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Social factors affecting litters in families of Mongolian gerbils, *Meriones unguiculatus*

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A b s t r a c t . Mongolian gerbils (*Meriones unguiculatus*) live territorially in families consisting of a reproducing founder pair and their non-reproducing young. Intra-family aggression occurs and is reported to be mainly caused by reproductive competition between females and the loss of reproducing founder animals. The current study investigated the impact of family traits (size, density and sex ratio) and aggressive inter-individual interactions on litters. Characteristics like pup mortality, litter size, sex ratio, and weekly body mass gain were tested. Across litters, significant correlations were found between litter size and family size ($r = -0.507$, $df = 25$, $p = 0.008$) and between litter size and family density ($r = -0.404$, $df = 25$, $p = 0.01$). Pup mortality was influenced by family size ($r = 0.556$, $df = 25$, $p = 0.003$) and by family density ($r = 0.328$, $df = 25$, $p = 0.04$). Unexpectedly, the influencing factor "occurrence of aggression" between adult family members or "expulsion of the mother" during lactation of the young had no influence on litters' features. Family size and family density could be shown to be the most dominant parameters affecting the fate of the offspring and regulating the reproduction of the family.

Key words: aggression, peri-natal factors, mothers, pups

Introduction

Life history was described by D a a n & T i n b e r g e n (1997) as the "distribution of major events over the lifetime of individuals". Such major events occur during the whole lifetime beginning with pre-natal ontogenesis. It is known that social and non-biological factors at the time of birth affect maternal care and mother-infant interactions. In rodents, care per individual declines with increasing litter size (G u e r r a & N u n e s 2001); mothers can limit their energy expenditure by adjusting maternal care and by infanticide (E l w o o d & B r o o m 1978, H a u s f a t e r & H r d y 1984, P a r m i g i a n i & v o m S a a l 1994). H a r p e r (1981) believes that it makes good economic sense for mothers to invest in offspring depending on individual and ecological resources. On the other hand, the loss of pups is equivalent to the loss of maternal investment (A g r e l l et al. 1998). Maternal care can be regulated further through the number of mother-infant interactions during the period of lactation (snowshoe hares: B o u t i n 1984, marmots: A r n o l d 1990, brown bears: D a h l e & S w e n s o n 2003). These patterns are less relevant in cooperatively breeding Mongolian gerbils, due to the presence of helpers, than in solitary rodents like the golden hamster (*Mesocricetus auratus*) (E l w o o d 1975, O s t e r m e y e r & E l w o o d 1984). Nevertheless, the ontogenesis of pups does generally depend on litter size and body mass of mothers (C o u r e a u d et al. 2000, R a u w et al. 2003). Moreover, body mass is important for an individual's life history because it influences the point at which maturity is reached and high body mass optimizes fecundity (D a a n & T i n b e r g e n 1997). In addition to

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these factors, body mass also influences the life history of the individuals because heavier individuals have advantages in occupying and defending their territories (Clutton-Brock et al. 1988, le Boeuf & Reiter 1988). Moreover, individuals of high body mass are favoured in aggressive interactions and therefore in their access to receptive females (Andersson & Wallander 2004, Szekely et al. 2004). Heavier females also have advantages in rearing more pups than lighter individuals and they are able to invest more resources during lactation (Malcolm & Marten 1982, Coureaud et al. 2000).

We used the Mongolian gerbil (*Meriones unguiculatus* Milne Edwards, 1867) as a model species for revealing to what extent individuals are influenced by peri-natal factors. These animals are rodents that occur naturally in the steppes and semi-deserts of Mongolia and northern China living in families based on a reproductive founder pair and their non-reproductive offspring (Gromov 1981, Ostermeyer & Elwood 1984, Salo & French 1989, Clark & Galef 2001). The families are strongly territorial with kin recognition based on a family odour spread by the ventral glands of the highest ranking family members, i.e. the founder pair animals and the oldest male offspring (Ginsburg & Braud 1971, Thiessen et al. 1971, Thiessen & Yahr 1977, Gromov 1990). If there is a loss of a founder animal, the vacant position is occupied by the oldest member of the family group of the appropriate sex. The replacement of founder females is one of the causal factors in the outbreak of aggression among family members in the Mongolian gerbils, (Roper & Polioudakis 1977, Swanson & Lockley 1978, Clark & Galef 2001). Further causal factors of aggression are changes in family composition and an increase in family size. The state of the family can be divided into short-term aggressive and long-term harmonious periods based on the occurrence of agonistic behaviour (Scheibler et al. 2005). We carried out an investigation of the effects of litter size, pup mortality, and sex ratio and body mass increase during these two different periods of family life. In previous studies, adult members of gerbil families were assigned to three different social categories (Scheibler et al. 2004). The first category was integrated family members, who were never attacked during aggressive periods and did not reproduce. The second category was expelled family members; they were attacked during aggressive interactions. A very small number of females from this category started to reproduce, but they were expelled by the time they weaned their pups. The third category included repeatedly successfully breeding animals; these were the founder pairs acting mostly as aggressors.

