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## Abstract

Parental care can be defined as any effort directed towards the offspring and consequently leading to an increase in juvenile fitness. The extent of parental care is highly variable and dependent of many factors. For a hibernator with a limited reproductive season, the Common hamster (*Cricetus cricetus*) has a very high reproductive output. Females can produce up to three litters per season, with litter sizes varying from one to nine pups. A population of free-ranging Common hamsters was examined in an urban area of Vienna (Austria) in the season of March until October 2012. Capture/recapture methods were used to gain information about maternal care as well as morphometric parameters in the juveniles. Furthermore we collected faecal samples to analyse glucocorticoid metabolite concentration as indicators of stress load in juveniles. Behavioural observations were carried out using focal sampling techniques. The reproductive output during the season was very low compared to previous results in nearby areas. Only two females managed to raise second litters and no third litters were produced. Different phases of maternal care were defined. The lactation phase, the phase of common burrow use of juveniles with their mother and the pre emergence phase, lasting from birth until natal emergence. Lactation duration and common burrow use were positively related, however, in about half of the litters common burrow use continued after weaning for about 10 days. This indicated that mothers stayed with their offspring although they had already regressed teats. We assume that the females provided food, cached in their burrows, which the pups could feed on. This would reduce predation risk and perhaps thermoregulatory costs by minimizing the activity outside the burrow. Extended periods of common burrow use seemed to have positive effects on the pups as indicated in larger tibia length and higher body mass. Furthermore FCM levels were lower, the longer the mother stayed with the pups, indicating reduced stress load. The larger the litter size, the longer was the period the females stayed with their offspring after natal emergence indicating higher maternal investment in litters containing more offspring. In 7 out of 15 litters maternal care was terminated at natal emergence, because the female left the burrow. Although the age of the juveniles at natal emergence varied, no significant body mass differences between the litters could be detected. This indicates that juveniles emerge at a certain body condition which is reached in different time spans.

## Introduction

Parental care can be defined as any effort directed towards the offspring and consequently leading to an increase in juvenile fitness (Royle et al., 2012). The increased survival of the offspring through parental care also increases parental fitness (Clutton-Brock, 1988). Therefore both the offspring and the parents benefit from parental care. On the other hand parental care is costly for the parents (Speakman, 2008) potentially resulting in decreased survival and future reproductive success (Roff, 1992). Due to this trade-off, parents have to find an optimum between the extent of parental care and their own future needs (Andersen et al., 2000). The extent of parental care is highly variable, and not only species specific, but also varying between individuals of the same species (Gross, 2005; Westneat and Sargent, 1996). This variation may be influenced by many different factors. Gross (2005) stated that mainly four parameters influence the extent of parental care; brood size, the preceding investment, future reproduction and genetic relatedness. Furthermore the body condition of the mother and the pups (Houston, 1999), offspring sex, parity and population density (Clutton-Brock, 1991) can affect the duration of maternal care. The Common hamster is a ground-dwelling rodent, mainly active in the morning- and evening hours (Eibl-Eibesfeldt, 1953). They are solitary, each animal inhabiting its own burrows, except for the period of maternal care (Weinhold and Kayser, 2006). Common hamsters have a breeding period of about 6 months (Franceschini-Zink and Millesi, 2008a). They have a promiscuous mating system and mating starts immediately after female emergence from hibernation (Franceschini-Zink and Millesi, 2008a). The timing of vernal emergence after the hibernation is regionally dependent, and in our study area commonly occurs between March and April (Weinhold, 1998b). During the hibernation period the Common hamster relies both on body fat and previously cached food stores (Weinhold and Kayser, 2006). Gestation durations of 17 to 37 days have been reported and after another 25 days in the burrow juveniles are weaned and disperse (Weinhold and Kayser, 2006; Vohralik, 1975). Sexual maturity can be reached with 2.5 months earliest (Niethammer, 1982). With up to three litters per season reproductive output in this species is relatively high compared to other hibernators (Seluga et al., 1996; Franceschini and Millesi, 2005). The litter sizes usually range from 1 to 9 pups (Franceschini, 2007; Franceschini-Zink and Millesi 2008a). It is known that in Common hamsters, late born juveniles have reduced chances to survive, due to less



time until hibernation (Seluga et al., 1996). Thus high investment in first litters would be more beneficial for the mother, than in second or third litters (Franceschini-Zink and Millesi, 2008a). In addition, parental investment could be lower for late born litters due to decreasing body condition of females in the course of the season (Franceschini-Zink and Millesi, 2008a). The extent of maternal care can vary during gestation, lactation and also after weaning (Rogowitz, 1996). For female mammals the lactation phase requires the highest energy expenditure during reproduction (Oftedal, 1985). The lactation phase is crucial for the offspring and can influence growth rates and other developmental parameters in the juveniles (Künkele and Trillmich, 1997; Weaver et al., 1988). Therefore shorter lactation durations may result in smaller body sizes of the juveniles, poorer body condition and correspondingly even lower survival rates. About three weeks after birth juvenile hamsters emerge from the breeding burrow for the first time. Commonly weaning occurs at or shortly after their natal emergence (Siutz and Millesi, 2012). After weaning a challenging time for the juvenile hamsters starts. Siutz and Millesi (2012) reported of increased faecal cortisol metabolite concentrations in juvenile hamsters during the post weaning phase. Glucocorticoids like cortisol are indicators of stress and are needed for the mobilization of energy (Romero 2002) which helps to deal with different challenges (Sapolsky, 1992). However permanent elevated stress levels have a negative impact on the immune system (Keay et al., 2006) and thus lead to diseases and reduced reproductive output. After weaning, juveniles are forced to increase their above ground activity mainly due to foraging activity. This leads to a higher exposure to adverse environmental factors, like cold temperatures or predators (Siutz and Millesi, 2012) and thus can be stressful for the juveniles causing lower survival rates.

