

**Female Reproductive Strategies in the
Striped Mouse (*Rhabdomys pumilio*):
Communal versus Singular Breeders**

Diploma Thesis

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submitted by

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from Köthen/Anhalt

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To Female 34

One who runs alone
cannot be outrun by another
ETHIOPIAN PROVERB

The present study was conducted from July 1st, 2004 to March, 31st, 2005 in cooperation with the chair of Animal Physiology, University of Bayreuth and the University of the Witwatersrand, Johannesburg.

Declaration

Hereby I declare that I independently wrote the present manuscript without using not – mentioned sources and support.

Melanie Schubert

Bayreuth; March 31st, 2005

Table of Contents

1	Introduction	1
1.1.	Predictions	4
1.1.1.	Influences on Over – winter Survival	4
1.1.2.	Female Reproductive Strategies	4
	Methods	5
2.1.	Study Area	5
2.2.	Study Animal	6
2.3.	Field Study	7
2.3.1.	Trapping and Marking of Animals	7
2.3.2.	Identification of Groups and Observations	7
2.3.3.	Radiotracking	8
2.3.4.	Plant Survey	9
2.4.	Captive Study	10
2.4.1.	Animals	10
2.4.2.	Procedure	11
2.3.2.1.	<i>Triplets</i>	11
2.3.2.1.	<i>Pairs</i>	13
2.5.	Definitions	14
2.6.	Data Analyses and Statistics	16
	Results	19
3.1.	Social relationships within a communal nest	19
3.2.	Over – winter Survival Probabilities	21
3.2.1.	Nest sharing and Thermoregulatory Benefits	21
3.2.2.	Ecological and Physiological Factors	22
3.3.	Reproduction in the Field	24
3.3.1.	Time Lag of Births	24
3.3.2.	Communal Breeding Societies	25
3.3.3.	Plural versus Singular Breeders	26
3.3.4.	Pup Survival and Ecological Situation	28
3.3.5.	Young individuals and Reproduction	30
3.3.6.	Home Ranges in two Seasons	32

3.4. Reproduction in Captivity	35
3.4.1. Time Lag of Births	35
3.4.2. reproductive Success	36
3.4.3. Body Mass and Weight Gain of Pups	40
3.4.4. Reproductive Success between Littermates	43
3.4.5. Parental and Allo – parental Care	45
3.4.6. Care of Adults concerning different Ages of Pups	47
3.4.7. Care in the Morning and Afternoon	51
3.4.8. Males: Paternal Care or Mating Strategy ?	53
3.4.9. Retrieval Experiment	55
4 Discussion	58
4.1. Over – winter Survival Probabilities	58
4.2. Reproduction	60
4.2.1. Synchronisation of Births	60
4.2.2. “Dispersing” of pregnant females	61
4.2.3. Reproductive Success	63
4.2.4. Parental and Allo – parental Care	66
4.2.5. Young Individuals and Reproduction	68
4.2.6. Home ranges in two Seasons	70
Conclusions	71
Literature	74

1 Introduction

Survival and reproduction are both crucial elements in the life history of animals (Krebs & Davis 1997). Thus consequences of different strategies are most readily related to an individual's fitness.

In the first place the reproductive strategy seems to be the most important factor in regard to the fitness of an individual. The trade – off between physiological demands and reproduction, in fact the ratio of costs (investment) to benefits (breeding success) are under strong pressure concerning their crucial effects on the fitness of a mother and her future reproduction (CLUTTON – BROCK et al. 1982; TRILLMICH 1986; LINDSTRÖM 1999). Therefore animals exhibit a variety of breeding systems to maximize their own fitness. For female mammals, one important factor regarding their reproductive strategy is whether they are solitary breeders or reproduce within a group (Hayes, 2000). Offspring of solitary breeding females mostly disperse after reaching sexual maturity. This system is found in cheetahs (CARO & COLLINS, 1987) and in many rodents (CHOATE, 1972; PERRIN, 1980; SCHRADIN & PILLAY, 2003). In contrast animals living in social groups develop extensive relationships with other group members. Three forms of breeding within group–living mammals are known: eusocial breeding, singular and plural breeding (HAYES, 2000). The main difference within these three breeding strategies is the number of reproductive females and males: In singular breeders one reproductive pair produces all the infants within the group (HAYES, 2000). Despotic systems or groups with helpers at the nest may occur (KÖNIG, 1997). In despotic groups one female reproduces all the offspring, whereas other females are reproductively suppressed (KÖNIG, 1993). Prairie voles, *Microtus ochrogaster* are known to live in singular breeding societies (HAYES & SOLOMON, 2004). The plural breeding strategy is characterized by the reproduction of several and sometimes even all sexually mature individuals within a single nest (HAYES, 2000). However reproductive suppression is likely to occur within this form of social system (SOLOMON & FRENCH, 1997).

Communal care, the sharing of parental responsibilities by multiple individuals, is found within all three breeding strategies. Individuals involved in communal care may gain fitness benefits as a result of thermoregulation and group defence (GITTLEMAN, 1985). Animals sharing a nest are most likely to be related, i.e. sister – units or mother – daughter units. Thus all individuals participating in communal care increase their indirect fitness benefits (HAMILTON, 1964).

In singular breeding mammals pups are reared communally in a nest and receive care from infertile and breeding individuals (SOLOMON, 1991).

Plural breeding mammals raise there together; and delayed dispersal (helper at the nest) (SOLOMON & FRENCH, 1997) is likely to occur within this form of social system. One hypothesis concerning the delayed dispersal of juveniles emphasises the cooperation of individuals when food and space become limited at high population densities (GETZ *et al.*, 1992). As population density increases suitable territories are filled. Thus young individuals remain philopatric and enjoy benefits of group living.

Plural breeding systems are best studied in house mice, *Mus musculus* under laboratory (GANDELMAN *et al.*, 1970; SAYLOR & SALMON 1971; KÖNIG 1994a, 1994b), semi – natural (MANNING *et al.*, 1995) and natural (WILKINSON & BAKER, 1988) conditions. Communal nesting is common in *Mus musculus* populations (MANNING *et al.*, 1992, KÖNIG, 1994a). Here females only nest solitary when opportunities to nest communally are restricted, e.g. in cases when no relatives survived (MANNING *et al.*, 1992). Females typically nest with close kin (WILKINSON & BAKER, 1988). Kin selection (HAMILTON, 1964) is known to favour cooperation due to indirect fitness benefits (GASTON, 1978). Furthermore the reproductive success of females depends on the relatedness to and the presence of a female partner (KÖNIG, 1989a, 1993).