Following hypotheses were tested in the long-term investigation of peri-natal factors in Mongolian gerbil's families under laboratory conditions: (1) An increasing number of helpers in the family leads to an elevated reproductive success marked by litter traits as size, pup mortality and weekly body mass gain. (2) Litters and pups in general will be negatively influenced by the outbreak of aggression. (3) The expulsion of the mother is followed by increased pup mortality and a reduced weekly body mass gain.

Materials and Methods

Animals and housing conditions

Seven gerbil families were investigated until all females for a given family died (1.3 to 2.4 years). The determined family size was up to 32 animals. Each family was based on a founder pair. Founder females were derived from our laboratory breeding stock (Zoh: CRW) going back to breeding pairs obtained by Charles River Wiga (Sulzfeld, Germany) in 1992. Founder males descended from wild animals caught in 1995. These founder pairs were set up for future paternity analysis based on differences in heterozygosity (Neumann et al. 2001). Each founder pair was put into a semi-natural enclosure made out of plastics and enriched by dens, a sand bath area, and tree roots and limbs and was lined with wood shavings (Allspan Animal bedding, The Netherlands). The enclosure sizes varied between 1.5 and 4.3 m^2 to favour different family densities. Tap water and food pellets (ALTROMIN GmbH Lage) were offered ad libitum and supplemented with sunflower seeds, walnuts, fruits and hay. The families were kept in windowless rooms with temperature of 25 ± 3 °C and light/dark conditions of 14:10 h (lights-on at 5 am) with the light intensity varying from 100-300 lux (light period) to 5 lux (dark period).

State of families and status of the mothers

In order to determine whether aggression occurred and which animals were involved in these interactions, all families were monitored at least five days per week between 7 and 9 am for 0.5 h per family. The individuals who had taken part into aggressive interactions were caught and identified by means of their transponder (see below). The observation period reflects one peak of the bimodal activity pattern under standard conditions, published earlier (Weinandy & Gattermann 1996/97). The kind of interaction was used to differentiate between harmonious and aggressive family situation. The following behaviours were recorded: chasing: one animal tried to escape by running while the aggressor followed closely behind; biting: one animal was attacked by the aggressor after ano-genital inspection; appeasement: one animal licked the mouth of the aggressor and rubbed its rear on the ventral gland of the aggressor; keeping distance: one animal hid in cage structures while the aggressor patrolled the enclosure; exclusion from food: one animal was excluded from food by the aggressor. If at least one of these behaviour patterns occurred repeatedly within one observation session and on subsequent days, such a period was labelled as “aggressive period”. Moreover, general activity of each of the families was recorded via passive infrared sensors during the course of the experiment. A higher level of activity indicated an increase of agonistic behaviour due to elevated amount of chasing and keeping distance. The activity data were calculated and analysed by “The Chronobiological Kit” (Stanford Software Systems, USA). Typical aggressive interactions occurred as follows: animals met in the enclosure and one remained passive while being inspected ano-genitally by the aggressor. Subsequently, biting attacks and chasing occurred and the victims of this targeted agonistic behaviour were labelled as “expelled family members”. The expelled family members were separated from the rest of the group by the aggressor due to attacking and excluding from feeding them. They were subsequently removed from the families by the observer, either immediately after this behaviour was observed or, if such fights were not observed, when wounds were detected. Some of the non-founder females also gave birth to a litter. These mothers were actively expelled by the founder female within 4 weeks after giving birth and were labelled as expelled mothers. The successfully reproducing animals were founders. Nearly all aggressors were recruited from this group.

Data collection

All individuals (> 50g body mass) were marked using a passive subcutaneous transponder (TROVAN Ltd., United Kingdom). Therefore an individual identification was possible by catching and reading their ID-number with a handy-reader. All litters were identified by date of birth, litter size, ID-number of mother, the social category of the mother, family size, family density and sex ratio of the family. Time of birth was characterized as either an aggressive or harmonious period. Mean litter body mass was measured weekly; except for the first three days after birth, pups were not weighed in order to prevent stress for the newborn litters. Sex ratio of litters was determined after weaning. Pup mortality was determined as the percentage of pups died post-partum until weaning.

