Reproductive performance in female common hamsters

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Abstract

We monitored individual reproductive timing and output in a common hamster population in Vienna over a 3-year period. Animals were live-trapped, weighed, individually marked, and reproductive status was determined at capture. Costs of reproduction were investigated by measuring body condition shortly before hibernation and overwinter survival. Our results indicated that early emerging females had more litters and weaned more offspring per season. Body mass throughout the active season did not differ significantly between females with high and low reproductive output. High reproductive output seemed to affect the duration of the active season. Successful females had a longer postreproduction period before hibernation than less successful ones, probably serving to balance the costs of reproductive effort by extended preparation for hibernation. Also, females that had emerged early in spring and had high reproductive success were more likely to survive the subsequent winter. Hence, we found female common hamsters to vary strongly in maternal investment capacity and to tailor reproductive strategies accordingly.

Keywords: Cricetus cricetus; Reproductive output; Seasonal timing; Overwinter survival

Introduction

The annual life cycle of many ground-dwelling animals alternates between above-ground activity and hibernation (Choromanski-Norris et al. 1986). During the short active period, individuals have to complete reproduction, molt and accumulate fat reserves and/or store food for hibernation. In contrast to other hibernators which produce only one litter per season (Hackländer et al. 1999; Millesi et al. 1999), common hamsters show a high reproductive potential resulting in up to three litters per season (Seluga 1996; Bekenov 1998; Franceschini and Millesi 2005). To maximise reproductive output in a limited active period, females showed a postpartum oestrus (Vohralik 1974; Grulich 1986; Franceschini and Millesi 2005) similar to several other small mammals (Norris and Adams 1981; Woodside et al. 1987; Fortun-Lamothe et al. 1999). They mated again shortly after parturition (Vohralik 1974). This strategy of concurrent lactation and gestation allowed common hamsters to raise more than one litter per season, but on the other hand might place considerable demands on the mother’s condition (Martinez-Gomez et al. 2004). High reproductive effort could in turn have consequences on future reproduction or survival (Clutton-Brock et al. 1982; Koivula et al. 2003). The timing of the active season might affect individual reproductive output. Studies on various hibernating small mammals have shown that early breeders achieved highest reproductive success.
Material and methods

The study was carried out in an urban area in southern Vienna, Austria. Common hamsters lived in the green areas associated with an apartment complex. Vegetation showed a very uniform distribution all over the study area and consisted mainly of plain grassland, some bushes and trees. The study site included 4.60 ha. Data were collected from spring 2003 until spring 2006. Live-trapping was done on 5 days/week mainly during the morning period from 5 a.m. until 11 a.m. (permit no. MA22-2605/02). Each focal individual was trapped in approximately 10-day intervals. Animals were captured using Tomahawk live traps baited with peanut butter. The hamsters were removed from the traps immediately after capture and put into a black cotton sack. This method minimised stress for the animals during the investigation and enabled us to handle the hamsters without anesthesia. Each manipulation lasted about 5–10 min and the hamsters were released near their burrows. At first capture, we implanted a transponder chip (PIT tag, Data Mars SA) subcutaneously for permanent identification (permit no. GZ 68.210/12- BrGT/2003). For all investigations, required legal authorisations were granted. For field recognition, the animals were marked with a commercial hair dye in individually recognisable patterns. Parameters recorded at capture were location, body mass (\( \pm 1 \) g), as well as teat and vulval development. Size and pigmentation of teats were classified in three classes from small (1) to swollen with milk remains (3). Vulval development was categorised on a four-point scale in terms of vagina size: completely closed (0), small opening (1), wide opening (2), wide opening with bloody mucus (3). At each capture, vaginal smears were collected and stained using the Papanicolaou stain protocol (Papanicolaou 1954). Vaginal cytology was classified under a Biovar microscope (Reichert) based on the proportion of cell components like nucleated epithelial cells, cornified cells and leucocytes. The only phase that could clearly be identified was vaginal oestrus. It was defined by a predominance of cornified cells in the smear (Weißbach 1996). Date of first conception was based on vaginal oestrous and observed sexual interactions with males. These data were validated by subsequent mass increases and teat development as indicators for pregnancy, supported by data on parturition and litter emergence. Indicators for parturition were rapid body mass loss, increased teat size and sometimes milk rests on the teats as a consequence of milk secretion. Date of parturition was calculated as the mean day between two recaptures within which a rapid decrease of body mass combined with an increase of teat status was protocolled. Signs of concurrent lactation and gestation were increasing body mass during lactation, bloody and mucous vagina status at the expected end of the postpartum pregnancy, rapid body mass loss at the expected end of postpartum pregnancy, and in some cases sexual interactions with males during postpartum oestrus. Litter size was determined at first emergence of the juveniles from a female’s breeding burrow. Each pup was individually marked (tattoo or transponder chip, fur-colour) to avoid double counts. As the pups began to disperse shortly after they had emerged (Franceschini personal observation), weaning date was determined by the appearance of the litter above ground. The reproductive