Females of close kin nesting communally often share parental duties (GANDELMAN *et al.*, 1970), including the nursing of own and alien offspring (KÖNIG 1994b). Polygynous female house mice (*Mus musculus domesticus*) produce more offspring during their lifetime. Moreover body mass of infants at birth is improved in communal nests compared to litters of solitary females (KÖNIG, 1993). Pups gain more weight in plural breeding (KÖNIG, 1993; HAYES & SOLOMON, 2004) than in solitary or singular breeding groups. For this reason communal breeding females can improve their reproductive success (KÖNIG, 1994a). In fact pup survival probabilities of house mice are higher in communal than in solitary nests (WILKINSON & BAKER, 1988; KÖNIG, 1994b). In contrary MANNING *et al.* (1995) could not confirm the improved development (weaning weight) of communally reared pups in their experiments. However they demonstrated that communal nesting provides a protection mechanism from conspecific infanticide in house mice under semi – natural conditions.

Reproductive skew is also likely to occur within communal breeding groups: In the wood mouse (*Apodemus sylvaticus*) females share reproduction in communal nests (GERLACH & BARTMANN, 2002), but reproductive success significantly differs among these individuals. Dominant female wood mice (mothers) have no advantage leading to an increased reproductive success by breeding communally. Moreover subordinates

suffer a decreased direct reproductive success and should therefore disperse when suitable ecological circumstances exist instead of breeding communally (GERLACH & BARTMANN, 2002).

Most studies investigating communal breeding in rodents were conducted in captivity. Since conditions in the nature are variable and energetically challenging for animals benefits of communal breeding and nesting might be even greater in the wild. Furthermore under laboratory conditions individuals were paired compulsory and had no opportunity to disperse leading to results, which might not apply under natural circumstances.

One mammal that provides a good opportunity for studying benefits of communal nesting within plural breeding groups in the field and under laboratory conditions is the African striped mouse (*Rhabdomys pumilio* (Sparrman 1784); as the genus is monotypic I refer to this species as *Rhabdomys* hereafter). SCHRADIN and PILLAY (2004) observed a regular occurrence of communal nesting and breeding by studying a *Rhabdomys* population in the succulent karoo in 2002. Furthermore they predicted factors influencing the formation of communal nests: predator avoidance, thermoregulatory benefits and an increase of fitness benefits by females breeding communally (SCHRADIN & PILLAY, 2004). Nevertheless detailed studies were missing so far. The main aim of the present work was to determine causes and consequences of communal nesting and breeding in the striped mouse.

The social system is likely to significantly influence a female's reproductive success. Especially the relationships between breeding females of the same group might be an important factor. It was expected that *Rhabdomys* live in an egalitarian social system since no dominance hierarchy was found in the past (SCHRADIN pers. commun.). Thus, all females were expected to start reproducing in springtime. Female mice of one nest breeding communally were expected to be descendants of the same group, i.e. to be related. If females raise their offspring in a communal nest, it was expected that they give birth synchronously, such that mothers could share care taking responsibilities and spent more time for foraging. Investment in offspring is particularly costly to females, because they experience extreme energetic demands during lactation (THOMPSON, 1992; ROGOWITZ, 1996). Since female striped mice undergo a postpartum oestrus they have doubled costs of lactation and pregnancy. This should result in a trade – off between current offspring and future fecundity. So it was expected that communally breeding striped mouse females can increase their fitness by the sharing of parental – and allo – parental duties.

One other element influencing the fitness of an individual is the survival probability, which is determined by ecological and physiological factors (RÖDEL *et al.*, 2004). In winter 2003 *Rhabdomys* formed huddling groups of unrelated individuals during the nights (SCHRADIN per. commun.). Here group affiliation changed in coherence with daily temperatures and more mice shared a nest during cold nights. In this study it was expected that individuals can increase their survival and therefore their fitness by the formation of huddling groups. It was assumed that more mice will share a nest concerning thermoregulatory benefits during cold nights.

1.1. Predictions

1.1.1. Influences on over – winter survival probabilities

- 1) More mice will share a nest during cold nights for thermoregulatory benefits

1.1.2. Female reproductive strategies

- 1) Births within communal nests are synchronized
- 2) Communal nests have higher fitness benefits in comparison to singular breeders
- 3) All members of a communal nest participate in rearing of offspring

2 Methods

2.1. Study Area

This study was conducted from 1st of July to 31st of December 2004 in the Goegap Nature Reserve (29°37'S;17°59'E) in South Africa. The nature reserve covers approximately 15 000ha and is situated about 15km south east of the town Springbok in the Northern Cape.



In this semi – desert area, the vegetation consists mostly of *Zygophyllum retrofractum* and *Lycium cinerum* shrubs. The vegetation type is succulent karoo (ACOCKS, 1988; COWLING *et al.*, 1999), one of 25 global hotspots (MYERS, MITTERMEIER, MITTERMEIER, FONSECA & KENT, 2000). In springtime this area is covered with approximately 600 different wildflower species,

which intersperse large patches of sand. The study area of 20ha is characterized by dry riverbeds and large sandy areas with patchily distributed shrubs. The annual rainfall of on average 160mm/year (RÖSCH, 2001) occurs mostly during wintertime and is highly predictable (COWLING *et al.*, 1999).

2.2. The study animal

The striped mouse is a diurnal, small (body mass: 40 – 60g) muroid rodent, that is widely distributed throughout southern parts of Africa. *Rhabdomys* is found in various habitats, such as grassland, marsh, forests, semi – deserts and deserts (KINGDON, 1974). In the grasslands of southern Africa *Rhabdomys* is a solitary breeder (BROOKS, 1974; PERRIN, 1980; WILLAN & MEESTER, 1989; SCHRADIN & PILLAY, accept, 2005a). Here females have exclusive territories, which are aggressively defended against female conspecifics. Male territories overlap several female territories



(WILLAN, 1982; WILLAN & MEESTER, 1989; PERRIN *et al.*, 2001; SCHRADIN, 2004). In contrast in the succulent karoo, a desert habitat, mice tend to live in persistent social groups of one to four breeding females, one to two breeding males and their offspring of both sexes (SCHRADIN & PILLAY, 2004). Here breeding males are permanently associated with the females and their offspring. Thus, in this habitat *Rhabdomys* can be defined as a plural breeder. The succulent karoo is characterized by a harsh climate, i.e. cold and wet winters as well as dry and hot summers. The breeding season starts in early spring with the occurrence of highly nutritious ephemerals and lasts for about three months (SCHRADIN & PILLAY, accept, 2005b). *Rhabdomys* requires a high protein diet during the breeding season including insects (PERRIN *et al.*, 2001). The average litter size is about five, with a sex ratio at birth close to 1:1, which also characterizes adult populations (BROOKS, 1974; PERRIN, 1980; DAVID & JARVIS, 1985). Females have a postpartum oestrus (CHOATE, 1972), with a gestation period of 23 days (BROOK, 1974), and produce two to three litters per breeding season (SCHRADIN & PILLAY, accept 2005a). Young mice reach sexual maturity at an age of one to three months (BROOKS, 1982). *Rhabdomys* builds nests above the ground, which resemble bird's nests; being about 15.2cm diameter with a single entrance hole (CHOATE, 1972).

