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Parental care and time sharing in the Mongolian gerbil

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Abstract

The biparental care behaviour of the social Mongolian gerbil (*Meriones unguiculatus*) was quantified from birth to weaning of the young under laboratory conditions. Nestbuilding, nest-residence, and retrieving of the offspring were measured. The behaviour of the parents was registered per video-observation on days 2, 5, 8, 13, and 20 after the birth of the young, each for 24 h. To obtain control data, we additionally observed all pairs for 24 h without progeny. The objective of our study was to evaluate the paternal and maternal efforts in rearing the young and to focus on parental time sharing in the nest.

The female made the greatest contribution to care since there was no paternal support in building of the litter-nest and retrieving of the young. However, both adults cooperated via their synchronized presence with the young (temporal coordination or time sharing in the nest). We suggest that via this mutual behavioural synchronization the physiological strains of the female caused, e. g., by lactational hyperthermia are reduced.

Key words: *Meriones unguiculatus*, parental care, time sharing

Introduction

Although in mammals the females mainly care for the young, paternal investment can also increase their chances of survival via direct support, such as warming, and more indirect assistance like nest-building or defending the young. Investigations on cooperative breeding and paternal care mainly refers to primates and carnivores (for a review see: Solomon and French 1997; for rodents: Ostermeyer and Elwood 1984; Solomon and Getz 1997; Gerlach 1998).

Based on short-term observations during the light period (90 minutes per family), Elwood (1979) showed that certain parental activities of the social Mongolian gerbils, e. g., nest-building, are influenced by the other parent. The aim of our long-term study was to quantify in greater detail paternal and maternal efforts from birth to weaning of the altricial young and to focus on parental time sharing in the nest.

Material and methods

Animals and housing

We selected six adult males and six females from a laboratory colony of Mongolian gerbils (*Meriones unguiculatus*). The animals came from different litters and were caged in pairs after weaning at 6–8 weeks. They were kept in climatised rooms with a photoperiod of 12 : 12 h light (200–300 lx per

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cage): dark (5–10 lx per cage) (light period: 0700–1900 h Central European Time). The room temperature was 24 ± 2 °C and the relative humidity varied from 65–70 %. The cages (size: 55 × 33 × 20 cm) were plastic with a wire mesh top and included a circular treadmill (30 cm in diameter and a running wheel area width of 10 cm). Water and food pellets (Altromin® 7024, Altromin GmbH, Lage) were provided ad libitum. The animal bedding was provided from Altromin GmbH, Lage. To facilitate nest-building, the animals were also provided with cellulose.

We confirm that the experiments have been performed in accordance with local animal welfare legislation and the legal requirements of Germany.

Data analysis and statistics

The parental care behaviour of five pairs towards their first litter and of one pair towards their third litter was observed over 1 600 h. The mean litter size was 5.1 pups (3–7). The behaviour of the parents was registered on days 2, 5, 8, 13, and 20 after the birth of the young (day of birth = day 0), each for 24 h. To obtain control data, we observed all pairs for 24 h without offspring, i. e., 2–3 weeks before birth or after weaning. We used the time-lapse videotechnic (Panasonic WV-CL352E u. AG-7350) and chose the 12 h mode. The analysis was performed using the software The Observer V 3.0 (Noldus, NL). For both pair partners we collected the following behaviours: nest-building (duration): time spent with the carrying-in and arranging of nesting material; nest-residence (duration): time spent in the nest; retrieving of the young (frequency): carrying the pups back to the nest. The parameters are given as mean values, the statistical measure of variance is the standard error. The Friedman analysis of variance and subsequently the two-tailed Wilcoxon test were used to assess the differences of the means. Differences were significant at $p < 0.05$ (* in the graphs). The computer package used for the statistical analyses was Winstat (V 3.1).

Results

Nest-building

The time the gerbils spent on nest-building depended on whether it was used as a nest for resting (rest-nest) or as a nest for the approaching litter (litter-nest), i. e., the nest had two functions. When the adults lived without young under laboratory conditions, both males and females built a rest-nest as a depression in the animal bedding which was located in a corner of the cage (Fig. 1, males vs. females: Wilcoxon test, $z = -0.94$, $N = 6$, $p > 0.05$). It was only slightly enlarged during the last activity period before and completed just after birth of the pups. This litter-nest was more compact and was also built by both sexes.