(e.g. Norris 1993; Millesi et al. 1999). The relationship between timing of reproduction and reproductive success has been well documented in birds (e.g. Verhulst and Tinbergen 1991; Olsson 1996) and in several rodent species (e.g. Hoogland 1995; Rieger 1996; Millesi et al. 1999).

Depending on the geographical range, common hamsters emerged from hibernation in March and April (Wollnik and Schmidt 1995; Weinhold 1998). Like in other hibernators (e.g. Murie and Harris 1982; Michener 1983), male hamsters appeared in advance of females (Franceschini and Millesi 2005). After female emergence in spring, the mating period started. Common hamsters have a promiscuous mating system and are known to show a long breeding season lasting for up to 5–6 months. Litter emergence from the natal burrow started in mid-May (Franceschini and Millesi 2005). In general, young reach sexual maturity at an age of about 2.5 months and are therefore able to reproduce in their first year (Niethammer 1982). Nevertheless, in our study population most females started to reproduce as yearlings (Tauscher 2006). In very few cases, juvenile females were observed to successfully breed in the year of birth (Franceschini, unpublished data). The last matings in the season were observed in mid-August (Franceschini, unpublished data). Shortly thereafter, males reduced activity and entered hibernation in late August, followed by females and finally juveniles (Franceschini and Millesi 2005). Preparation for hibernation in these animals included both accumulation of body fat reserves as well as preparing food stores in the burrow. This strategy provided additional food resources for the winter. Previous studies indicated that common hamsters show a rather facultative hibernation behaviour (Waßmer 1998). Body temperature patterns of individuals ranged from regular torpor bouts to almost continuous euthermy over winter. During the euthermic phases, hamsters even left their hibernacula and were active above ground (Bekenov 1998; Waßmer 2004).

Our study investigates individual reproductive output in free-living female common hamsters. Seasonal timing, body mass changes and overwinter survival were compared with individual reproductive output.

Material and methods
period was defined as the time span between first conception and weaning of the last litter. The post-reproductive period was defined as the time period when the females had terminated reproductive activities in a season. It started after weaning of the last litter and lasted until the onset of hibernation. Data on teat and vulval development, vaginal cytology and body mass were used to document that no further oestrus, gestation or lactation period had occurred until the subsequent spring.

Focal individuals reduced above-ground activity during a time span from late August until the end of October. Within this time span, we checked for immersgence into hibernation by frequently observing the burrow and by recapture attempts. Hibernation duration was defined as the time period from the last sighting in autumn until emergence in the subsequent season. To determine spring emergence date, regular trapping sessions and observations were conducted on a daily basis starting in early March. The duration of the active season was defined as the time period between spring emergence and immersgence into hibernation.

**Statistics**

Tests for normality were done by applying Wilk-Shapiro tests (SPSS 11.5 for Windows). Correlation statistics were done with Pearson correlations in case of normally distributed samples, otherwise Spearman rank correlations were performed.

In case of related samples, Wilcoxon tests were used. Mann–Whitney U-tests were applied in case of independent samples. Normally distributed samples were tested with one-way ANOVA, others with Kruskal–Wallis tests. Significance values were obtained from two-tailed statistics. If not stated otherwise, means ± S.D. are shown.

We were able to monitor only one complete breeding season of each focal female. Seasonal reproductive success (number of litters, total offspring) of 18 females could be determined. Unfortunately, reliable data on emergence or immersgence date, body mass or conception and parturition date was not always available for all individuals. The sample sizes in the analyses vary due to this lack of information.