In the succulent karoo, nesting sites are typically within dense shrubs (SCHRADIN & PILLAY, 2004).

2.3. Field study

2.3.1. Trapping and Marking of Animals

All mice were trapped alive using metal (26 x 9 x 9cm, like Sherman traps) and plastic (29,5 x 8 x 6,5cm) traps. Traps were baited with a mixture of bran flakes, currants, sea salt, salad oil and peanut butter and placed around bushes, which were occupied as a nesting site, as revealed by radio-tracking (see below). Furthermore, in wintertime a piece of cotton was put into the traps. Depending on the outside temperature, traps were placed in the sun (mainly in winter) or in the shade (in summer). Trapping was performed in the morning and in the afternoon, but not during the hottest time of the day. All traps were checked 30 to 60 minutes after setting. Trapped mice were weighted and sexed. Females having a perforated vagina or visible nipples were regarded as being reproductively active; males when they were scrotal. Furthermore all mice were marked individually with black hair dye (Inecto Rapid, South Africa) by writing a number on each side of the mouse. This method had no effects on their behaviour (SCHRADIN & PILLAY, 2004). Furthermore every mouse received two ear tags (National Band and Tag Co., USA). Since the colour started fading soon, the markings had to be refreshed every second week. Trapping was performed to refresh markings, to mark juveniles and mice which immigrated onto the grid. During this study a total of 186 mice (71 females and 85 males) were trapped at the field site. However only the females were used in this project.

2.3.2. Identification of Groups and Behavioural Observations

Mice occupying one nest were regarded as one group. Every group received a number ranging from G 1 to G 11. Scrotal males were regarded as breeding males of the group. All females weighting over 60g were regarded as being pregnant and thus breeding.

Behavioural observations were performed for the duration of 45 minutes in front of the nest in the morning and in the afternoon, which represent the main activity periods of *Rhabdomys* (SCHRADIN & PILLAY, 2004). On average 56 behavioural observations were performed for each group (range: 35 – 68). The group composition was recorded during each observation, including the number of individuals emerging out of the nest or withdrawing into the nest.

An electronic scale, which was baited with peanut butter was placed in front of the nest, so that individuals were able to climb onto it. Peanut butter was chosen, because it presented a highly nutritious food source for the mice. Furthermore individuals could not remove the peanut butter from its place and therefore had to remain longer on the scale. Thus the body mass of females could be determined without disturbing the mice. Using this balance, it could be determined when females gave birth, as indicated by a large loss of body mass of 10 – 15g.

2.3.3. Radiotracking

Radiotracking was performed with an AOR 8000 wide range receiver and a Telonics RA – 14K antenna. On average two females and one male of each nest received a radio – transmitter (MD – 2C). The mice were trapped (see above) and were brought to the research station. Here animals were briefly anaesthetized with ether (Barrs Pharm Industries, South Africa) and the radio collars were put around their necks. Tags used for females weighted 2.5g including the collar and represented less than 10% of the body weight (average: 5.59%, variation: 5.07 – 6.11%). Radio tags were perishable to eight to twelve weeks and had to be replaced by new ones after this time. No indication for negative effects of equipping mice with radio-collars were found in the past (SCHRADIN & PILLAY, 2005a). Altogether seventeen females from nine different groups were equipped with radio collars. Of these seventeen females two were eaten by a raptors, two died of human failure, one died of natural causes and two more mice disappeared from the study grid. However, radiotracking – data of these animals could mostly be included in the analyses.

Radiotracking was performed for the entire study period, for three different reasons: (1) determination of individual sleeping sites; (2) home range size in non – breeding season and (3) during the breeding season. To determine the home ranges, females were radio – tracked for nine days, six times a day (a total of 54 fixes) and every two hours from 8:00 – 18:00. A radio – tagged mouse was approached until the animal was either seen or known to be hidden in a particular shrub (homing in method). By using a GPS (eTrex Venture, GARMIN International, USA) the position was recorded with an accuracy of five meters.

Home range size was determined using the 95% minimum polygon method (RANGES 6). This method is widely used in rodents (MADISON *et al.*, 1984; TEW & MACDONALD, 1994) and has previously been used in studies on the same *Rhabdomys* population (SCHRADIN & PILLAY, 2004a; SCHRADIN & PILLAY, 2005a).

2.3.4. Plant Survey

By knowing the home range size and the distribution in the field for each female, the dissemination of plants, their quality and condition could be investigated. All corner points of the 95% minimum convex polygon home range were located using the GPS and marked with iron rods that were then connected with barrier tape. The vegetation was investigated every three square metres by using a 20m measuring tape and classified at each 3m point into different categories: (1) plant species, (2) condition (alive or dead), (3) potential cover for the mouse and (4) food plant. In several cases no plant grew directly at the 3m point, then a zero score was marked in the map. However sometimes a plant species could not be identified. In these cases the plant was defined as unknown shrub or ephemeral.



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ephemeral.

Eleven plant surveys were carried out in wintertime (June) for individual survival measurements. This data was provided by Dr. C. Schradin. In breeding season (spring) plant surveys were carried out for seventeen females. The habitat quality, e.g. the number of food plants and dissemination of ephemerals, which are highly nutritious

plants only occurring in spring, were determined of each female mouse. Ephemerals contain a high proportion of protein, which is essential for reproduction (PERRIN, 1980).

2.4. Captivity Study

2.4.1. Animals

The experimental individuals were born in captivity (third generation from a founder generation trapped in Goegap in 2002) and were housed under semi – natural conditions on the veranda at the research station. The animals were protected from wind, rain and direct sunshine through a shade cloth. The sun only shone directly on the enclosure in the early mornings. Then all cages were placed in the sun for about an hour. Thus mice were allowed to bask in the sun, an important activity for mice in the field (SCHRADIN & PILLAY, 2004). In wintertime the whole enclosure was surrounded with a wind – and rainproof cloth during the night to avoid a too extreme decline in temperature (frosty nights were common). The minimum and the maximum temperatures were recorded daily by a thermometer situated on the veranda next to the cages.

Water was provided *ad libitum*, whereas the main food was given in the mornings. Each mouse received a daily portion of 4g of a mixture of seeds (Marltons



Pets & Products, USA; Lopis Hamster Food, South Africa; Brencco Hamster Food, South Africa; Seeds from Agricol, South Africa). Furthermore a piece of fruit or lettuce was given six times a week at midday. In the evenings three pieces of tissue paper were supplied for nest building and

each individual received Fifteen sunflower seeds. Food was allocated during the day to prevent adiposis. Furthermore under natural circumstances mice spent most of the day searching for food. For this reason the allocation of food turned out to be a useful method for behavioural enrichment of captive mice.