The main goal of our study was to examine the impact of maternal care on juvenile development in Common hamsters. We mainly concentrated on the relationship of varying durations in maternal care and juvenile development. There are different phases of maternal care which can be mainly divided in pre weaning and post weaning phases. We aimed at investigating if those different phases of maternal care are related to juvenile development. As the body condition of the juveniles can influence the duration of maternal care (Houston, 1999) and vice versa we assumed that juveniles in a poorer condition may need higher maternal investment and thus longer periods of maternal care. Former studies reported higher body mass and faster growth

rates of pups in small litters (Hufnagl, 2009; Tauscher, 2006). Petzsch (1943) indicated that faster growth rates in small litters may be caused by higher maternal care. Based on the assumption that juveniles originating from large litters have a lower body mass at birth and that pups in a poorer condition receive more maternal care, we expected longer maternal care durations in females with large litters. Furthermore we assumed seasonal effects of maternal investment. Previous studies indicated higher maternal care in first litters, than in second or third ones (Franceschini-Zink and Millesi, 2008a; Siutz and Millesi, 2012). Generally we assumed longer maternal care durations to have positive effects on juvenile development.

## **Material and methods**

### **Study site**

A population of free- ranging Common hamsters living in an urban area in the southern district Favoriten, in Vienna was examined. The study area (22 ha) included parts of the Volkspark and the surrounding apartment complexes (48° 9'22.31"N, 16°23'1.99"E). Vegetation mainly contained regularly mowed grass with bushes and trees crossed by paths at the park site. Vegetation between and around the apartment complexes was similar. Potential predators, especially for the juveniles, were feral cats and dogs, Common kestrels (*Falco tinnunculus*) and foxes (*Vulpes vulpes*).

### **Field techniques**

Data collection lasted from the beginning of May until the end of October 2012. Hamsters were trapped 5 days per week in the morning hours from 5 a.m. until 10:30 a.m. using Tomahawk live traps baited with peanut butter (Siutz and Millesi, 2012). We tried to capture individual hamsters in weekly intervals using capture-mark/recapture techniques. The traps were controlled every 20 minutes. Captured hamsters were immediately released into special shaped cotton sacks laterally equipped with Velcro fasteners (Franceschini and Millesi, 2001). Hence no anaesthesia was needed during the examination. The procedure lasted about 10 minutes and the animals were then released at their burrows. Recorded parameters were body mass ( $\pm 1$ g), length of head, tibia and foot ( $\pm 0.1$ mm), state of moult and reproductive status. Age (yearling/adult) was defined based on the animals' body mass at vernal emergence (Lebl and Millesi, 2008). The reproductive status was determined in males based on testes size, being sexually reproductive from a testes length of 18 mm (Grulich, 1986). In females the determination of reproductive status was based on vaginal and teat status. Teats were categorised from small to swollen with milk remains and vaginal size was categorised from completely closed, small opening, wide opening and wide opening with bloody mucus (Franceschini-Zink and Millesi, 2008a).

Faecal samples were collected at capture and stored at -20°C until analysis (Siutz and Millesi, 2012). We further recorded location and time of trapping, temperature and weather conditions.

A transponder chip was implanted subcutaneously in the abdominal region (PIT tag, Data Mars SA) at the animal's first capture. For distant recognition the animals were marked with individual symbols using commercial hair dye, red colour for females and black colour for males.

### **Behavioural observations**

Observations were mainly done in the evening hours from 5 p.m. until sunset. Focal sampling methods were used, each lasting 15 minutes divided into 20 sec intervals. The distance of the focal animal from the burrow was recorded in five categories (near burrow, two, five and ten meters distance from burrow, >20 meters distance from burrow). Recorded behaviours of the juveniles were foraging (food caching, feeding above ground) and vigilance (bipedal posture). Interactions were included in the protocol but were excluded from analysis due to the rare occurrence.

### **Juveniles**

We tried to capture individual juveniles at natal emergence (+2 days). The expected date of natal emergence was about 21 days after parturition (Nechay et al., 1977). We were able to predict the date of natal emergence for each litter by monitoring the mother's body mass, vulval development and teat status as well as behavioural observations quite precisely (Franceschini-Zink and Millesi, 2008a). All juveniles emerging of the same breeding burrow were assigned to the same mother and litter.

### **Phase definitions**

The following dates and phases were defined.

#### Dates

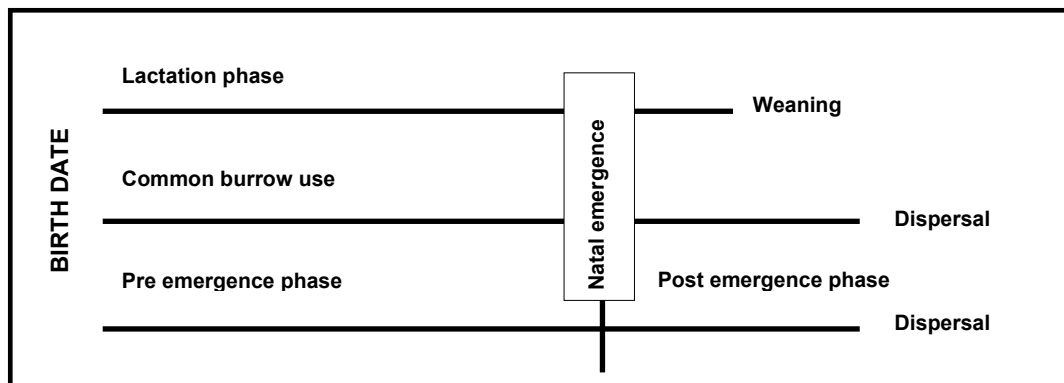
Natal emergence was defined as the date when the juveniles left the breeding burrow for the first time (+2 days).

Independence date was the date when either the juvenile or the mother dispersed from the breeding burrow.

#### Phases

The lactation phase lasted from birth until the total regression of the mother's teats (Franceschini et al., 2007).

Common burrow use included the time from birth until the dispersal of either the mother or the juvenile. This phase can exceed the lactation phase, if the mother stays with the juveniles beyond weaning (Fig.1). Hence, the lactation phase and common burrow use are two distinct phases with different durations.



**Fig.1:** Overview of the defined phases.

Common burrow use was composed of two phases, the pre emergence phase and the post emergence phase (Fig.1). The pre emergence phase lasted from the day of birth until natal emergence. The post emergence phase lasted from natal emergence until the dispersal either of mother or juvenile.

Body measurements (body mass, head, tibia, foot) were measured in weekly intervals, starting at natal emergence, until 4 weeks thereafter. For further analysis these four weeks were divided into two 14-day intervals.

### **Faecal cortisol metabolites (FCM)**

For FCM extraction faeces were dried and bruised before 0.2 g of each sample was dissolved in 4.0 ml of 80% methanol (Franceschini et al., 2007; Touma and Palme, 2005). FCM concentrations were analysed using an 11-oxoetiocholanolone enzyme immunoassay (EIA) (Möstl et al., 2002). FCM-concentrations were given in ng/g faeces. Intraassay coefficient of deviation was <15% and the interassay coefficient of deviation was <25%.