Statistics

Statistical analysis was carried out with SPSS 12.0. Normally distributed data (Shapiro-Wilk: litter size z = 0.987, p = 0.969, pup mortality z = 0. 915, p = 0.5, litter sex ratio z = 0.973, p = 0.897, time an animal lived in its natal family z = 0.926, p = 0.513) were given as mean values, the statistical measure of variance is the standard error of mean (SEM). The parametric t-test and Pearson correlations were used for these data. As body mass increase was non-parametric data (Shapiro-Wilk: z = 0.963, p = 0.04), it was given as median values and the interquartile range and were analyzed with non-parametric Mann-Whitney-U-tests and Spearman correlations. In order to prevent pseudo-replication, the data of the animals or litters were analysed first per family and subsequently the family data were compared with each other, i.e. the N in these cases was seven. Altogether 76 litters were registered, one family had 20, one had 15, two families 11, one had 10, one had 5 and the last one 4 litters.

Results

Effects of family trait on litters

Litter characteristics in the seven families studied were: mean litter size of 5.1 ± 0.5 pups per litter; pup mortality of 36.9 ± 6.2 %; mean sex ratio across litters of 1:1.24 ± 0.18; and median of weekly body mass increase within the first six weeks of life of 6.4 g (interquartile range 0.48) per litter. These values were calculated from seven families and their 76 litters. Family and litter characteristics were analyzed by Pearson correlations (Table 1). An increase in family size, as well as family density, resulted in increased pup mortality and reduced litter

Table 1. Correlation of family characteristics and litter features. Given are Pearson coefficients of correlations for parametric values of litter size, pup mortality and sex ratio of litters and Spearman coefficients of correlation for non-parametric values of weekly body mass gain. Data were calculated family-wise (N=7).

Litter feature	Litter size	Pup mortality %	Sex ratio	Mean weekly body mass increase
Absolute family size	- 0.507 df = 25 p = 0.008	0.556 df = 25 p = 0.003	- 0.271 df = 22 p = 0.2	- 0.475 df = 16 p = 0.054
Family density n/m²	- 0.404 df = 39 p = 0.01	0.328 df = 39 p = 0.04	- 0.173 df = 32 p = 0.3	- 0.338 df = 25 p = 0.09
Sex ratio of family	0.100 df = 26 p = 0.9	- 0.062 df = 26 p = 0.8	- 0.021 df = 21 p = 0.9	0.145 df = 16 p = 0.6

size, with family size having a stronger effect. The sex ratio of the adult family members at the time of birth had no impact on litter traits and the sex ratio of the pups at weaning was not influenced by the families and litter characteristics measured.

In the mean, animals lived for 21.9 ± 1.4 weeks (N = 311) with their family until expulsion or natural death. Elevated family size around birth significantly influenced this period (r = -0.347, df = 310, p<0.0001) negatively as it did family density (r = -0.253, df = 310, p<0.0001).

Effects of aggression and status of mothers on litter trait

A minority of adult family members were directly involved in aggressive interactions, these were the aggressors and the animals expelled. Aggressors mainly (> 80 %) acted alone and the number of animals attacked was low (2.4 ± 0.3) during an aggression period which corresponded to 16.7 ± 3.3 % of the absolute family size at the beginning of such an aggressive period. Males and females acted aggressively, but mostly founder females were determined as the attacking ones. There was no relation between the sex of the attacking and of the attacked animal. Pups were rarely involved directly; mostly they were influenced by the shortened time of warming and lactation or the destruction of the nest. However, some of them were killed by different family members including their own mother. Aggressive periods (N=36) were shorter (17.4 ± 1.4 days) as periods without any aggressive interactions observed (N=29) with a mean duration of 53.9 ± 13.2 days.

Effects of the occurrence of aggressive behaviour (harmonious vs. aggressive periods) on litter traits are shown in Table 2 for the seven families. There was a non-significant trend towards a reduced reproductive rate shown by elevated pup mortality and a reduced litter size in families exhibiting aggression. Aside from the fact that it was mainly the founder pairs that produced litters, the social category of the mothers (founder females vs. expelled females) was also tested (Table 2). A non-significant trend was found for the sex ratio of litters with expelled mothers having a higher proportion of sons. With respect to the time

Table 2. Effects of family state and social category of the mothers at time of birth on litter characteristics. Data were calculated family-wise (N=7). Given values are means ± SEM and the values of non-paired t-test.