Nevertheless, regarding the whole observation period, the respective effort of male and female was different (Fig. 1). In the mean a male invested 15.9 ± 7.4 and a female 27.3 ± 4.7 minutes per day (males vs. females: Wilcoxon test, $z = -1.99$, $N = 6$, $p < 0.05$). Whereas males did not intensify the nest-building behaviour (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 8.3$, $N = 6$, $df = 5$, $p > 0.05$), it was significantly elevated in the females until day 13 (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 15.64$, $N = 6$, $df = 5$, $p < 0.05$; Wilcoxon test, day 2 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 5 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 8 vs. control: $z = -2.2$, $N = 6$, $p < 0.05$; day 13 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 20 vs. control: $z = -1.36$, $N = 6$, $p > 0.05$).

Nest-residence

Both males and females stayed for approximately the same time alone in the commonly established nest (Fig. 1). There were no intersexual differences in that respect either in the rest-nest (Wilcoxon test, $z = -1.36$, $N = 6$, $p > 0.05$) or in the litter-nest (Wilcoxon test, $z = -0.52$, $N = 6$, $p > 0.05$). In the presence of the young this separate nest-residence of the

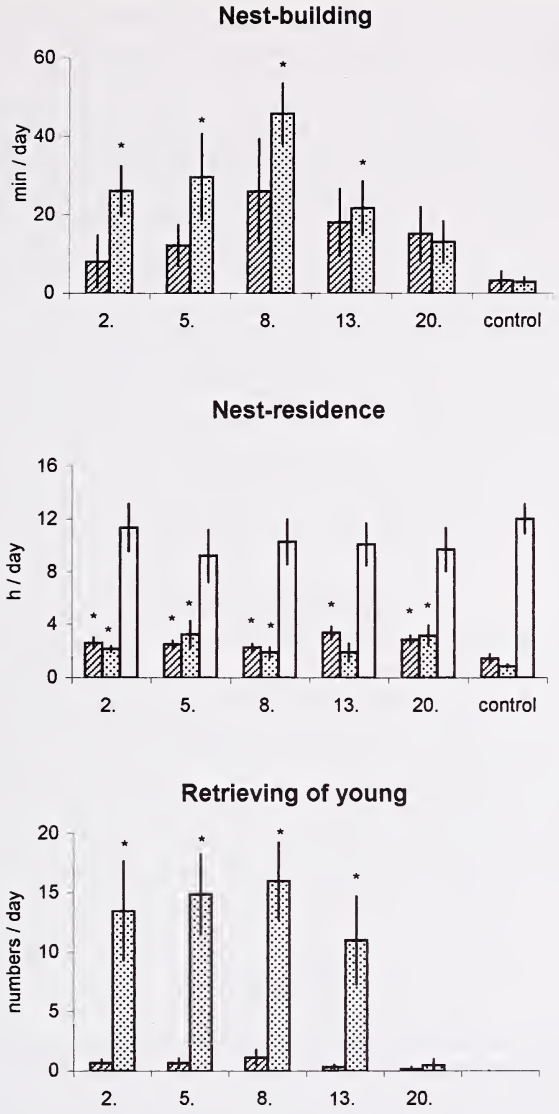

Fig. 1. Biparental care in Mongolian gerbils. Data of six pairs. Day 2 to day 20: with young (day 0 = day of birth); control: without young; scattered columns = males; dotted columns = females; blank columns = both parents together; bars = standard error of mean. * $p < 0.05$; The Friedman analysis of variance and subsequently the two-tailed Wilcoxon test were used to assess the differences of the means (for details, see text).

adults increased, i. e., the two parents showed time sharing in the litter-nest. This increase of the sole care for the progeny was always significant for the males (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 13.38$, N = 6, df = 5, $p < 0.05$; Wilcoxon test, day 2 vs. control: $z = -1.99$, N = 6, $p < 0.05$; day 5 vs. control: $z = -1.99$, N = 6, $p < 0.05$; day 8 vs. control: $z = -2.2$, N = 6, $p < 0.05$; day 13 vs. control: $z = -2.2$, N = 6, $p < 0.05$; day 20 vs. control: $z = -1.99$, N = 6, $p < 0.05$). The same applies to the females ex-

cept for day 13 (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 17.4$, N = 6, df = 5, $p < 0.05$; Wilcoxon test, day 2 vs. control: $z = -2.2$, N = 6, $p < 0.05$; day 5 vs. control: $z = -2.2$, N = 6, $p<0.05$; day 8 vs. control: $z = -2.2$, N = 6, $p < 0.05$; day 13 vs. control: $z = -1.4$, N = 6, $p > 0.05$; day 20 vs. control: $z = -2.2$, N = 6, $p < 0.05$).