### **Statistics**

All statistics were done with PASW Statistics 18. Shapiro-Wilk tests were used for tests of normality. For normally distributed data we used Pearson correlations other-

wise Spearman bivariate correlations were applied. For early and late born juvenile comparisons T-Tests for normally distributed data were used and Mann-Whitney-U-Tests for not normally distributed data.

Because of the low sample size we were unable to compare juveniles of female's first with that of second litters in a season. However we compared litters born early in the season (end of April until the end of June) with late (end of July until beginning of August) born litters. There were no significant differences between early and late born juveniles using correlations in the morphometric parameters. Furthermore, using T- Tests/ U-Tests, we found no significant differences in behavioural parameters and FCM levels between early and late born juveniles. Therefore the data were pooled in all further analyses.

Means per litter were used in the analyses. Varying sample sizes are due to the available data set.

We tried to compare the relationship between FCM levels and behavioural data in the post emergence phase and an interval of 4 weeks post emergence. Due to low sample size in the post emergence phase, only the 4 weeks interval post emergence was statistically analysed.

If not stated otherwise means and standard deviations are given in parentheses (mean  $\pm$  SD).

## Results

In our study 15 litters, containing 13 first (first litter of a female in the season) and 2 second (second litter of a female in the season) litters, were studied. From these 72 individuals, 40 were males and 32 females. Thus the sex ratio was slightly male biased ( $1.25 \text{ m/f}$ ).

Litter size ranged from 2 to 9 pups ( $4.9 \pm 2.2$ ). Because of the low number of second litters we were unable to compare female's first with second litters. Litter sizes of the second litters were in the range of first litters with 5 and 9 pups.

Birth dates ranged from April 20<sup>th</sup> to June 29<sup>th</sup> 2012, and natal emergence dates ranged from May 2<sup>nd</sup> to August 1<sup>st</sup> 2012. The juveniles stayed 23 days ( $\pm 7.1$ ) in the breeding burrow until natal emergence. Most of the litters were born in May and least in April (Tab.1).

**Tab.1:** Number of litters born per month in the season of 2012.

Month of birth	April	May	June
Number of litters	2	9	4

## Phases

The lactation phase and the phase of common burrow use were quite similar in duration. As expected, lactation duration ( $22.7 \pm 6.4$ ) was significantly related to common burrow use ( $r=0.561^*$ ,  $p=0.030$ ,  $N=15$ ). However, in some cases ( $N=4$ ) common burrow use exceeded the lactation phase for 9 to 15 days ( $10.57 \pm 3.3$ ). Females had already regressed teats but continued to stay with the offspring at the breeding burrow.

The phase of common burrow use was composed of the pre- and the post emergence phase. The pre emergence phase, lasting from birth until natal emergence, ranged from 10 to 33 ( $23.2 \pm 7.1$ ) days. The post emergence phase, lasting from natal emergence until dispersal either of mother or juvenile, had a lower range from 0 to 11 days ( $3.3 \pm 3.8$ ). Although these two phases were parts of the common burrow use, they were not related to each other ( $r=-0.087$ ,  $p=0.769$ ,  $N=14$ ). In 7 litters out of 15, common burrow use was terminated at natal emergence because the mother had

left the burrow. In these cases the post emergence phase was noted with zero. These 7 litters had litter sizes of 2, 3, 5 and 8.

### Lactation phase

The lactation phase, lasting from birth until weaning, had a relatively broad range of 11 to 51 days ( $22.7 \pm 6.4$ ,  $N=15$ ). The lactation phase was positively correlated with the pre emergence phase ( $r=0.688^{**}$ ,  $p=0.007$ ,  $N=14$ ). However we found no significant relationship between the post emergence phase and lactation duration ( $r=0.232$ ,  $p=0.469$ ,  $N=12$ ).

We further examined potential relationships between lactation duration and the morphometric parameters. But neither body mass, nor head, tibia or foot length, showed significant correlations with the lactation phase. In addition, lactation duration did not vary with litter size ( $r=0.296$ ,  $p=0.283$ ,  $N=15$ ).

Moreover, with regard to FCM excretion as an indicator of stress levels, no relationship between lactation duration and FCM concentrations was found ( $r=0.464$ ,  $p=0.294$ ,  $N=7$ ).

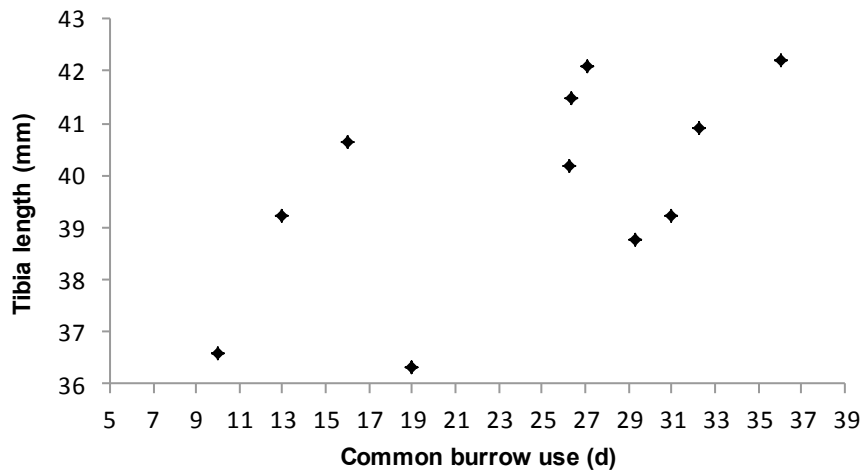
### Common burrow use

The common burrow use phase, including the time from birth until dispersal of mother or juvenile (pre- and post emergence phase), ranged from 10 to 36 days ( $25.8 \pm 7.8$ ,  $N=15$ ). The longer the pre emergence phase lasted, the longer was also the duration of common burrow use ( $r=0.852^{**}$ ,  $p=0.000$ ,  $N=14$ ). Thus the older the juveniles were at emergence the longer was the period they stayed with their mother at the breeding burrow.

Similar to lactation, litter size did not correlate with the duration of the common burrow use ( $r=0.124$ ,  $p=0.660$ ,  $N=15$ ).