Features	State of the family			Social category of mothers		
	Harmonious period N=7	Aggressive period N=7	t-test	Founder females N=11	Expelled females N=2	t-test
pup mortality %	31.5 ± 9.0	56.3 ± 9.4	-1.331 df = 11 p = 0.08	45.7 ± 9.4	37.9 ± 22.8	- 0.960 df = 14 p = 0.4
litter size	5.3 ± 0.5	4.2 ± 0.7	1.899 df = 11 p = 0.2	5.0 ± 0.4	6.3 ± 1.3	0.314 df = 14 p = 0.8
litter sex ratio	1 : 1.5 ± 0.5	1 : 0.9 ± 0.1	-1.276 df = 10 p = 0.2	1.3 ± 0.2	0.6 ± 0.2	2.292 df = 11 p = 0.05
time of living in natal family in weeks	21.8 ± 4.4	11.1 ± 4.5	1.169 df = 11 p = 0.1	20.7 ± 4.5	9.6 ± 1,7	1.025 df = 11 p = 0.3

an animal lived with its family, the status of the mother affected (t-test: T = 1.025, df = 11, p = 0.3) the time an animal lived in its family. Offspring of founder females tended to stay longer within their families as pups from expelled females. No differences were found for weekly body mass gain of pups born in harmonious (6.7g interquartile range 0.7) periods versus pups born in aggressive ones (6.7 g interquartile range 2.1; Mann Whitney U-test: U=7.0, p=0.3). Offspring of founder females showed nearly the same weekly body mass gain than these of mothers expelled. (Pups of founder females 6.4g per week, interquartile range1.0; pups of mothers expelled 6.1 g per week, interquartile range 1.1; Mann Whitney U-test: U=8.0, p=0.2).

Discussion

The main issue of this current long-term laboratory study was to investigate the impact of perinatal factors in a cooperative breeding rodent species. As a possible parameter, general family traits as their size, density and sex ratio were used to present the influence of a varying number of helpers. Moreover, the occurrence of aggressive behaviour between their mothers or other adult family members was further tested concerning their influencing power on the litters.

The first influencing factor was the family traits. It was shown that an elevated family size or family density had negative consequences for the youngest offspring. Although a large number of family members was described as advantageous for other mammals like African wild dogs (Malcolm & Marten 1982), snowshoe hares (Boutin 1984) and marmots (Arnold 1990), an increased family size and density led to a reduced litter size and an elevated pup mortality in the Mongolian gerbils. This resulted in a delayed increase of the families. Therefore, the first hypothesis, that an increased number of helpers would cause improved condition for the young, had to be rejected under the restricted laboratory conditions used. It was shown that reproductively suppressed helpers have an advantage in getting experience and fitness gain, but beyond it they compete with the pups for resources (Trivers 1972, Daan & Tinbergen 1997). Such dynamic processes were well described and explained by Emlen (1995) in his generalized economic model in which family size and family composition were the main controlling elements. He wrote that there occurs a trade-off between the advantages of family-living and the disadvantages of being reproductively suppressed. Therefore, family dynamics reflect regulatory mechanisms for optimizing the direct fitness of individuals within the family. The effect of the delayed population increase in highly density populations was also described by Christian & Davis (1964) with respect to the regulation of population growth in house mice.

Litters were generally also exposed to intra-family interactions as the time of warming and lactating was thereby reduced and the nest was moved or destroyed repeatedly while aggressive behaviour occurred. The assumed disadvantages on the litters born during aggressive periods could not be shown. Neither the litter size, pup mortality, sex ratio nor the body mass gain was affected. A slight but not significant increase (15 %) of pup mortality of those litters born in aggressive periods was observed. Moreover, the weekly body mass gain of the young tended to be reduced (8 g less). Therefore, the second hypothesis of a disadvantage of these young could not be proven, intra-family conflicts between some of the offspring and founder pairs seemed to affect reproductive success less. This might be explained by the social structure of the Mongolian gerbil families. The young were cared by the non-involved family members who acted as helpers at the nest (Ostermeyer

& Elwood 1984, French 1994, Clark et al. 2004), a phenomenon which was generally described by Daan & Tinbergen (1997).

Moreover, the expulsion of the mother and therefore the massive disturbance of the mother-offspring relationship had no measurable effects on the young. Neither their mortality nor their ontogenesis (e.g. body mass gain) differed from those of the pups raised by their own mother. This can most probably be explained by the fact that these females reproduced synchronously with the founder female. Therefore, the young were lactated and raised jointly. In that way, there was a compensating strategy which led to a survival and growth of the young. However, due to the fact that this only happened in two cases, it is yet not possible to evaluate it in terms of future consequences.

In conclusion, litters of the cooperatively breeding species *Meriones unguiculatus* are mainly influenced by the number of helpers and competitors. It seems that there is an optimum range in the number of helpers. Beyond it, this promoting effect is reversed into a competitive situation in which the youngest were impaired the most. However, the helping behaviour of all family members compensates intra-family aggressive behaviour and even the loss of the mother which is possible due to synchronous births. Warming the young was therefore performed by non-involved family members. Founder females lactated all young despite the fact that they acted as aggressors.

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