The common nest-residence, i. e., the time the adults spent together in the nest as a pair, was about four times longer than the separate stay (Fig. 1). However, in contrast to this, it was not affected by the offspring (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 11.5$, N = 6, df = 5, $p < 0.05$; Wilcoxon test, day 2 vs. control: $z = -0.94$, N = 6, $p > 0.05$; day 5 vs. control: $z = -1.57$, N = 6, $p > 0.05$; day 8 vs. control: $z = -1.36$, N = 6, $p > 0.05$; day 13 vs. control: $z = -1.57$, N = 6, $p > 0.05$; day 20 vs. control: $z = -1.78$, N = 6, $p > 0.05$).

Summing up the data of the separate and the paired nest-residence results in the total time the adult gerbils spent in the nest. It ranged from 14.4 ± 1.2 h per day (control) and 15.4 ± 1.8 h per day (mean of day 2–day 20). As for the common nest-residence, the statistical analysis showed that there was no difference between these two periods (day 2–day 20 vs. control: Friedman ANOVA chi-square approximation, $\chi^2 = 11.98$, N = 6, df = 5, $p < 0.05$; Wilcoxon test, day 2 vs. control: $z = -1.21$, N = 6, $p > 0.05$; day 5 vs. control: $z = -0.52$, N = 6, $p > 0.05$; day 8 vs. control: $z = -0.37$, N = 6, $p > 0.05$; day 13 vs. control: $z = -1.36$, N = 6, $p > 0.05$; day 20 vs. control: $z = -1.36$, N = 6, $p > 0.05$).

Retrieving of young

Until day 5, the progeny were passively dragged out of the nest while attached to the mothers nipples. Nevertheless, to an even greater extent they were thrown out of the nest by digging movements of the adults. With advancing age and increased locomotor activity the pups actively left the nest and were retrieved essentially by females (Fig. 1, males vs. females: Wilcoxon test, day 2: $z = -2.2$, N = 6, $p < 0.05$; day 5: $z = -2.2$, N = 6, $p < 0.05$; day 8: $z = -2.2$, N = 6, $p < 0.05$; day 13: $z = -2.2$, N = 6, $p < 0.05$; day 20: $z = -0.48$, N = 6, $p > 0.05$). The mothers grabbed the young in the neck or other parts of the body with their teeth. At day 20 the retrieving behaviour of females ended.

The males also tried to retrieve their offspring but they pushed the young back to the nest with their snout. However, they failed in all observed cases.

Discussion

In nature Mongolian gerbils live under territorial conditions in groups which are established by a founder pair (Bannikov 1954; Agren 1984; Hendrie and Starkey 1998). In addition to the female, the male and the other family members also participate in promoting the development of the offspring (Elwood 1975; Ostermeyer and Elwood 1984). During their first days they have an incompleted ability to thermoregulate and are warmed and sheltered in a nest by the parents in order to stay alive. Paternal behaviour is described also in other rodent species. Wolff and Cicirello (1991) showed that *Peromyscus maniculatus* males retrieved pups and nested with females and newborn pups. In the laboratory adult gerbils built plain nests for common resting (rest-nest). For rearing the altricial young, the nests were enlarged and constructed more compactly mainly by the females (litter-nest). As shown in the golden hamster, the size of the nest and the amount of the female nest-building activity do not depend on the sexual cycle or the state of gravidity but on the environmental temperature (Richards 1966; Bhatia et al. 1995). Since the room temperature in our experiments was high (23–25 °C), the nest-building activity was relatively low. The increase in the female nest-building behaviour immediately after the birth of the pups is a response to parturition and the presence of

the young. Besides the temperature, the nest-building behaviour in house mice and other myomorph rodents is intensified according to olfactorical and acoustical (ultrasonic-) stimuli of the young (Noirot 1972, 1974; Sales and Smith 1978). Two weeks after birth the coat of the pups is well developed and the reduced relative surface of the body diminishes the loss of body heat. This shift of the young gerbils from being "heat sinks" to "heat sources" is reflected in a reduction of the nest-building effort following day 13.