A total of 47 females and 33 males were used in this study. Females were mated with a male, which was unknown and not related to them. The weight of all individuals was recorded before pairing. Two kinds of groups were established: 21 pairs and 13 trios consisting of two sisters which were litter mates and a strange male. Groups containing three individuals were housed in two glass tanks (490 x 335 x 400mm), which were connected through a PVC- tube (110cm length, 4cm diameter).

This was done such that females had the choice whether to share one nest and rear their offspring communally or to use one tank for themselves and their offspring. Each glass tank contained a PVC – nest box (13 x 10 x 10,5cm). All females were weighted twice a week (Tuesday and Friday) to determine the reproductive status of each individual. Pairs were housed in 400 x 250 x 120mm macrolon cages (Labotec, Halfway House, South Africa). All cages and glass tanks were provided with hay and were cleaned weekly. Additionally, different kinds of pasteboards and branches were supplied to the cages to enrich the environment and to reduce stress in captivity.

To ensure that the environment was new to the individuals, all mice were placed simultaneously into the tank and their behaviour was recorded for 15 minutes. If no aggression was observed, all study animals remained together and pairing was regarded as successful.

2.4.2. Procedure

2.4.2.1. Triplets

Determination of Social Relationships

To differentiate between the three, female mice were individually marked with black hair dye (Inecto Rapid, South Africa). One female was marked on the head, whereas the other one received a black back. All individuals were observed three times in the mornings (6:30 – 9:30) and three times in the afternoon (17:00 – 19:00) for 15 minutes using scan sampling with continuous recording (MARTIN & BATESON, 1993).

The observed behaviour pattern was classified into three categories (see Tab. 2): (1) agonistic behaviour (chasing, biting, fighting, kicking, replacing), (2)

defensive behaviour (dodging, running away and being replaced) and (3) socio-positive behaviour (allo-grooming, sitting together (1. in body contact, 2. being in proximity of $< 5\text{cm}$)).

Development of Pups

Body mass, number and mortality of pups per female were determined during different stages of the pup's development (Day 0 = day of birth, Day 3 = pups are still in the nest, Day 10 = pups leaving the nest, Day 16 = pups are weaned). To differentiate between the pups of the two females, one group of pups was marked with "Gentian

Violet" at the tail, ("Gentian Violet" is purple and non-toxic). The second group (including the adults) was sham marked (with a dried "Gentian Violet" on a cotton bud), so that all the individuals (pups and adults) had the same smell, whereas only one litter was marked with colour (PILLAY, 2000). Since the colour faded quickly, the back fur of the marked litter was shaved of at Day 3 and Day 10. Thus, the observer was able to distinguish between the pups. Additionally all terrariums were checked for death pups daily. All pups were removed from the cage at Day 16 and were placed in a separate cage with their litter mates or were sacrificed with Fluothane (AstraZeneca Pharmaceuticals (Pty) Ltd.).

Parental and Allo – parental Care in Communal Nests

Sixteen observations per litter (scan sampling for 15 minutes, instantaneous recording after MARTIN & BATESON, 1993) were carried out to measure aggressive and amicable behaviour towards pups. The scan sampling method was chosen to distinguish the amount of shown behaviour between mothers, their sisters and the father. Thus a comparison between the three individuals was possible. Instantaneous recording turned out to be the best method as it was hard to keep track by using continuous recording. Observations were divided into four different stages concerning the age of offspring: Stage 1 (Day 0 – 3), Stage 2 (Day 4 – 6), Stage 3 (Day 7 – 10) and Stage 4 (Day 11 – 16). In each case two observations were performed in the morning and two in the

afternoon. Additionally, at Day 0 – 2 pups were removed from the nest and were placed in the tank not containing the nest. During this period the retrieval behaviour of mothers, their sisters and the males was recorded. Thus it was possible to determine who took an active part in the offspring care.

Both females of the triplet were allowed to give birth twice. If the females had produced two litters after three months, the experiment was terminated. Three months represented the duration of the natural breeding season (SCHRADIN & PILLAY, 2005c). After the last female gave birth for the second time, the most successful female in regard to survival of pups was chosen for a second experiment. If there was no difference between the siblings regarding reproductive success one female was chosen by chance. The chosen female was placed with the male in a cage and kept under the same conditions as pairs. Then this female gave birth again and one could compare her reproductive success when she was living in a trio or a pair. The other female was sacrificed (either with Fluothane or by cervical dislocation).

2.4.2.2. Pairs

The litter size and the body mass of pups was investigated during the first sixteen days of the pup's live (Day 0, 3, 10, 16; see above). Furthermore all cages were checked daily to determine the mortality in pups. All females were allowed to give birth twice. In some cases females didn't produce any litters after two months of pairing. Then the pair was separated and both individuals were kept alone in a cage for seven days. After this each individual was paired again with an unknown mouse. The experiments were terminated after 3 months, even if no second litter was produced by this time.

2.5. Definitions

Tab. 1 Terms used in this study (based on HAYES, 2000)

Term	Definition
Reproductive success (field study)	Number of offspring per female surviving from 10–35 days (35 days were chosen, as mice might disperse at an older age.)
Reproductive success (captivity study)	Number of offspring per female surviving the first 10 days
Singular breeder	One female and one male are responsible for producing all offspring
Plural breeder	Multiple females breed and rear their offspring in the same nest
Communal breeding	Multiple reproductively mature individuals breed and rear their offspring together; communal care is a condition for communal breeding
Communal nesting	Sharing of a single nest by several individuals

Female 1 (captivity)	Produced earlier offspring in comparison to her nest mate
Female 2 (captivity)	Delivered her pups in comparison to her sibling later
Breeding season	August – November
Non – Breeding season	December – July
Winter	June – July
Summer	November – May
Spring	August – October

Tab. 2 Behaviour

Behaviour between adults

Aggressive behaviour

Chasing	Follow an individual with high speed
Biting	The opponent was in general bitten on the back or tail
Replacing	Pushing the opponent from it's place
Fighting	Violent kicking, biting and wrestling behaviour
Kicking	Kick the opponent by using forepaws or hind legs

Defensive behaviour

Running away	The individual rapidly moves away from the chasing
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	or attacking animal
Being replaced	The animal was pushed away by the opponent
Dodging	By changing the location, the animal avoided contact with the opponent

Amicable behaviour

Allogrooming	An individual licked, wiped and nibbled the other animals' fur with forepaws and tongue
Sitting in proximity	The mice sat close together at a distance of less than 5cm
Sitting in body contact	The animals sat in body contact

Behaviour towards pups

Amicable behaviour

Licking	The individual licked the body of the pup
Sitting in body contact	An adult sat in body contact with a pup
Sitting in proximity	The adult sat close to a pup at a proximate distance of 5cm
Huddling	The individual huddled the pups by sitting over them
Retrieving	The animal carried the pup in its mouth to the nest
Nursing	The pups were attached to the nipples of the female
Grooming	An individual licked, wiped and nibbled pups' fur with forepaws and tongue
Spending time in nest	The mouse stayed with the pups in nest

Agonistic behaviour

Bite	In general the individual bit the pup in the neck; resulting in the death of the pup
Replace	The animal removed the pup from the nest

2.6. Statistics and Data Analysis

Over – winter survival probabilities

To test the occurrence of winter huddling groups, the ratio of family to non-kin groups of 2004 was compared with the ratio from 2003 (data from SCHRADIN & PILLAY, subm). For eleven females the home range size and the quality as well as the individual body mass and the group affiliation was tested concerning their

influences on survival probabilities. All data was collected in June (winter) and was provided from Dr. C. Schradin.

