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# Male expulsion in cooperative Mongolian gerbils (*Meriones unguiculatus*)

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**Abstract**

Mongolian gerbils are territorial rodents of steppes and semideserts of Mongolia and Northern China. At least under laboratory conditions, the family life is characterized by long-term harmonious and short-term aggressive periods in which some members are expelled. The purpose of this study was to clarify which features of male offspring promote their expulsion. Therefore body mass, absolute and relative weight of testes and epididymis, histology of testes and testosterone concentrations were analyzed in males derived from five families living in semi-natural enclosures with food and water ad libitum. Males expelled (EFM, $n=40$) had significantly higher relative testes and relative epididymis weight and higher testosterone concentrations in harmonious periods than it did non-attacked ones (IFM, $n=13$). A stepwise discriminant analysis has established the relative testes weight as decisive for the affiliation to EFM or IFM. Based on this parameter, 71.7% of the offspring could be classified correctly. Moreover, histological results showed that 50.0% of integrated and 29.4% of the expelled family members had incomplete spermiogenesis, indicating a reduced fertility. It is concluded, that males do compete for reproduction within the families which triggers the expulsion of the males with the highest reproductive capacity.


*Keywords:* Aggression; Reproductive competition; Spermiogenesis; Expulsion

## 1. Introduction

Living in social groups is well known for many species. This way of life is associated with harmonious and aggressive interactions. In the wild, expulsion or coercive migration of some group members might follow these interactions. Such dynamic processes are especially important and effective for animals living in closely related units like families. In a current long-term study such a comparable mechanism was investigated under laboratory conditions in families of the Mongolian gerbil (*Meriones unguiculatus*), which is a typical rodent of steppes and semi-deserts in Mongolia and northern China. This species is described as a cooperative breeder with a single breeding pair [1,2]. Within the families, it was frequently shown that the reproduction of the female offspring is suppressed [3–5]. However, concerning the role of the males, only little information is available [6].

The social life of the Mongolian gerbil is described as harmonious within a family group, but they show intense intraspecific aggressive behaviour against non-littermates and unfamiliar animals [7,8]. Aggression against related animals occurs after the loss of the founder female or male. As a result, the vacant position of founder females was later occupied by a single female offspring depending on her outcome in aggressive interactions. Therefore, physical condition, age and aggression level influenced a female individual's position in its family. The vacant position of founder males was occupied by different male offspring. Resulting from their age and their ventral gland pad size, these group members were characterized as the oldest ones [9].

The replacement of founder females is often associated with aggression amongst the female offspring and is therefore one of the causal factors for agonistic interactions [10–12]. The replacement of founder males did not lead to aggressive interactions, although also founder males were attacked seriously in rare cases.

As shown recently, general changes in family structure including age, rank and reproductively active animals, and an increase in family size are possible causal factors as well [13]. Based on these findings, the family life could be divided into

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short-term aggressive (17.2±3.8 days) and long-term harmonious periods (up to 21 weeks). Depending on their respective role and agonistic behaviour in these periods, the adult members were assigned to three different social categories. The first category summarized the integrated family members (IFM), who were non-attacked and non-reproducing animals. The second category was the expelled family members (EFM), who were attacked during aggressive interactions. In females, reproductive efforts could be observed. The third category was defined as repeatedly successfully breeding animals, the founder pair animals (FPA). These animals acted in nearly all cases as aggressors. Similar findings were reported about the social life of marmots (*Marmota marmota*) [14]. Moreover, the underlying dynamic processes was also described in Emlens' theoretical model [15] in which the trade-off between advantages of group-living and the disadvantages of being reproductively suppressed is emphasized for the members of a family. That is why mature offspring is waiting for acceptable reproductive opportunities and vacancies. Conflicts of interest lead to aggressive interactions in cases of limited resources. Therefore, family dynamics reflect regulatory mechanisms for optimizing the direct fitness of individuals within the family.