**Results**

In all study years, female common hamsters showed high individual variation in reproductive output: individual females produced zero to three litters per season and litter size ranged from one to nine pups per litter (4.34±2.14, n = 18). A female’s first litter in the season was significantly larger than the second one (first litter: 6.00±2.23; second litter: 3.23±2.52; p = 0.01, n = 13). No significant inter-year differences were found in the number of litters (Kruskal–Wallis test: p = 0.49, n = 18) and offspring number (Kruskal–Wallis test: p = 0.99, n = 18). We compared body mass at spring emergence and body mass at first conception with reproductive output in individual females. Neither the number of litters (rS = −0.27, p = 0.42, n = 11) nor total offspring number per season (rP = −0.24, p = 0.48, n = 11) correlated with body mass at spring emergence. Similar results were found with body mass at first conception (number of litters per season: rS = −0.07, p = 0.85, n = 10; total offspring number: rP = −0.22, p = 0.55, n = 10).

The timing of the active season varied among individual females and potentially plays an important role for reproductive success. Females emerged from hibernation between 4 March and 12 May. Similar variation was found in the onset of hibernation: immersgence dates ranged from 29 August to 21 October. Thus, the duration of the active season in female hamsters ranged from 144 to 200 days (171.67 days ± 19.65, n = 9). Examining potential relationships between timing and individual reproductive output revealed that the spring emergence date was significantly correlated with individual reproductive output: the earlier a female emerged, the more litters (rS = −0.71, p = 0.01, n = 11) and the more total offspring per season (rS = −0.69, p = 0.02, n = 11) were produced (Fig. 1a and b).

To analyse these potential timing effects in more detail we attempted to determine if early-emerging females became oestrous earlier than those that had emerged later in the season. As expected, early spring emergence corresponded with early breeding, as reflected in a significant relationship between spring emergence date and both first conception and parturition date: the earlier a female emerged from hibernation, the earlier she mated (rP = 0.75, p = 0.01, n = 11) and the earlier she gave birth to her first litter (rP = 0.55, p = 0.04, n = 15).

The relationship between timing of reproduction and offspring number could indicate that early emerging females had a longer reproductive period than later ones. However, our results showed that this was not the case; the duration of the reproductive period – defined as the time span between first conception and termination of reproduction in a season – did not vary with spring emergence date (rP = −0.34, p = 0.33, n = 10). Thus, early emerging females had a similar time span for reproduction as later ones.

A potential strategy to maximise reproductive output in a limited time period is to mate shortly after parturition during a postpartum oestrus. This enables a female to simultaneously lactate while being pregnant with the second litter. In our study population, a postpartum oestrus and gestation was determined in
eight focal individuals. Nevertheless, only in four of these females a postpartum litter could be observed above ground. The other four females showed signs of concurrent gestation and lactation and even of a second parturition at the expected time, but no young appeared from the natal burrow. In these cases, we therefore assumed that the young died after birth. We compared females that successfully produced a postpartum litter with those that lost their pups. Spring emergence date differed significantly between the two groups (Mann–Whitney U-test: $p = 0.03, Z = -2.18, n = 4/4$; Fig. 2), with the former having emerged earlier than the latter.

To estimate potential costs of high reproductive effort and success, we determined female condition shortly before hibernation. Prehibernatory body mass was apparently not affected by individual reproductive output. Neither the number of litters ($r_S = 0.17, p = 0.57, n = 13$) nor total offspring number ($r_P = 0.24, p = 0.44, n = 13$) was related to body mass at the end of the active season.

In general, body mass loss during hibernation ranged from 0.00% to 38.11% (22.86% ± 11.30, $n = 8$). In our population no significant relationships were found between body mass loss during hibernation and the number of litters per season ($r_S = 0.41, p = 0.36, n = 7$) or total offspring ($r_P = 0.64, p = 0.17, n = 6$). Reproductive success also did not seem to affect the duration of the subsequent hibernation period. We found no significant correlations between hibernation duration and number of litters per season ($r_S = -0.20, p = 0.66, n = 7$) or total offspring ($r_P = -0.39, p = 0.45, n = 6$) in the previous season.

Another potential cost factor could be reflected in overwinter survival. However, females with high reproductive output had higher overwinter survival rates than less successful ones (Mann–Whitney U-test: $p = 0.01, Z = -2.46, n = 6/10$; Fig. 3).

Although reproductive output did not seem to affect hibernation duration, it was significantly related to the length of the active season. The number of litters per season ($r_S = 0.79, p = 0.02, n = 8$) and total offspring number (Fig. 4) correlated significantly with the duration of the active season. Thus, successful females were active longer than individuals with lower offspring numbers ($r_P = 0.85, p = 0.01, n = 8$).

