, 1993) or coterries (in *C. ludovicianus*; Hoogland, 1981, 1995). Polygynous family groups typically contain one breeding male and two to four breeding females, but some extended family groups contain two or three breeding males (Travis *et al.*, 1996). Females of two species (*C. ludovicianus* and *C. leucurus*) were found to be mostly monandrous, and females of the other two species (*C. gunnisoni* and *C. parvidens*) — mostly polyandrous (Hoogland, 1981, 2001, 2007, 2013).

The study in a population of *C. gunnisoni* (Travis *et al.*, 1996) based on DNA fingerprinting analysis has shown that females living in a social group often produced litters of mixed male parentage. Moreover, 61% of all progeny were sired by extraterritorial males. Thus, Gunnison's prairie dog litters were frequently sired by multiple males, and a large proportion of these males resided extraterritorially. According to Hoogland (1998), the probability of pregnancy and parturition was 92% for females that copulated with only one or two males, but was 100% for females that copulated with at least three males. Litter size at weaning has been found to be positively correlated with the mother's number of sexual partners. Therefore, MMM might be necessary to guarantee pregnancy. Because each female Gunnison's prairie dog comes into estrus only once each year, such a guarantee is important so that females do not forfeit an entire breeding season. Therefore, this finding supports the hypothesis of cryptic direct benefit (fertility assurance). Besides, MP promotes genetic diversity among littermates and thus maximizes the advantages of sexual reproduction. Assurance of bringing pregnancy to term and larger lit-

ters are supposed to be independent benefits that female Gunnison's prairie dogs reap by copulating with more than one male (Hoogland, 1998). Haynie *et al.* (2003) have drawn similar conclusions for *C. parvidens*.

Frequency of MP estimated for *C. gunnisoni* (77%) and *C. parvidens* (up to 90%) was found to be greater than that detected for *C. ludovicianus* (5–10%; Hoogland, 1995). The study conducted by Hoogland (2013) has shown that females of three species (*C. leucurus*, *C. gunnisoni* and *C. parvidens*) benefited from polyandry by rearing more yearlings, but females of *C. ludovicianus* evidently did not benefit from polyandry. This finding supports the hypothesis that polyandry might enhance female annual reproductive success due to a higher probability of fertilization/conception (Sakaluk & Cade, 1980; Torok *et al.*, 2003; Uller & Olsson, 2005): polyandrous females were significantly more likely than monandrous females to conceive (Hoogland, 2013). Females of two species (*C. gunnisoni* and *C. leucurus*), however, paid a cost from copulating with more than one male, because they were less likely to survive until the next mating season. The lower survivorship of polyandrous females was resulted from increased susceptibility to predation while searching for additional males with which to copulate. In particular, the observed number of predations on polyandrous females was higher than the number expected by chance alone, and the observed number of predations on monandrous females was lower than the number expected by chance alone (Hoogland, 2013).

Studies on muroid rodents with a family-group lifestyle also deserve special attention. Within this category of species, mating systems are ranging from monogamy to polygyny, often within the same species (Solomon & Keane, 2007; Waterman, 2007; Gromov, 2022), and unimale family groups are the most common association (Gromov, 2008). Nevertheless, extra-pair copulations have been reported even in socially monogamous species, such as *Meriones unguiculatus* (Ågren *et al.*, 1989; Gromov, 2022), *Microtus socialis* (Gromov, 2023), and *Microtus ochrogaster* (Carter & Getz, 1993; Wolff & Dunlap, 2002). Multiple paternity was also found in litters of *Apodemus flavicollis* (Gryczyńska-Sięmiątkowska *et al.*, 2008) and *Lasiopodomys brandti* (Huo *et al.*, 2010) with plural breeding females. The authors of these studies concluded that MP mechanistically increased offspring genetic diversity.