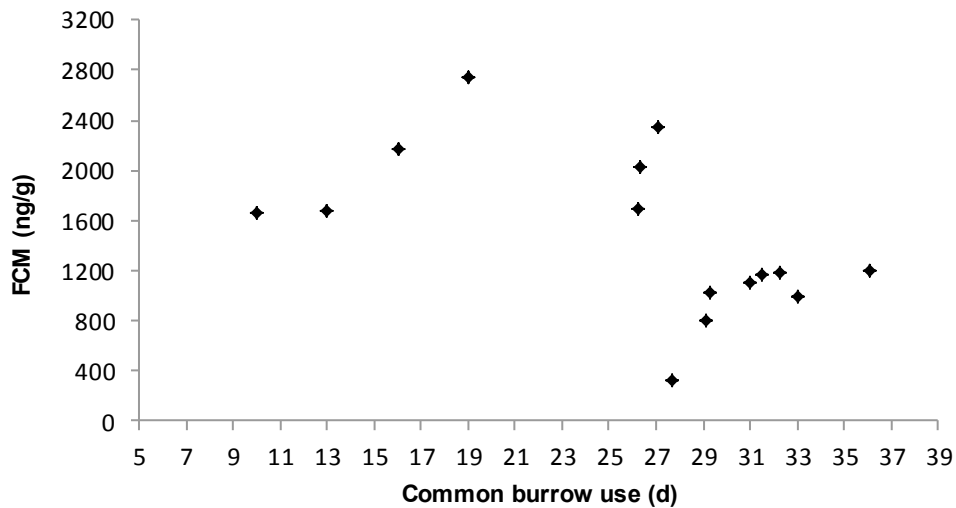
Considering the morphometric parameters we found no correlations between body mass, head and foot length with common burrow use. However, the longer the duration of common burrow use lasted, the higher was the tibia length in the second two-weeks interval post emergence (week 3+ 4) ( $r=0.603^{*}$ ,  $p=0.049$ ,  $N=11$ ) (Fig.2).





**Fig.2:** Relationship between common burrow use and the tibia length in the second two- week interval after natal emergence.

In contrast to the lactation phase, FCM concentrations were significantly related to common burrow use. The shorter the duration of common burrow use was, the higher were the FCM levels ( $r=-0.575^*$ ,  $p=0.025$ ,  $N=15$ ) (Fig.3).

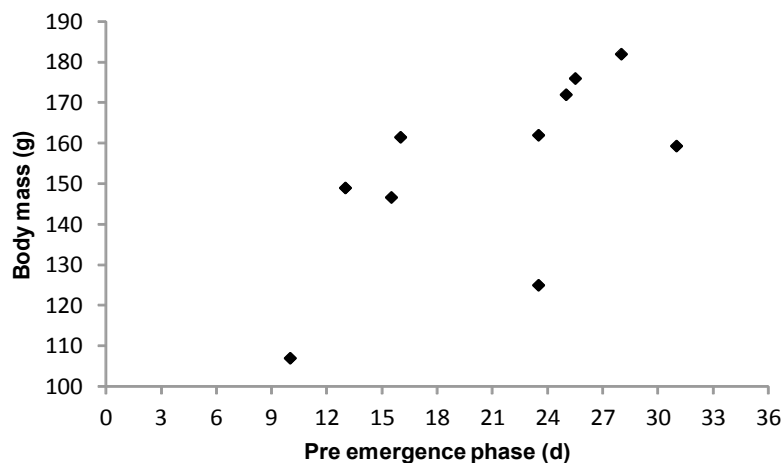


**Fig.3:** Relationship between FCM concentrations and the duration of common burrow use.

As the phase of common burrow use included the pre- and the post emergence phase we also looked at those two phases separately. Both varied highly in their durations, thus different relationships to the morphometric measures and litter size could be assumed.

### Pre emergence phase

Similar to the lactation phase and common burrow use, litter size did not correlate with the pre emergence phase ( $r=-0.189$ ,  $p=0.517$ ,  $N=14$ ). Juvenile's body mass was however related to this period in that, the longer the duration of the pre emergence phase lasted, the higher was the juveniles' body mass 3 weeks post emergence. ( $r=0.635^*$ ,  $p=0.048$ ,  $N=10$ ) (Fig.4). No relationship with head, tibia and foot length was found.



**Fig.4:** Relationship between juvenile body mass 3 weeks after natal emergence and the duration of the pre emergence phase.

### Post emergence phase

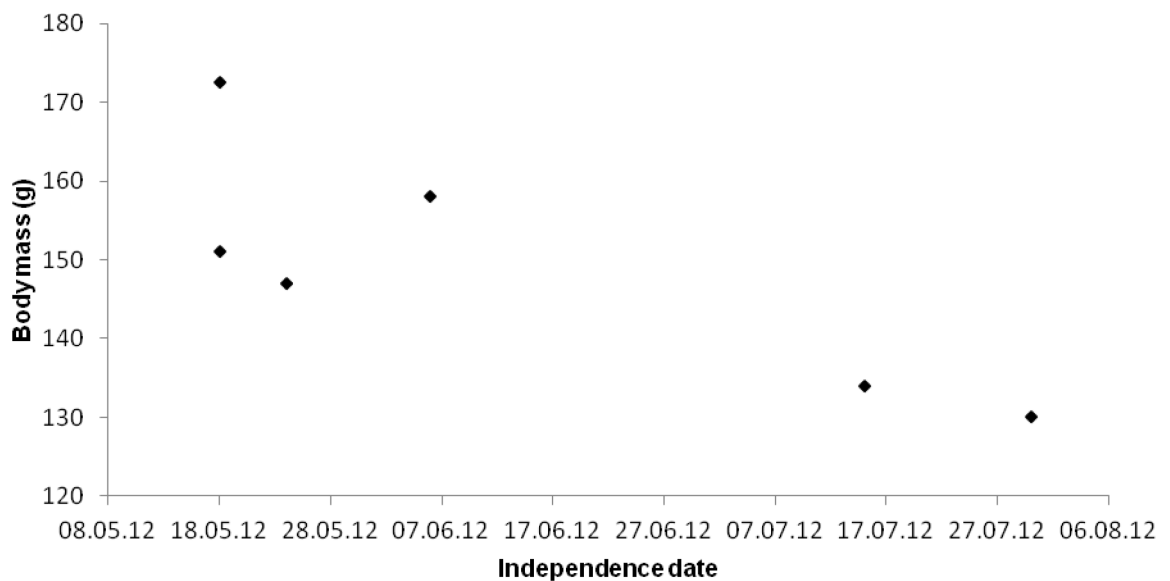
In contrast to lactation duration, common burrow use and the pre emergence phase, we found a significant relationship between litter size and the post emergence phase. The larger the litter size was, the longer was the duration of the post emergence phase ( $r=0.574^*$ ,  $p=0.025$ ,  $N=15$ ). Mothers with larger litters stayed longer with their offspring after natal emergence.