Social relationships within communal nests in captivity

Behavioural observations were performed in twelve communal nests. Socio – positive data (see Tab.2) shown by females towards their sisters and their males were evaluated. To avoid pseudoreplications one mean per siblings per nest (n= 12) and one mean per male per nest (n=12) were calculated and compared.

Reproduction

In order to test for synchronisation within communal groups, the time lag (in days) between births within social groups was compared to the population average (definition below), which would have been the time lag expected by chance. The two ratios were obtained and compared. Births, which were 23 days apart from each other (birth interval), were excluded from this analysis. In such cases one female was regarded as not have given birth for this period. Females that did not give birth (n= 3) were excluded. Altogether, data for 35 births from 17 females were available. The data of one female had to be excluded, because the date of her delivery could not be determined accurately.

1. Calculation of population average (PA)

For every birth event, the time difference (in days) to all other birth events in the population was determined (condition: All births must occur in a time slot of ± 23 days). From this, the average per birth event was taken. Additionally, for each female the average for all her births was taken (providing an average per female). Finally, the averages of all females were taken and divided by the number of female mice included in the analyses. This was the population average. The procedure avoided any pseudoreplications.

2. Calculation of group average (GA)

For each social group, the time intervals between all births that occurred in a time frame of ± 23 days were calculated. The average is the GA for this group. Calculating one value per group avoids pseudoreplications.

3. Calculation of solitary average (SA)

Births could also occur synchronously by chance, or because of ecological factors, which might affect the entire population. Thus for each solitary female the time intervals between all her births and the births of all other females that occurred in a time window of ± 23 days were calculated. The average is the SA for this female.

In captivity data of 59 births from 30 females were available. Seven pairwise housed females did not give birth at all. In one additional case the male was extremely aggressive towards his female after she gave birth, so this pair had to be separated. Six females housed in communal nests did not produce any offspring: In two cases both females and in two cases one female did not reproduce. Pairs and trios where all females did not give birth at all, were excluded from these analyses (pairs: $n=7$, trios: $n=2$).

Data on survival probabilities of pups of plural and singular breeders:

In the field study, the percentage of offspring and the number of offspring surviving until an age of 35 days was determined from the trapping data. 35 days were chosen, because some juveniles left their natal nest and emigrated around an age of six weeks (Brooks, 1982). Thus it was impossible to determine survival and therefore females' reproductive success at an older offspring age. To determine the percentage of offspring survival an average per communal nest was calculated and compared with that of singular breeders. Data of 64 juveniles was available.

One problem which all analyses on reproductive success had in common is that the litter size at birth could not be investigated accurately. In the field young mice started to emerge from the nest at the age of ten days. Thus the occurrence of pup mortality caused through predation, infanticide or any other event resulting in the death of young mice could not be determined within the first ten days of the pups' life. So the time interval from Day 10 until Day 35 was chosen as a measurement for reproductive success.

In captivity pup mortality rates were recorded until Day 10 of their life, the age when the young started to leave the nest to explore the environment. Thus accidents caused through environmental factors can be excluded regarding pup mortality rates.

Injuries could have resulted from terrarium covers, which were made out of wire. Additionally some pups managed to escape from the cage in the beginning. So it was impossible to determine survival probabilities of some trios at Day 16 of the pups' life. These females were included in the analysis by choosing the period until Day 10.

Furthermore the occurrence of infanticide within the communal nest and between singular breeders was determined. Dead pups without visible bite marks were excluded from the analysis for the reason that causes of mortality could not be determined accurately.

In captivity parental and allo – parental care was investigated in regard to the sex of the caregiver, the reproductive status (aunt or mother), the time of the day (morning or afternoon), the time alone in nest, the retrieval behaviour and the age of pups. Concerning the age of offspring, data were evaluated, when only one litter was present in the nest, since most litters of the two females were born several days apart from each other making an investigation regarding behaviour pattern during different ages of pups impossible. Data on behaviour differences of mothers, aunts and fathers between mornings and afternoons were transformed with *arcsin (square root)*.

All tests were scrutinized of normality (Shapiro – Wilk test) and performed two-tailed. According to data distribution either parametric or non – parametric tests were chosen. The Fisher's Exact Test was calculated using the software InStat (Demo version, GraphPad Software Inc.). All other tests were checked by the software SPSS (version 11.5, SPSS Inc.). Diagrams were drawn by using SigmaPlot 2000 (version 6.0; SPSS Inc.).

3 Results

3.1 Social Relationships within Communal Groups

Aggression was rarely noticed during behavioural observation. However two of thirteen communal groups had to be separated because of highly aggressive behaviour shown by one female. In one case aggression towards the sister occurred soon after pairing the siblings with an unfamiliar male. In the second case one female showed highly aggressive behaviour after the birth of her second litter towards her sister. The defensive female was not allowed in the terrarium containing the nest with the young anymore.

Males never took part in these interactions. In both cases it was observed that they tried to protect the defensive females. Male mice interrupted agonistic interactions by shielding and following the attacked female. In addition these males exhibited amicable behaviour (grooming) to a large extent towards the attacked female after aggressive interactions ended.

However agonistic behaviour was not noticed in the other trios. For this reason socio – positive interactions towards littermates and males by females were analysed. There was no difference concerning socio – positive behaviour shown by females towards their sisters and males (paired t – test: $n = 12$, $t = 1.691$, $df = 11$, $p = 0.119$, Fig. 1). Females were involved on average 7 ± 3 min/h, mean \pm standard deviation (SD), with their littermates and 5 ± 2 min/h with the male in socio–positive interactions.