The most thorough studies have been conducted on the prairie vole, *M. ochrogaster* (Evans & Dewsbury, 1978; Wolff & Dunlap, 2002; Solomon *et al.*, 2004). Prairie voles live as male–female pairs, single females (presumably remnants of male–female pairs), or in groups formed primarily through retention of offspring at the nest of a male–female pair (Getz *et al.*, 1990). Other than one field study in which MP was found in one of three litters examined (Carter & Getz, 1993), virtually nothing is known about MMM in prairie voles in the wild. This study has shown several males in the vicinity of females at the time of conception. Under laboratory conditions, females were found to mate with

more than one male (Evans & Dewsbury, 1978). In an experimental study conducted by Wolff and Dunlap (2002), it was found that litter size and probability of pregnancy were not significantly different for females that mated with one, two or three males. Increasing numbers of copulations, regardless of the number of males, also did not increase litter size but did significantly increase the probability of pregnancy. Therefore, MMM, at least in prairie voles, must serve some function other than increasing litter size and probability of conception. The percentage of females mating with one, two, or three males was 45, 34, and 21%, respectively. Thus, polyandrous mating in the supposedly socially monogamous prairie vole was relatively frequent, at least in the laboratory setting. It has been also shown that females play an active role in mate choice and seeking multiple partners. Wolff and Dunlap (2002) have concluded that gaining greater paternal care or obtaining material benefits are not good explanations for MMM in *M. ochrogaster* because additional mates do not provide additional parental care.

Solomon *et al.* (2004) examined allelic polymorphism at microsatellite loci to assess mating exclusivity in wild prairie voles and found evidence of MP in five of nine litters (56%) analyzed; the minimum possible number of sires per litter was two in each case. These findings are consistent with the results of the laboratory studies in which females mated with more than one male (Evans & Dewsbury, 1978; Wolff & Dunlap, 2002).

General discussion

The secretive lifestyle of most rodent species means that much of their reproductive biology and social behavior remains unknown. Although male reproductive success is typically constrained by the number of mates obtained (Bateman, 1948), the link between mating tactics and reproductive success is more imperceptible in females and not easily observable (Jennions & Petrie, 2000; Solomon & Keane, 2007). This review presents data obtained from studies on 48 rodent species. Unfortunately, very few studies provided direct evidence of MMM in natural environments of these species. Many studies (e.g., Huck *et al.*, 1989; Berteaux *et al.*, 1999; Ratkiewicz & Borkowska, 2000; Bartmann & Gerlach, 2001; Wolff & Dunlap, 2002; Klemme *et al.*, 2006, 2007; Klemme & Firman, 2013; Thonhauser *et al.*, 2013, 2014b) have been carried out on captive rodents. In most field studies, evidence of MMM was provided only on the basis of the occurrence of MP in the litters examined. Moreover, the available data provided an opportunity to test various hypotheses regarding the potential fitness benefits to females mating with multiple males in a relatively small number of the species only.

Nevertheless, multiple mating by females has been revealed in all rodent species in question, regardless of their social structures and mating systems. In other words, multiple paternity as a result of MMM could be found in any rodent species. The only possible ex-

planation for this phenomenon is that MMM plays an important role in rodent populations, increasing their genetic diversity, which in turn confirms the relevant hypothesis (Loman *et al.*, 1988; Watson, 1991; Madsen *et al.*, 1992; Jennions & Petrie, 2000; Zeh & Zeh, 2001; Tregenza & Wedell, 2002; Head *et al.*, 2005), although some studies on promiscuous rodents (e.g., Lane *et al.*, 2008; Baxter *et al.*, 2009; Thonhauser *et al.*, 2013, 2014b; Sommaro *et al.*, 2015) revealed no correlation between MMM and offspring quality, MP or litter allelic diversity. However, it can be assumed that MP probably evolved as a mechanism to prevent inbreeding (Bergeron *et al.*, 2011; Ratkiewicz & Borkowska, 2000). It should be also noted that the frequency of MP was found to be much higher in solitary and gregarious rodents compared to species with a family-group lifestyle. However, because of shortage of these data and the small number of species compared, it is impossible to draw valid conclusions from this finding.