We found no correlations between the post emergence phase and either of the morphometric parameters.

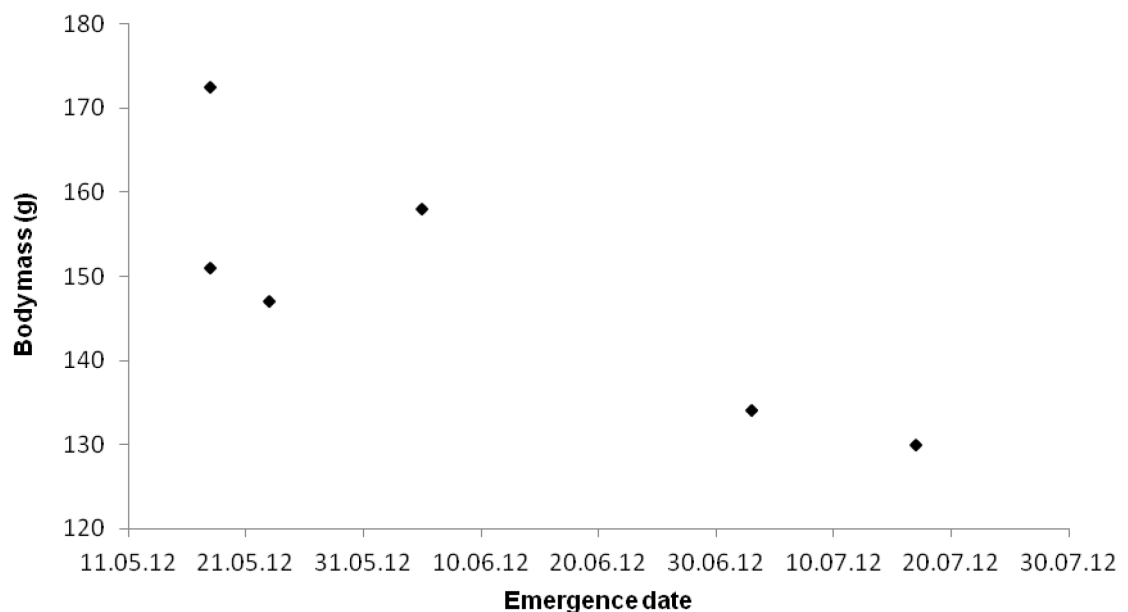
To look for potential sex differences, all defined phases, dates and morphometric parameters were tested separately for both sexes. Body mass in females was related to emergence and independence dates. The earlier in season the juvenile females

emerged ( $r=-0.819^*$ ,  $p=0.046$ ,  $N=6$ ), the higher was their body mass 4 weeks later (Fig.5). Female age at emergence ranged from 13 to 31 days ( $21.9 \pm 7.4$ ,  $N=6$ ).

A similar relationship was found for independence date, the earlier the date, the higher was the female's body mass 4 weeks post emergence ( $r=-0.827^*$ ,  $p=0.042$ ,  $N=6$ ) (Fig.6). The age of the female juvenile hamsters at independence date ranged from 13 to 33 days ( $24.3 \pm 8.1$ ,  $N=6$ ).



**Fig.5:** Relationship of emergence dates and female body mass 4 weeks after natal emergence.



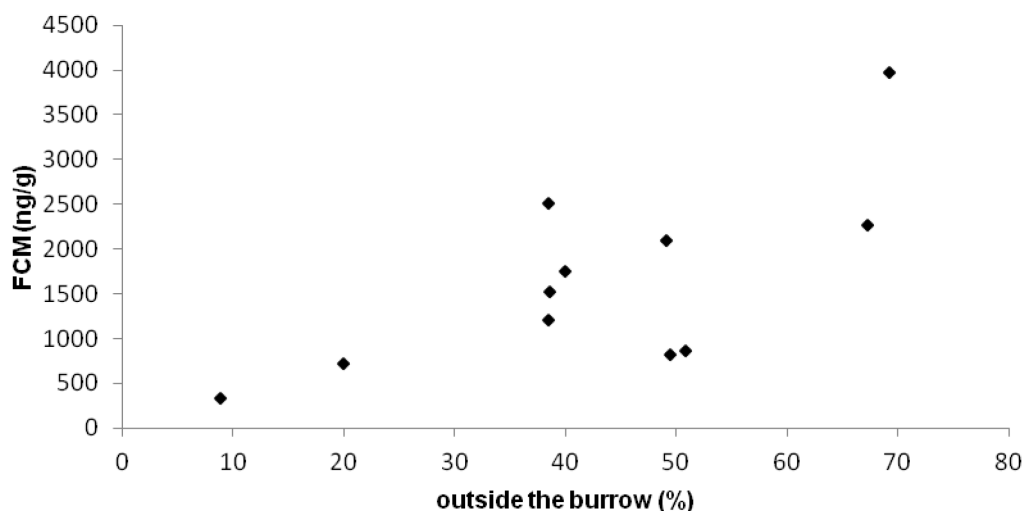
**Fig.6:** Relationship between independence dates and female body mass 4 weeks after natal emergence.

## Behavioural analysis

To investigate relationships between the attendance of the mother and juvenile behaviour we compared the behaviour during the post emergence phase, where the mother was still present with an interval of 4 weeks thereafter when the mother already was absent. As mentioned above, the sample size in the post emergence phase was too small for statistical analysis. FCM levels had no relationship with the age of the juvenile hamsters.