![Figure 1](image1.png)  
**Fig. 1.** Emergence from hibernation and reproductive success in female European hamsters. (a) Spring emergence date and number of litters per season. (b) Spring emergence date and total offspring per season.

![Figure 2](image2.png)  
**Fig. 2.** Spring emergence date (mean ± S.D.) in female hamsters that were successful and unsuccessful in producing a postpartum litter.

![Figure 3](image3.png)  
**Fig. 3.** Total offspring number per season (mean ± S.D.) in females that survived the subsequent winter and females that died over winter.
The prolonged active season in successful females was evident in the postreproductive period. This period, defined as the time span between the termination of reproductive activity and hibernation onset was highly variable among individual females (53.57 days ± 28.86, n = 14). Our results demonstrate that early-reproducing females had a longer postreproductive period than later-breeding ones ($r_p = -0.64, p = 0.01, n = 14$).

This period might be important for overwinter survival because the duration of the postreproductive phase was negatively correlated with overwinter mass loss ($r_s = -0.76, p = 0.05, n = 7$). Thus, mass loss over winter was lowest in females that prolonged the postreproductive period before entering hibernation.

**Discussion**

Due to the short active season, most hibernators only raise a single litter per year (e.g. Hackländer et al. 1999; Millesi et al. 1999). Common hamsters, however, are known to have a high reproductive potential (Grulich 1986). Accordingly, individual females in our study population were able to wean up to three litters per season, with a maximum litter size of nine juveniles. Similar data on reproductive output in this species were found in other field studies. Seluga (1996) and Bekenov (1998) reported females that produced two litters per season. Grulich (1986) claimed that common hamsters can even have up to five litters per season under very beneficial environmental conditions. Regarding maximum litter size, Weinhold (1998) documented nine juveniles, Seluga (1996) seven pups. Reproduction at our study site was therefore in the range of populations in habitats with less human impact. The reproductive output was characterized by high individual variation as reflected in the number of litters and total offspring per season. Females with more litters also had more total offspring per season indicating that reproductive output was maximized by producing more than one litter. Most females had two litters (67%); 17% of females had only one litter per season. Very few individuals had no offspring and, exceptionally, females could successfully raise three litters in a season (Franceschini and Millesi 2005).

A female’s first litter per season was significantly larger than the second one. The strategy to produce larger litters early in spring might be adaptive because early born young could have higher survival rates due to several aspects. First, early born pups have more time to grow, gain body mass and prepare for hibernation than later born juveniles (Tauscher 2006). Moreover, food resources may decline seasonally. Second, an early birth date might enable early puberty and perhaps successful reproduction in the first year of life. Niethammer (1982) observed first-year puberty in common hamsters. In Vienna, two females produced offspring in their first year (Franceschini, unpublished data); those two females were born early in the season. Because they have more time for growth and development, early born young may show greater competitive ability than later born ones. Especially at our site, this could be important because the population density was about seven times higher (Franceschini and Millesi in press) than in other habitats (Seluga 1996; Weinhold 1998).

An important factor determining juvenile survival is maternal investment. Females are confronted with increasing energetic and temporal constraints during the active season. Conditional factors may therefore limit parental investment in second or third litters. This situation may allow higher maternal investment early in the season, resulting in comparatively smaller litters later in the year (Rieger 1996; Millesi et al. 1999).

Hibernating species underlie rigid time and energy constraints (Choromanski-Norris et al. 1986; Bieber and Ruf 2004; Millesi et al. 2004). As in a number of mammalian species (e.g. Microtus townsendii – Anderson and Boonstra, 1979; Spermophilus armatus – Rieger, 1996; Cynomys ludovicianus – Hoogland, 1995; Spermophilus citellus – Millesi et al., 1999), the timing of spring emergence date was related to individual reproductive success. In the studied population, early emerging female hamsters had more litters and more offspring per season. A potential advantage of early emergence might be more time for reproduction and consequently more litters. However, the duration of the reproductive period was similar in early and late emerging female hamsters. Hence, early reproduction did not provide more time for gestation and lactation. At our site, several females mated shortly after parturition and lactated the first litter while being pregnant with the second one. This may reflect a time-saving strategy to maximize seasonal reproductive output. However, in half of the cases where a postpartum litter was born, the
juveniles apparently did not survive the first postnatal weeks until emergence. Postnatal mortality could occur due to infanticide or insufficient maternal care. Infanticide has been observed in several other hamster species in captivity (Da Silva et al. 1989; Edwards et al. 1995), but in the field no evidence was found. Females were very aggressive during lactation (Franceschini personal observation) and stayed close to the breeding burrow when feeding above ground (Franceschini personal observation). We also never observed an individual entering the breeding burrow of another hamster. Data on faecal cortisol metabolites indicate higher stress levels in females that lost their postpartum offspring than in the successful ones (Franceschini et al. 2007). Stress during lactation was observed to negatively affect survival of postpartum young in house mice (Krackow, 1990). Declining resources and increasing competition, especially in a high-density population, may lead to elevated stress levels in individual females. Especially when food is scarce, it may be advantageous for females to reject the postpartum-conceived litter in order to breed again later in the season (Krackow 1990). This is supported by the observation that three of the four female hamsters that lost the postpartum litter reproduced successfully later in summer.