An increase of genetic variability per litter in unpredictable environments that results from MP may provide a plausible explanation for why females mate with several males (Hanken & Sherman, 1981; Madsen *et al.*, 1992; Murie, 1995). Field studies have provided evidence that MMM allows females to increase the genetic variability of their progeny in some species with a family-group lifestyle (*C. leucurus*, *C. ludovicianus*, *M. marmota*, *L. brandti*; Chesser, 1983; Daley, 1992; Goossens *et al.*, 1998; Cohas *et al.*, 2006; Huo *et al.*, 2010), as well as in some promiscuous rodents, such as *M. musculus* (Thonhauser *et al.*, 2014a) and *G. glis* (Moska *et al.*, 2021). Increasing genetic variability within litters can increase the survival probability in habitats that experience unpredictable changes from one generation to the next (Yasui, 1998; Crean & Marshall, 2009). Some authors (reviewed in Karl, 2008) proposed that MP would reduce the effective population size and decrease the genetic variability of the population (because each mating may result in fewer offspring per male than the expected in a genetic monogamy), but others suggested that MP might increase the effective population size and genetic variability of the population (Pearse & Anderson, 2009).

The hypothesis that MMM promotes fertility assurance and an increasing probability of conception (Birkhead *et al.*, 1993; Hunter *et al.*, 1993; Sheldon, 1994; Zeh & Zeh, 1996, 1997, 2001; Hoogland, 1998; Jennions & Petrie, 2000; Colegrave *et al.*, 2002; Mays & Hill, 2004) leading to increased litter size received weak support, and relevant evidence was obtained from studies on five species only: *C. gunnisoni* (Hoogland, 1998), *C. parvidens* (Haynie *et al.*, 2003; Hoogland, 2013), *A. uralensis* (Bryja *et al.*, 2008), *S. tereticaudus* (Munroe & Koprowski, 2011), and *M. musculus* (Thonhauser *et al.*, 2013). However, females of two *Cynomys* species with a family-group lifestyle (*C. gunnisoni* and *C. leucurus*) appear to have incurred the cost of copulating with more than one male, as they are less likely to survive to the next mating season (Hoogland, 2013). On the other hand, a decreased probability in

conceiving following MMM has been detected in two promiscuous species: *Peromyscus maniculatus* (see Dewsbury, 1982) and *Phodopus sungorus* (see Wynne-Edwards & Lisk, 1984). In most species examined, MMM had no effect on litter size. Recent studies (Keil *et al.*, 1999; Wolff & Dunlap, 2002; Stockley, 2003; Sommaro *et al.*, 2015) provide evidence that mating with several males does not increase litter size in promiscuous rodents.

The mechanism by which MMM may increase conception rates or litter size in some species of rodents is still not well understood, but it may be either to guard against male sterility or sperm depletion (Haig & Bergstrom, 1995) or just to stimulate ovulation (Jennions & Petrie, 2000; Kraaijeveld-Smit *et al.*, 2002). The importance of inducing ovulation by multiple copulation has been examined in some rodent species. Specifically, it was found that a larger number of intromissions resulted in a greater percentage of eggs ovulated in *M. pennsylvanicus* (Gray *et al.*, 1977; Milligan, 1982) and *R. norvegicus* (Zarrow & Clark, 1968). However, a decreased probability in conceiving following MMM has been detected in two other muroid rodents (*P. maniculatus* and *P. sungorus*; Dewsbury, 1982; Wynne-Edwards & Lisk, 1984). Such a decrease following MMM might be the result of a strange-male-induced pregnancy block (Dewsbury, 1982; Wynne-Edwards & Lisk, 1984). It was also shown that MMM had no effect on conception in *S. tridecemlineatus* (Schwagmeyer, 1986), *S. columbianus* (Murie, 1995), *C. ludovicianus* (Hoogland, 1995), and *M. ochrogaster* (Wolff & Dunlap, 2002).