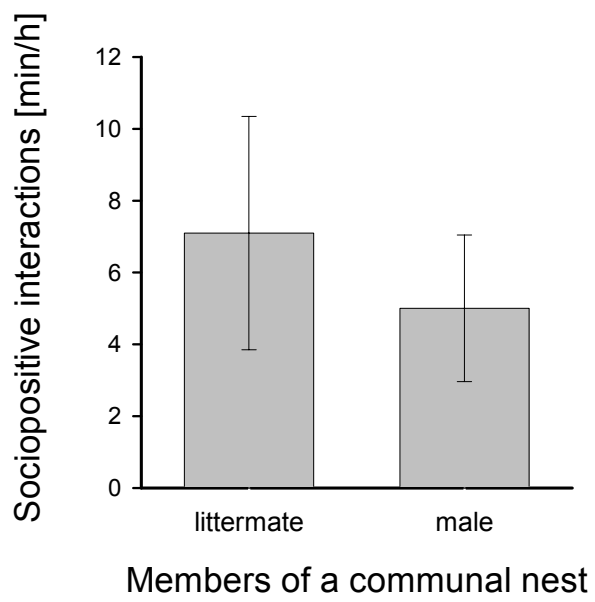


Fig. 1 Socio – positive interactions (mean \pm SD) of females towards their siblings and males ($p = 0.119$)

3.2. Over – winter Survival Probabilities

3.2.1. Nest Sharing and Thermoregulatory Benefits

In contrary to previous expectation mice did not form huddling groups with unfamiliar mice in wintertime. In addition the number of individuals sharing a sleeping place did not increase with decreasing of night temperatures. Thus mice lived in stable family groups with an average size of 3.8 individuals (range: 2 – 6). This was in contrast to sleeping associations of unrelated mice in 2003. In winter 2003, all 22 mice slept in huddling groups of unrelated individuals and affiliation changed from night to night (data from Schradin & Pillay, subm), while in wintertime 2004 most of the mice lived in family groups. Only three mice pursued a solitary lifestyle, but they did not form huddling groups with unfamiliar ones. Trapping data revealed that family groups consisted mainly of sisters and brothers or males, which immigrated into the group before June.

With the onset of breeding season all females and males became solitary in 2003, whereas group affiliation mostly remained constant in 2004. The social system switched from solitary to group living within one year in this population ($p < 0.001$, Tab. 3, Fisher's exact test).

Tab.3 Comparison of social systems between 2003 and 2004 at the start of breeding season

	Solitary mice	Group living mice
2003	n = 22	n = 0
2004	n = 3	n = 34

3.2.2. Ecological and Physiological Factors

The survival probability of an individual is determined by many factors. In the following body mass, group affiliation, home range size and food availability were analysed regarding their influence on individual survival probabilities. It was supposed that predation risks have the same effect on all studied animals. Seven females surviving and four female mice dying in winter were included in the analyses. Data of all aspects was collected in June.

There was no difference in home range sizes between surviving and non – surviving females (Fig. 2). Nevertheless a great variation of home range sizes of the surviving females is recognizable. Home range sizes were on average 0.24 ± 0.06 ha for non – surviving female mice and 0.25 ± 0.18 ha for surviving animals. The food availability, which was measured as percentage of points with food plants during plant surveys in winter did not significantly differ between individuals surviving till 1st of September and those dying before. However areas of surviving females were on average covered with 12.38% of food plants, whereas food availability was only 9.03% in home ranges of non – surviving individuals.

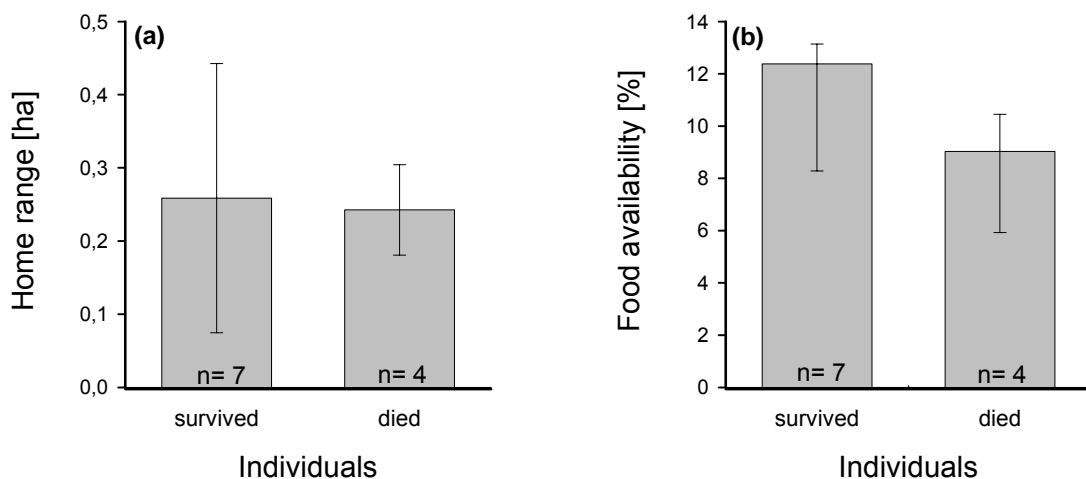


Fig. 2 Home range size and food availability of females that survived till 1st of September and those that died during winter time: **(a) Home range size** (mean \pm SD): Mann Whitney U – test: $Z = -0.189$, $p = 0.850$

(b) Food availability (median, percentiles): Mann Whitney U – test:
 $Z = -1.134$, $p = 0.313$

Individual physiological condition, measured as body mass did not differ between female mice that survived till 1st of September and those that died during wintertime ($p = 0.788$, Fig 3a). The average weight for surviving females was $37.1 \pm 6.5\text{g}$ and for non – surviving individuals $37.0 \pm 8.9\text{g}$.

Furthermore an influence of group size in regard to survival probabilities of female mice could not be determined ($p = 0.648$, Fig. 3b). Groups of individuals that died during the winter consisted on average of 5.5 ± 1.5 mice, whereas the average group size of surviving female was 5.0 ± 1.5 members.