Several life history traits could determine reproductive success. First, age might play an important role: in many species, first breeders often had lower reproductive success (e.g. Myers and Master 1983; Festa-Bianchet and King 1991; Huber et al. 1999) than more experienced older individuals. Considering the short life expectancy in the study area (females: mean life span 14 months in the study area) a rather opportunistic reproductive strategy is assumed to be adaptive.

Females with more litters per season had more overall offspring than those that produced only one litter. However, offspring recruitment in future breeding periods is another important factor determining individual lifetime fitness. There might exist alternative reproductive strategies in females, to produce either high offspring quantities or fewer but high quality offspring. Unfortunately, due to juvenile dispersal and high mortality rates we are not able to answer this question.

High reproductive output is associated with high energetic costs and could therefore negatively affect physical condition in females. Nevertheless, prehibernation body mass did not differ between females with high and low offspring numbers, indicating either that high output did not require more energy or that the costs of high maternal effort could be compensated. For example, in Richardson’s ground squirrels (Spermophilus richardsonii – Michener, 1978) and Columbian ground squirrels (Spermophilus columbianus) successful females hibernated later than females that did not wean a litter (Neuhaus 2000). In our population, early-emerging females with high offspring numbers had a prolonged postreproductive period. This additional time could be used to gain body mass before hibernation. Common hamsters do not rely solely on body fat reserves during winter, but also accumulate food stores in the burrow (Niethammer 1982). The time between reproduction and hibernation was mainly used for food caching (Franceschini personal observation).

High reproductive effort in one season can impact future reproduction and survival (Clutton-Brock et al. 1982; Partridge and Harvey 1985; Koivula et al. 2003). In our study population, however, females with high reproductive output had significantly higher overwinter survival rates than less successful individuals. No significant relationships with age or body mass were found. Differences in the amount and/or quality of individual food stores might affect overwinter survival. We have no information on individual food stores but females with a longer postreproductive period could spend more time with food caching. This is supported by the result that the duration of the postreproductive period was negatively correlated with mass loss during the subsequent winter. We therefore suggest that a prolonged postreproductive period served not only to compensate the costs of high reproductive success but also allowed more and/or better food storage.

Of course, one has to keep in mind that the results presented in this study are based on correlations and therefore factors determining individual reproductive decisions still remain unclear. However, the data indicate high maternal plasticity in the focal females. As has been shown in several studies mainly on reproductive success in birds, individual plasticity is an important component in reproductive traits (Tinbergen and Both 1999; Tinbergen and Sanz 2004; Nussey et al. 2005). Phenotypic quality can play a role in response to environmental variation and in differing parental quality. In our studied females it seemed that some individuals were more successful in reproduction and survival. This could be due to better access to resources in these individuals. Food abundance may decline during summer but was distributed equally in the study area. Therefore, we found no evidence for pronounced variation in the quality of female territories. Another aspect that could contribute to the high variation might be carry-over effects of maternal effort in the previous season. High reproductive output in 1 year might lead to reduced subsequent fecundity (Olsson 1996; Huber et al. 1999; Hanssen et al. 2005) or delayed emergence in the following spring. We were able to monitor only one breeding season of the focal females and therefore do not have sufficient information on reproductive effort and output in the previous year. Most females dispersed or died after their first reproductive season. Finally, individual birth date, early or late in the season, could determine the timing of puberty and future reproductive...
performance. This is supported by the fact that early born females sometimes even manage to breed in the same season.

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