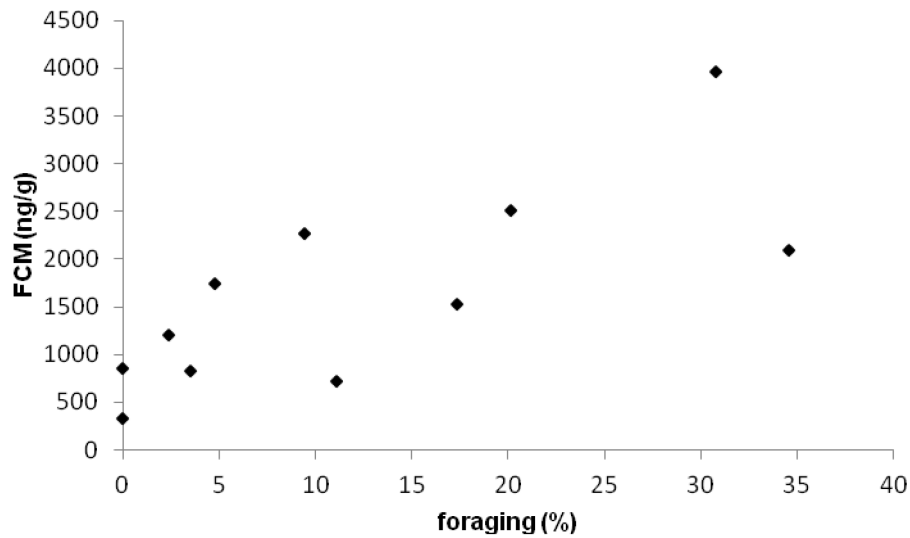
To look for potential age effects the behavioural parameters were correlated with the juveniles' age. No relationships with foraging behaviour ( $r=0.290$ ,  $p=0.387$ ,  $N=11$ ) or vigilance behaviour ( $r=-0.020$ ,  $p=0.953$ ,  $N=11$ ) could be found. Age also did not correlate with the time spent outside the burrow ( $r=-0.115$ ,  $p=0.736$ ,  $N=11$ ).

However, FCM concentrations were higher the more time the juveniles spent outside the burrow ( $r=0.711^*$ ,  $p=0.014$ ,  $N=11$ ) (Fig.7).



**Fig.7:** Relationship of FCM concentrations and time spent outside the burrow.

In addition foraging behaviour correlated with FCM levels. Individuals that showed foraging behaviour more frequently had higher FCM concentrations ( $r=0.752^{**}$ ,  $p=0.008$ ,  $N=11$ ) (Fig.8).



**Fig.8:** Relationship of FCM concentrations and foraging behaviour.

No significant correlations could be found between FCM concentrations and vigilance behaviour ( $r=-0.476$ ,  $p=0.139$ ,  $N=11$ ).

Furthermore we wanted to know if behavioural parameters varied with lactation duration. There were neither relationships between lactation duration and the behavioural parameters (vigilance:  $r=0.470$ ,  $p=0.171$ ,  $N=10$ ; foraging:  $r=-0.089$ ,  $p=0.806$ ,  $N=10$ ) nor with the time spent outside the burrow ( $r=0.321$ ,  $p=0.365$ ,  $N=10$ ).

FCM concentrations ranged from 327.1 ng/g to 2744.1 ng/g faeces ( $1474.2 \pm 648.6$ ,  $N=15$ ) throughout the season. No significant relationships between FCM levels with litter size ( $r=0.038$ ,  $p=0.893$ ,  $N=15$ ) or sex ratio ( $r=-0.424$ ,  $p=0.131$ ,  $N=14$ ) were found.

## Discussion

The reproductive period of a Common hamster population in Vienna was recorded between April and August 2012. Birth dates of the litters ranged from May to August 2012. Previous studies on Common hamster populations in Vienna, in similar surroundings, reported of vernal emergence dates of adult females between March and May (Franceschini and Millesi, 2005; Franceschini-Zink and Millesi, 2008a). Studies of other Common hamster populations referred of vernal emergence in March in France (Kayser, 1975) and in Slovakia and Germany in April (Grulich, 1986; Wendt 1991). Kayser and Stubbe (2003) determined litter birth dates in Germany from May until August. Considering this, the juvenile emergence dates of our study season are well within the range of other populations.

Results of previous studies in Vienna, indicated that females which emerged early in the season reproduced earlier and had more offspring than those that stayed longer in their hibernacula (Franceschini-Zink and Millesi, 2008a). In our season the earliest emerging females had a higher total reproductive output with 11 pups/individual, compared to the later emerging females with 4.5 pups/individual. The total reproductive output compared to previous studies in Vienna was rather low. Franceschini and Millesi (2008a) had a total reproductive output of 9 pups/individual. Whereas Hufnagel et al. (2011) reported of 6.9 pups/individual in a season of delayed reproduction due to harsh winter conditions. The total reproductive output of our study season with 5.5 pups/individual was even lower although there were no conspicuous environmental conditions. In several seasons at study sites in Vienna two to three litters per female could be detected (Franceschini and Millesi, 2001; Pluch, 2013; Roiser-Bezan, 2010). Most females produced one to two litters but third litters were produced only occasionally (Pluch, 2013, Roiser-Bezan, 2010).

In our study season only two females were observed to produce a second litter and none of the individuals raised a third litter. This two second litters were produced by two females which emerged earliest in the season (conception of the first litter was determined in early April). Emergence dates of the second- litter offspring even exceeded some of other females' first litters. This indicates that some individual females reproduced very late in the season. None of these females showed signs of gestation or lactation earlier in the season, thus late reproduction was unlikely to be

due to the previous loss of a litter. Reproduction late in the season could further be due to a poor condition of the mother. There was no conspicuous difference between the body mass of early and late emerging females at emergence, thus late reproduction of some females due to poor mother condition can be rejected. Yearling females tend to reproduce later than older individuals due to energy investment in growth before mating. As this was the first investigation at this specific field, the exact age of the females was unknown. Low reproductive output at a similar study site compared to previous years was assumed to be due to harsh weather conditions (Hufnagl et al. 2011). This factor can be excluded in our study season. Franceschini (2002) suggested in her study area a low litter number due to high population density, leading to stress and limited resources. Weinhold (1998b) reported a population density of 3.6 individuals/ha on agricultural regions in Germany. In Vienna population densities could reach 36 individuals/ha in some years (Franceschini and Millesi, 2001). Population density in our study area varied within the location, but overall was 5.2 individuals/ha. Therefore a low reproductive output due to high population density is unlikely. There was enough space to disperse and sufficient food resources at the study site. Litter sizes of 2 to 9 pups were similar to those of other studies (Franceschini- Zink and Millesi 2008a, Tauscher et al., 2003). First litters often contained more juveniles than second or third ones (Tauscher et al., 2003; Franceschini and Millesi, 2008a). The two second litters in our study site however, had litter sizes of five and nine, thus were in the range of first litters.