According to Humphries and Boutin (2000), McAdam *et al.* (2002), and Réale *et al.* (2003), exceeding optimal litter size can have long-term fitness consequences both for offspring growth and survival and/or female survival and future reproductive success. These authors suggested that these associated costs might only be avoided in species with biparental or communal offspring care. The costs (in terms of time and energy expenditure, injuries, and sexually transmitted diseases) of mating with several males in order to increase litter size seem to be not justified in females of promiscuous rodents.

Based on the results of the study on *C. musculus*, Coda *et al.* (2011) and Sommaro *et al.* (2015) suggested that females of this species would mate with multiple males as a counter-strategy against infanticide by males. This can be explained by the hypothesis of uncertainty of paternity preventing infanticide (Hrdy, 1977; Agrell *et al.*, 1998; Wolff & Macdonald, 2004), which suggests that copulation inhibits males from killing the future young pups for a period of time long enough for the young to be weaned (Agrell *et al.*, 1998). Therefore, infanticidal males should not kill the offspring of previous sexual partners (Ebensperger, 1998; Thonhauser *et al.*, 2013). This hypothesis seems to be supported also by the results of the studies on *M. musculus* (Thonhauser *et al.*, 2013) and *M. marmota* (Goossens *et al.*, 1998).

The female mate choice hypothesis (Andersson, 1994) when females select their optimal sexual partners with “good genes” seems to be justified in two species only: *S. columbianus* (Murie, 1995) and *M. marmota* (Cohas *et al.*, 2006). The results of the study on *T. striatus* suggest that MMM can act as a bet-hedging strategy (Yasui, 2001; Fox & Rauter, 2003) that may effectively provide indirect genetic benefits for females by reducing the risk of inbreeding in this species where mating among close relatives is common (Bergeron *et al.*, 2011).

The relationship between OSR and MP in species with polygynandrous or promiscuous mating systems is not clear. Male-biased OSR was associated with increased multiple mating by female *S. tridecemlineatus* (Schwagmeyer & Brown, 1983), but somewhat reduced multiple mating by female *S. columbianus* (Murie, 1995). In *S. richardsonii* (Michener & McLean, 1996) and *X. inauris* (Waterman, 1998), female rate of multiple mating was independent of changes in OSR. In *S. lateralis*, OSR also did not affect rates of MP (Wells *et al.*, 2017), though through postcopulatory female choice (Eberhard, 1996), it is possible for OSR to have increased the rate of MMM without affecting the rate of MP (Murie, 1995). One can suggest that the variation in MP likely results from the interaction between encounter rates and the active strategies of males or females.

Studies examining Bateman’s gradients (Bateman, 1948; Jones *et al.*, 2002) have been conducted on two rodent species only: *S. tereticaudus* (Munroe & Koprowski, 2011) and *S. lateralis* (Wells *et al.*, 2017). The mating system in *S. tereticaudus* defined through genetic analyses and Bateman’s gradients was found to be polygynandrous compared to the previously suggested polygynous mating system as established by behavioral observations. From Bateman’s gradients, there was found no direct fitness benefit of MP for *S. lateralis* females. Thus, Bateman gradients turned out to be useful for clarifying data on the mating system of these species and identifying possible advantages of MMM.

The results of some studies (Klemme *et al.*, 2007b; Hoogland, 2013; Thonhauser *et al.*, 2014a) have shown that MMM may have negative fitness effects for females and their offspring. Specifically, MP was found to be associated with reduced mean and variance in offspring body mass in *M. domesticus* and *M. musculus* (Thonhauser *et al.*, 2014a). As for other conceptual models, it should be noted that the hypothesis of promotion of parental care due to MMM (Davies *et al.*, 1996) has been examined on one species only — *M. ochrogaster* (Wolff & Dunlap, 2002). This study has shown that additional mates did not provide additional parental care. The hypothesis of enhanced access to resources due to MMM (Gray, 1997) has not been examined on rodents.