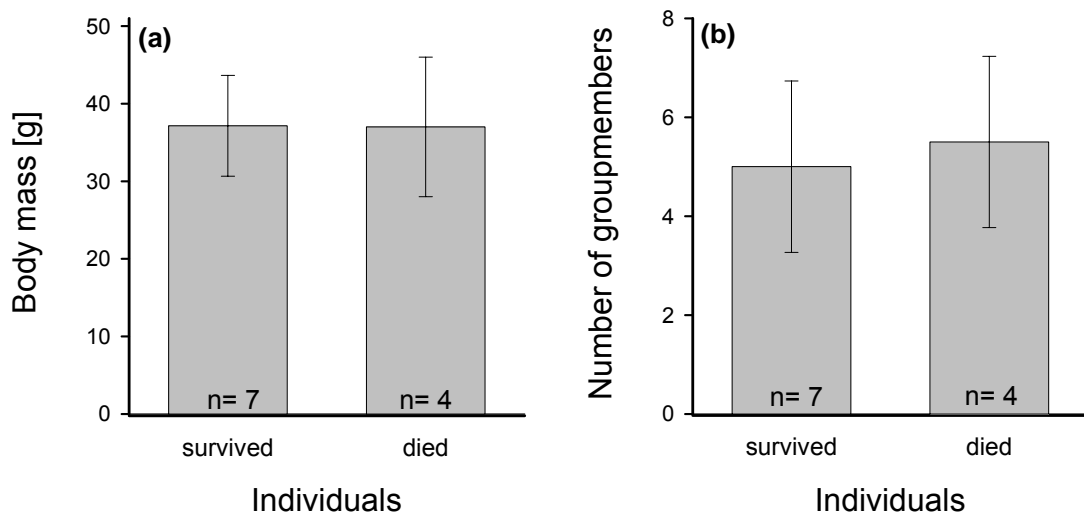


Fig. 3 Body mass (mean \pm SD) of individual weight and number of members within a family group in regard to survival probabilities of an individual:
(a) Number of group members: Mann Whitney U – test: $Z = -0.592$, $p = 0.648$ **(b) Individual body mass:** Mann Whitney U – test: $Z = -0.284$, $p = 0.788$

3.3. Reproduction in the field

3.3.1. *Time Lag between Births within Social Groups and in Comparison with Singular Breeders*

The time lag of births within a communal nest (one average for each communal group) and for each group of singular breeder was compared with the population average (10 days). Births of communal breeding females were highly synchronized (average 2.5 day, range: 0 – 9 days) while singular breeders had an average time lag of 11 days (range: 9 – 12 days).

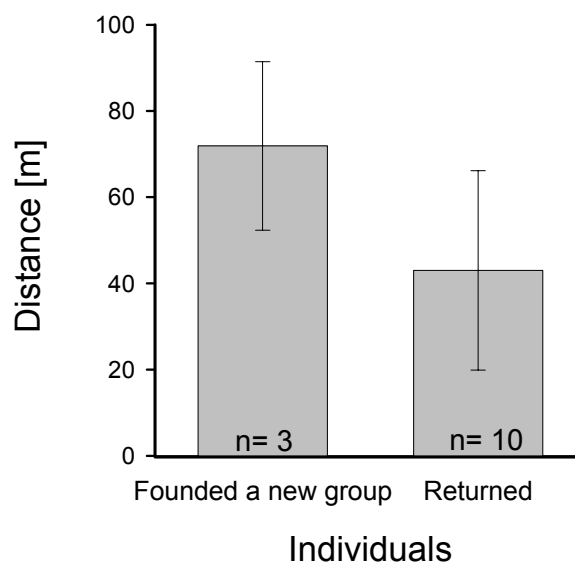
Tab.4 Births that occur synchronously or not synchronously concerning the population average (Fisher's exact test: $p = 0.015$)

	Birth interval > PA (not synchronously)	Birth interval < PA (births occur synchronously)
Within groups (n =5)	0	5
Singular breeders (n = 7)	6	1

3.3.2. Communal Breeding Societies

The main aim of this project was to study reproductive strategies in the striped mouse with giving special attention to communal breeders. Data from the last year revealed that females nesting communally were related, i.e. sister, half – sisters or mother – daughter units. Communal nests mostly contained of half sisters, i.e. females had the same mother. In one case two littermates nested communally with other half – sisters and in one case a mother nested with their two daughters. Fourteen females were identified as a member of a communal nest. During the breeding season most communally nesting females left their original nest approximately 2 ± 1 days before giving birth. Data of twenty births from eleven communal nesting females were available. In fifteen cases females left their original nest to deliver their pups in temporary nesting sites. However in ten out of fifteen cases females returned to their communal nest again, whereas five founded new groups. Females leaving their nest stayed on average eight days away from their group ($n = 9$, range: 3 – 12 days) and it was observed in two cases that mothers retrieved their newborn pups to the communal nest. Furthermore most females stayed in their original area with a mean distance of 49.7m (range: 14.8 – 92.7m, $n = 13$) from the communal nest. Although females founding new groups dispersed farther away from the communal nest (71.9 ± 20 m), the difference was not significant regarding the distance from the communal nest between females which returned to their group and those which founded new once (Mann Whitney U – test: $Z = -1.693$, $p = 0.91$; Fig. 4).

Fig. 4 Distance from the communal nest to the “birth nest” between females, which founded new groups, pursuing a singular breeder strategy and those which returned to their original nest.
(mean \pm SD)



3.3.3. Plural versus Singular Breeders: Reproductive Success

Since litter size could not be determined within the first ten days, reproductive success had to be defined as survival of offspring from Day 10 till Day 35 (see data analysis).

The number and the survival probabilities in percentage of juveniles did not differ between females pursuing a singular breeder strategy and those which were a member of a communal nest (number of pups: Mann Whitney U – test: $Z = -0.221$, $p = 0.825$, Fig. 5; percentage of offspring survival: Mann – Whitney U – Test, $Z = -1.465$, $p = 0.143$, Fig 6). On average 3.0 ± 1.8 pups growing up in a communal nest reached the age of 35 days, whereas 2.75 ± 0.9 pups of singular breeding nests survived the first 35 days. In singular nests on average 98.0% (range: 75.0 – 100.0%) pups survived till an age of 35 days. In contrast on average only 81.0% (range: 33.3 – 100.0%) of young mice survived till day 35 of communally nesting females.

Three females from three different communal nests were not producing any offspring at all. These females shared a nest with two to three conspecifics.

In one case both females of a communal nest died soon after the delivery of their first litter making a distinction in regard to pup survival rates impossible. Thus this communal nest and the mentioned females not reproducing were excluded from all analyses.