The phases of maternal care as defined in our study showed interesting relationships with one another. Lactation duration, common burrow use as well as the pre emergence phase were positively related to each other. Juveniles that emerged at an older age were lactated longer and shared the burrow with their mother for a longer period than juveniles that started surface activity at an earlier stage. In our study seven litters received no further maternal care after natal emergence. The mother terminated lactation and left the breeding burrow. Dispersal of the mother may be due to death or to future reproduction and investment in another litter.

If natal emergence is triggered by the mother for instance by reducing lactation and/or leaving the burrow for longer periods, cannot be answered by our data. However it is known that in case of the mother's death juveniles leave the burrow in a

relatively early state of development due to the need to find food. In our study, the pre emergence phase did not vary with litter size. Thus the differences in the timing of natal emergence cannot be due to the number of pups in a litter. Again the condition of the mother was unlikely the cause for varying juvenile age at emergence. There were no obvious differences in the mothers' body mass at lactation onset. Moreover, in contrast to age, juvenile body mass at natal emergence did not vary significantly among litters. This indicates that pups at a young age at emergence already had reached a sufficient body condition and therefore started to explore outside the burrow earlier.

In eight litters the mothers continued maternal care after natal emergence. This post emergence phase was neither correlated with the pre emergence phase, nor with lactation duration or common burrow use. Lactation duration ranged between 11 and 51 days and was often continued after the juveniles had started surface activity. This high variation within one species is not unusual (Langer, 2003). The duration of lactation depends on several factors, such as body size, with small mammals generally having shorter lactation periods (Peters, 1986). Lee et al. (1991) and Rehling and Trillmich (2007) suggested that the onset of weaning is triggered by a certain body mass threshold of the juveniles, resulting in longer lactation durations of pups in poor conditions. Therefore beneficial environmental conditions, resulting also in a good condition of the mothers, may lead to earlier weaning. In Columbian ground squirrels (*Urocitellus columbianus*) a high body mass at weaning and rapid growth rates of the juveniles during the lactation phase were due to a good body constitution of the mother (Skibieli et al., 2009). Furthermore in guinea pigs a good body condition of the mother, resulting also in higher milk quality, led to earlier weaning dates (Rehling and Trillmich, 2007).

In our study there were no significant correlations of the lactation phase and body mass of the juveniles, as well as head, tibia or foot length. Several studies refer to litter dependent differences in the extent of lactation within species (Kounig et al., 1988; Kenagy et al., 1990). However, we could not find a significant relationship between lactation duration and litter size.

Weaning does not obligatory lead to the cease of maternal care. The phase of common burrow use exceeded the lactation duration in four cases for about ten days.



That means that the females weaned their offspring, as reflected in regressed teats but continue to stay at the breeding burrow for up to 15 days. Maternal care after weaning mainly occurs in vertebrates with a longer lifespan (Clutton-Brock, 1991). Maternal care after weaning is rather rare in small rodents, but was reported for American red squirrels (*Tamiasciurus hudsonicus*) by provisioning solid food for the offspring (Boutin et al. 2000). Milk is a very energy-rich food source and very important for the juveniles. Therefore pups should try to get lactated as long as possible (Rehling and Trillmich, 2007). Usually the pups get lactated as long as the mother is present. In many ground dwelling sciurids, weaning is initiated by the mother by leaving the breeding burrow (Millesi et al., 1999). However in our study some mothers managed to wean the pups while still living in the same burrow. The suckling of the pups is the important stimulus initiating milk flow and production (Bronson, 1989). For weaning of the pups this stimulus has to be prevented somehow. The easiest way would be to keep the pups away from suckling. The independence of the pups from the mother mainly is enforced by the mother in her own interest (Rogowitz, 1996). In Common hamsters the mother could provide food hoards for the offspring in addition to or- in a later phase- instead of milk. This could keep the juveniles from dispersal, and decrease predation risk. An additional effect of feeding on food stores in the burrow would be lower energy expenditure by juveniles, reduced foraging time and thermoregulatory costs.

The relationship between the post emergence phase and the litter size leads to the conclusion that pups of large litters stayed longer at the breeding burrow after natal emergence than those of smaller litters. Several studies reported of longer maternal care durations or more intensive maternal care in larger litters (Andersen et al. 2000, Guerra and Nunes 2001, Huber et al. 1999). In Columbian ground squirrels (*Urocitellus columbianus*) growth rates were lower in big litters (Skibieli et al., 2009). In addition, in the golden hamster (*Mesocricetus auratus*) offspring body mass had a negative relationship with litter size (Guerra and Nunes, 2001). This could lead to the conclusion that large litters require more maternal care than small litters. A large number of pups in a litter could lead to higher competition in suckling (Fey and Trillmich, 2008). Mothers may compensate this disadvantage via longer durations of maternal care. In our study, mothers of large litters, did not prolong lactation duration but interestingly seemed to stay longer with their offspring when they had already reached a

developmental state enabling them to feed on solid food. Guerra and Nunes (2001) found out, that pups are able to influence the maternal behaviour through different stimuli. They noted that a litter size of just one pup may be an insufficient stimulus for the mother to give sufficient maternal care.

Due to the low reproductive output in the season, females may invest more in their litters. Maternal care is very important for juvenile survival (Franceschini-Zink and Millesi, 2008a), effects the postnatal development (Rogowitz and McClure, 1995 ) and also the growth rates of the pups (Künkele and Trillmich, 1997). Tauscher et al. (2003) indicated that high investment in early litters may result in costs for the next litter. Some of the females in our study site raised their first litters relatively late in the season, therefore chances of further reproduction in the same season may be low. Thus a high investment in the current litter seems beneficial for the mother.

Positive effects of maternal investment could be seen in some morphometric parameters and also in FCM levels. The phase of common burrow use was positively related to growth rates of the juvenile hamsters. The longer the pups shared the burrow with their mother, the longer was the tibia in the second two-weeks interval after natal emergence. Altmann and Alberts (2005) reported of larger body sizes in juveniles with longer maternal care durations. Furthermore a positive relationship between the pre emergence phase and the body mass of the juveniles could be found. In our study juveniles showing a long pre emergence phase had a higher body mass three weeks after natal emergence. In the pre emergence phase the energy expenditure may be lower compared to the post emergence phase, where the pups already leave the burrow. A higher body mass may also result in higher survival rates (Festa-Bianchet and King, 1991).