In general, the potential fitness benefits to females mating with multiple males including fertility assurance, an increase in genetic diversity of offspring and litter size, as well as reduction in the probability of infanticide have been revealed, at least partially, in 23 species in question. It should be also noted that these potential fitness benefits of MMM have been confirmed

for solitary and gregarious species, as well as for species living in family groups, that is, regardless of their social structures and mating systems. As for the other 25 species, the findings are limited to stating the fact of occurrence MMM or MP. Moreover, none of the hypotheses concerning the potential fitness benefits to females mentioned in the Introduction can be considered universal, and in most cases one or another hypothesis is confirmed only for a limited number of species. With regard to other factors, such as population demographics or annual variation in food abundance, that may influence MMM and thus MP, the available data are insufficient to draw valid conclusions.

The results reported in the present review show that even in species where pronounced behavioral and physiological mechanisms promoting social monogamy are seen, the social mating system is not necessarily tightly linked to the genetic mating system. This raises the intriguing question of why females and males form a long-term pair bond and then females mate multiply. Evidence from other vertebrates indicates that MP may provide direct or indirect benefits to females (Jennions & Petrie, 2000; Brotherton & Komers, 2003; Sommer, 2003). However, because of the lack of data on the fitness consequences of mating with multiple males, the benefits of this behavior still remain an unanswered question.

Multiple paternity observed in many socially monogamous (e.g., *M. unguiculatus*, *M. ochrogaster*, *M. socialis*, *P. californicus*) as well as polygynous rodents (e.g., *L. brandti*, *P. polionotus*) is also an intriguing phenomenon (Gromov, 2008). Extra-pair paternity was found to be rare among species living in solitary pairs (e.g., *P. californicus*, Ribble, 1991), but frequent among species living in extended family groups (e.g., *P. polionotus*, Foltz, 1981). According to the fitness-enhancing hypothesis (Trivers, 1972; Maynard-Smith, 1977), paternal care evolved because there was an initial direct benefit to offspring, fathers and/or mothers. The prevailing paradigm assumes that a male’s fitness can increase through providing care if his offspring survive and reproduce, and certainty of paternity is presumably a contributor to the evolution of paternal care. However, many males in socially monogamous rodents with biparental care of young provide parental care for both own offspring and young sired by other males. Therefore, “careful fathers” promote distribution of not only their own but alien genes as well. This phenomenon does not fit into the framework of the concepts accepted in behavioral ecology, and therefore deserves further research.

Future studies must identify the precise genetic benefits of multiple paternity from the female’s perspective and evaluate the causality of the relations in order to understand the rather complex variation in multiple paternity in the wild. Further studies are also needed to estimate the adaptive significance of multiple mating in rodents. The resulting paternity pattern after multi-male mating seems to be a combination of sperm competition and cryptic female choice. The lack of observations of copulation makes it impossible

to determine whether selectivity was the result of pre- or postcopulatory mechanisms. Such observations are quite challenging to obtain on wild populations. These are required to provide a better understanding of how animals cope with contrasted population demographics and environmental conditions to ensure that their own and their offspring's fitness are optimized.

In most cases, the differences in MP proportions are considered a result of the differences in MMM proportions. However, the MP proportion is determined not only by the MMM proportion but also by litter size. Therefore, the explanatory power of the MP proportion should be reconsidered. When a high MP proportion is observed, the population undoubtedly has a high MMM proportion, but a low MP proportion does not always indicate a low MMM proportion (Wakabayashi & Saitoh, 2019). Further investigation is thus needed to determine if benefits of polyandry are likely to differ for polytocous and monotocous species. Estimating the lifetime reproductive success of offspring of monandrous and polyandrous females may also clarify the adaptive significance of polyandry.

The extent to which the consequences of MMM observed under laboratory conditions manifest under natural conditions and the level to which these benefits, relative to extrinsic influences of the populations' mating system, govern female mating behavior will require further investigations within the context of each species' natural history. Experimental studies of the benefits of genetic promiscuity in both female individuals and the population would be a very important task for future research. Accumulating the empirical data will enable a more comprehensive review of the genetic benefits of MMM.

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