In contrast to the female-biased nest-building both males and females cared for the progeny in the nest. While one animal stayed in it and warmed the young, the other left it. This ensues from the increased separate nest-residence of the father and the mother after the litter, i. e., there was an intersexual time sharing in the nest. Even in the prairie vole, *Microtus ochrogaster*, the female does leave the nest more often when the male takes part in the care of the litter (Wang and Novak 1992). Nevertheless, in this case the data were not calculated for timed synchrony. Wynne-Edwards (1995) observed the care behaviour of *Phodopus campbelli* for 30 minutes per day during the activity phase and during rest, respectively. She was also able to prove a temporal synchronisation in the care behaviour between the parents and additionally between mother and sister, i. e., the aunt of the offspring. The cooling down of the pups is prevented due to this temporal coordination of parental behaviour. Furthermore, the mother is able to satisfy her increased need for nutrients following the litter and during lactation (Galef 1983) and to reduce the physical strain caused by the lactational hyperthermia. This phenomenon of an increased core body temperature while in physical contact with the young is described in various small mammals (Adels and Leon 1986; Scribner and Wynne-Edwards 1994 a, 1994 b). In gerbils the daily mean values of core body temperature during the whole period of lactation are elevated by 0.6 °C (Weinandy and Gattermann 1995).

Although the common nest-residence of the pair partners was longer than the separate ones, it was not influenced by the pups. In accordance to their nocturnal activity pattern (Weinandy and Gattermann 1996/97) and their social behaviour gerbils rest together during most of the light phase, irrespective of the presence of young. They were left alone in the nest for about 8.6 h per day, i. e., the pups were not constantly warmed by the parents. Our assumption is that this is a consequence of the relatively high temperature conditions in the laboratory. Furthermore, the mutual warming of the young also reduced the loss of heat.

Retrieving the offspring is another direct nursing effort, which was in our study only successfully carried out by the female. The observed increase of retrieval behaviour was most likely triggered by ultrasonic vocalisation and the growing locomotor activity of the young, which left the nest more frequently. Furthermore, they were thrown out of the nest due to the species-specific stereotypic digging behaviour of both adults (Wiedenmayer 1997). Nevertheless during the rearing period, the females tended to dig more often (67 to 88 minutes per day; unpubl. obs.). Similar results for this species were obtained by Kaplan and Hyland (1972) and they considered this phenomenon an indication of female hyperactivity connected with litter and lactation.

In conclusion, in gerbils there is no paternal support in the building of the litter-nest and the retrieving of the young. Both adults cooperate via their synchronised presence with the young (temporal coordination or time sharing in the nest). We suggest that via this mutual behavioural synchronisation the physiological strains of the female caused by lactational hyperthermia are reduced.

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Zusammenfassung

Elterliche Jungenpflege und zeitliche Kooperation bei der Mongolischen Wüstenrennmaus

Das elterliche Pflegeverhalten der sozial lebenden Mongolischen Wüstenrennmaus (*Meriones unguiculatus*) wurde von der Geburt bis zur Entwöhnung der Jungen unter Laborbedingungen quantitativ erfaßt. Nestbau, Nestaufenthalt und das Eintragen der Jungtiere wurden analysiert. Die Registrierung dieser Verhaltensweisen der Elterntiere erfolgte per Videobeobachtung an den Tagen 2, 5, 8, 13 und 20 nach der Geburt der Jungen (Tag der Geburt = Tag 0) für jeweils 24 Stunden. Als Kontrolle wurden alle Paare darüber hinaus einmalig für 24 Stunden ohne Nachwuchs beobachtet. Neugeborene Mongolische Wüstenrennmäuse sind typische Nesthocker. Ziel dieser Studie war es, den väterlichen und den mütterlichen Aufwand bei der Jungenaufzucht zu ermitteln. Das Weibchen leistete insgesamt den größten Anteil an der Jungenpflege, da es keine männliche Unterstützung beim Bau des Wurfnestes oder beim Eintragen der Jungtiere gab. Dagegen kooperierten beide Elterntiere aufgrund ihrer synchronisierten Anwesenheit bei den Nestlingen miteinander (temporale Koordination). Wir vermuten, daß durch diese wechselseitige Verhaltenssynchronisation die physiologischen Belastungen des Muttertieres, beispielsweise verursacht durch die Laktationshyperthermie, reduziert werden können.

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