Another indication for positive effect of extended common burrow use with the mother was indicated in FCM-concentrations. FCM levels of juvenile hamsters increased with decreasing durations of common burrow use. This result indicates higher stress load in individuals that were left by their mothers shortly after natal emergence compared to those which stayed with their mother for a longer period. Siutz and Millesi (2012) showed that FCM levels varied with birth dates of the juveniles. In juveniles born late in the season, FCM levels rose from weaning until post-weaning. Furthermore they assumed that the higher FCM levels of those late born

juveniles could be due to less maternal care. High stress levels can have negative effects on the immune system, developmental parameters and survival (Keay et al., 2006).

Siutz and Millesi (2012) indicated higher stress levels of juveniles born late in the season at a similar study site in Vienna. Late born juveniles are forced to an increased surface activity and foraging activity due to less time of preparing for hibernation. A high surface activity coincides with an increased exposure to predators and may lead to higher stress levels. This assumption is supported by FCM levels of juveniles being higher, the more time they spent outside the burrow and correspondingly the more time they spent foraging above ground.

The only sex difference we found related to a seasonal aspect. The earlier in season the emergence date and the independence date of juvenile females were, the higher was their body mass 4 weeks post emergence. Juveniles born early in the season have advantages in gaining body mass until hibernation, because they have more time to grow and preparation for the winter (Tauscher, 2006). A high body mass early in the season could enable female juveniles to reproduce in their first season. Juvenile hamsters reach sexual maturity with about 2.5 months earliest (Nechay et al., 1977). Nevertheless females usually reproduce for the first time as yearlings (Franceschini-Zink and Millesi, 2008a ). However some cases of successful juvenile reproduction were reported in Vienna at a nearby field site (Siutz and Millesi, 2012). In our study season we noticed one juvenile female with an opened vagina by the beginning of July, indicating sexual activity. However no successful reproduction of any juvenile female could be observed. Still, even if early-born females in a good body condition do not reproduce in their first season, they may benefit in the following year via earlier conception and higher reproductive output. This relationship was not found in male juvenile hamsters. Larger males usually have a higher reproductive success (Clinchy et al., 2004). In our study season just three juvenile males approximately reached the body mass of yearling males in poor conditions by the end of the season. All the other juvenile males stayed far below yearling and adult male body mass. Therefore it seems quite unlikely that juvenile males get access to a receptive female.

## **Zusammenfassung**

Als elterliche Pflege kann allgemein geltend jede Investition, die die Fitness des Nachwuchses steigert, gesehen werden. Dies führt unweigerlich zu Kosten auf Seiten der Eltern. Deswegen sollte ein optimaler Mittelweg zwischen dem Ausmaß der Brutpflege und den Nachteilen, die die Eltern dadurch erfahren, gefunden werden. Hohe Investitionen in den Nachwuchs können die Überlebenschance und auch den künftigen Fortpflanzungserfolg der Eltern vermindern. Dadurch kann der elterliche Aufwand in Abhängigkeit von unterschiedlichen Faktoren wie z.B. Alter und Kondition der Mutter sehr stark variieren und ist von einigen Faktoren abhängig. Der Feldhamster weist im Gegensatz zu anderen Winterschläfern eine relativ lange Fortpflanzungsperiode von bis zu 6 Monaten auf. In dieser Zeit produzieren die Weibchen bis zu 3 Würfe, mit Wurfgrößen von 1-9 Jungtieren wodurch eine hohe Fortpflanzungsrate erreicht werden kann. Ziel dieser Studie war es, mehr über die Variation der mütterlichen Pflege und deren Auswirkungen auf die Entwicklung der Jungtiere zu erfahren. Die Studie wurde an einer frei lebenden Hamsterpopulation im südlich gelegenen Bezirk Favoriten, in Wien, durchgeführt. Durch Fang/Wiederfang-Methoden konnten sowohl Daten über die Brutpflegeperioden der Weibchen als auch morphometrische Parameter bei den Jungtieren ermittelt werden. Zusätzlich wurden Kotproben zur Analyse von Glucocorticoidmetaboliten als Indikatoren für Stressbelastung gesammelt und Verhaltensbeobachtungen durchgeführt. Die Reproduktionsrate in unserer Saison fiel relativ niedrig aus. Die meisten Weibchen hatten nur einen Wurf, zwei Weibchen konnten zwei Würfe produzieren und es gab keine dritten Würfe. Als Brutpflegeperioden wurden die Laktationsphase und die Phase der gemeinsamen Baunutzung von Jungtier und Mutter definiert. Letztere setzte sich aus der Zeit von der Geburt bis zum ersten Auftauchen aus dem Wurfbau und der in einigen Fällen darauffolgenden Phase zusammen in der Mutter und Jungtiere weiterhin denselben Bau bewohnten. Laktationsdauer und die Periode gemeinsamer Baunutzung zeigten zwar einen signifikanten Zusammenhang waren aber nicht identisch da einige Weibchen nach Entwöhnung der Jungen und damit einhergehender Rückbildung der Zitzen für weitere ca. 10 Tage beim Wurfbau blieben. Diese länger andauernde mütterliche Pflege hatte einen positiven Zusammenhang mit der Wurfgröße. Würfe mit mehr Jungtieren waren länger mit der Mutter im Bau zusammen, wurden allerdings nicht länger laktiert als kleinere Würfe.

Ein längeres Zusammenleben mit der Mutter schien sich günstig auf die Jungen auszuwirken. Es zeigte sich ein positiver Zusammenhang mit der Tibiallänge, einem der Wachstumsparameter. Die Cortisolmetabolitenkonzentration war bei Jungtieren die lange mit der Mutter zusammen waren niedriger als bei denen die früher verlassen wurden, was auf weniger Stress bei lang andauernder mütterlicher Pflege hinweist. Bei 7 von 15 Würfen endete die mütterliche Pflege allerdings mit dem ersten Auftauchen der Jungtiere aus dem Wurfbau. Das Alter der Jungtiere variierte dabei teils stark. Einige Junge begannen mit der Oberflächenaktivität bereits mit 10 Tagen andere waren bereits 4 Wochen alt. Trotz dieser starken Altersvariation war kein eindeutiger Gewichtsunterschied beim ersten Auftauchen ersichtlich. Dies deutet darauf hin, dass einige Jungtiere einen entsprechenden Körperzustand früher erreichten als andere.

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