In well described polygyny breeding species like the red deer (*Cervus elaphus*) and the elephant seals (*Mirounga angustirostris*), the role of the males is well described. Here dominant males are adults with optimal adaptation for the ecological conditions and reproductive capacity [16,17]. Comparative studies have shown that there are relationships between mating systems, relative testes sizes and sperm morphology, phallic morphology, circulating testosterone levels and sexual behaviour in male mammals [18]. Furthermore, a correlation between breeding system and testes weight in 33 species of primates was found [19]. Males living in single male breeding systems had smaller testes than males from multi male breeding systems. This was explained by the need of a larger deposit of sperm for competing with other males, possibly necessitating a higher volume of spermatogenic tissue. In general, a positive correlation between sperm number and testes weight and size in mammals was hypothesized [20] and moreover, summarized data of mammals and confirmed this by calculating data of diverse mammal species [21]. They found that smaller males showed an increased investment in sperm production, which was associated with an increase of testes size. Such a compensating mechanism developed independently in species where heavier males performed guarded mating and smaller males acted as sneakers. Further studies supporting this theory were undertaken in the solitary and promiscuous common shrew (*Sorex araneus*) [22] and in the yellow-pine chipmunk (*Tamias amoenus*) [23], revealing that successful sperm competition is correlated with higher testes size.

Testosterone is ascribed an important role with respect to mammalian reproductive success [24] and to aggression [25,26]. Such an effect was investigated in male mice [27], here the rank of the animals was determined influenced by the level of testosterone and modulated by castration. Although the relationship between aggression and social dominance is therefore well documented [28], it was argued by another study [29] that aggressiveness is just the manifestation of social dominance.

The complex family dynamics of the Mongolian gerbil is influenced by the individual traits of its members including age, sexual maturity, phenotypical fitness, and the social rank. In this study, the focus was on male–male interaction and the fate of the male offspring within the family. Therefore, the two different social categories, integrated males (IFM) and expelled males (EFM) were compared in order to find predetermining factors along the reproductive axis, which might explain the selective expulsion of some of the male offspring. The following hypothesis was tested: expelled males differ from the integrated ones with respect to reproductive characteristics. Moreover, a possible pattern of sexual-specific expulsion was investigated in further detail in order to elucidate whether founder males attack mature male offspring and founder females attack mainly the infertile males with incomplete spermiogenesis.

## 2. Materials and methods

### 2.1. Animals and housing conditions

Five families were kept in enclosures, lined with wood shavings (Allspan Animal bedding, The Netherlands) and enriched by wooden roots, limbs and sand bath. Tap water and food pellets (ALTROMIN GmbH Lage, Germany) were offered ad libitum and were complemented with sunflower seeds, walnuts, fruits and hay. The temperature was 25±3 °C in the windowless rooms. The light/dark conditions were 14:10 h (lights-on at 5 am), the light intensity varied from 100–300 lux (light period) to 5 lux (dark period). Animals were kept in their natal families and they lived on an area of 1.5 to 4 $m^2$. The different enclosure sizes were used in order to determine a possible influence of the area-dependent number of animals per family. From these families together 58 males were analyzed (distribution: two families 15 males, one family 14 males, one family 9 males and one family 5 males). The relative share per family of IFM was 22.8±7.1% and respectively 67.2±8.3% for EFM. The exclusive category of FPA had a share of 10.1±3.0%.

Families of *Meriones unguiculatus* were each based on a founder pair. Females derived from our own laboratory breeding stock (Zoh:CRW) going back to three breeding pairs obtained by Charles River Wiga (Sulzfeld, Germany) in 1992. The founder males descended from wild animals caught in 1995. These founder pairs were set up for future paternity analysis based on different heterozygosity [30].

### 2.2. Family member expulsion

The individual differentiation of all individuals was possible due to the use of passive subcutaneous transponders (TROVAN Ltd., United Kingdom), with which all animals were supplied at a body mass of more than 50 g. For the determination of whether an animal was excluded from its family or not, all families were monitored at least five days per week for 0.5