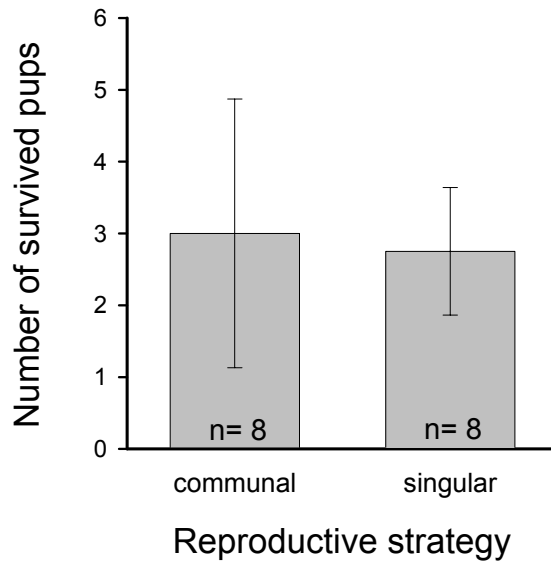
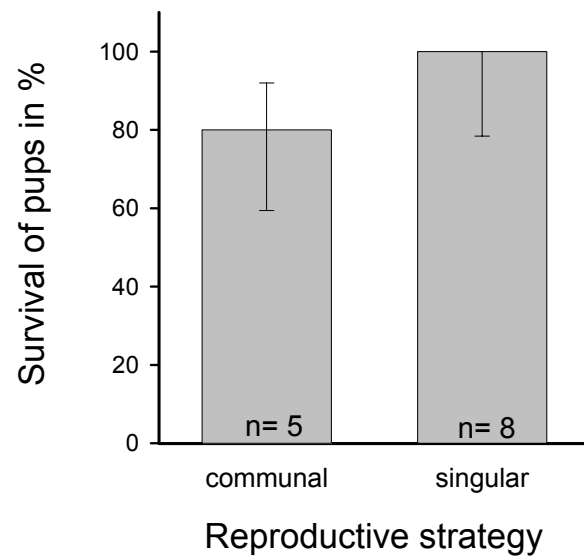


Fig. 5 Number of pups (mean ± SD) surviving till Day 35 between singular breeders and females of a communal nest ($p = 0.825$)

Fig. 6 Reproductive success (median ± percentiles) between singular and communal nesting females ($p = 0.289$) An average was calculated for every plural breeding groups



3.3.4. Pup Survival and Ecological Situation

In this analysis the influence of ecological factors in regard to pup survival probabilities was tested. There was no correlation between pup survival and home range size of the mothers (Spearman – rank – correlation: $n = 14$, $r_s = -0.201$, $p = 0.491$; Fig. 7a) Furthermore the survival probabilities of young mice was not correlated with the dissemination of ephemerals (Spearman – rank – correlation: $n = 12$, $r_s = -0.102$, $p = 0.752$; Fig. 7b).

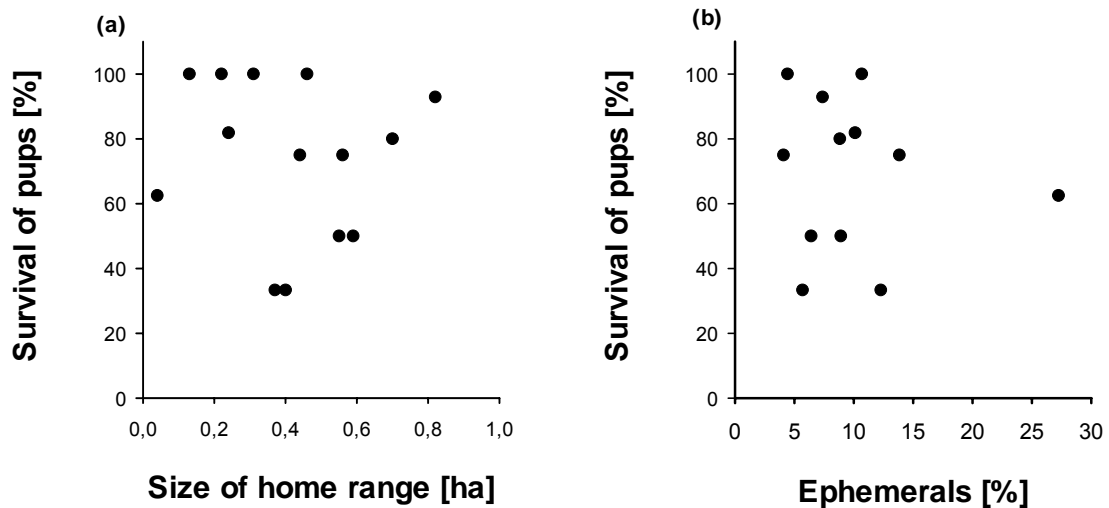
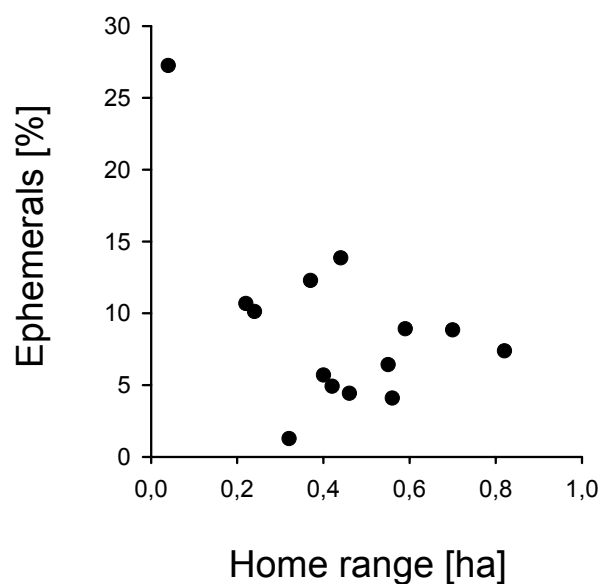


Fig. 7 Coherence of (a) home range size and (b) dissemination of ephemerals concerning pup survival probabilities

Moreover the dissemination of highly nutritious plants did not correlate with home range size of females (Spearman – rank – correlation: $n = 14$, $r_s = -0.336$, $p = 0.240$, Fig. 8). Home ranges were on average 0.4 ± 0.2 ha and covered with 9.0% (range: $1.27 - 27.24\%$) of ephemerals.

Fig. 8 Home range size and dissemination of ephemerals ($p = 0.240$)



3.3.5. *Young Individuals and Reproduction*

Trapping data revealed that some juveniles became reproductively active in the same year they were born. It was determined, whether there was a relationship between time of birth and sexual maturity.

Individuals born early in breeding season (August/September) were much more likely to become reproductively active than individuals born in October or November (females: Fisher's exact test: $p = 0.001$, Tab. 6; males: Fisher's exact test: $p < 0.001$, Tab. 7)

Tab. 6 Reproductive and non – reproductive females and their date of birth

FEMALES (n = 23)	Reproductive active	Not reproductive active
Born in August/September	13	2
Born in October/November	1	7

Tab. 7 Reproductive and non – reproductive males and their date of birth

<i>MALES (n = 43)</i>	Reproductive active	Not reproductive active
Born in August/September	28	4
Born in October/November	2	9

No difference between the sexes was evident regarding dispersal or philopatric behaviour (Fisher's exact test: $p = 0.681$, Tab. 8). But significant more individuals remained philopatric than dispersed (Binominal test: females: $p = 0.008$; males: $p = 0.010$, Tab. 8). Several young females started to breed communally with their mothers in the natal nest.

Tab. 8 Comparison of individual that dispersed and those staying at their natal nest

	Left natal nest	Stayed in natal area
Females	n = 2	n = 13
Males	n = 5	n = 18

All dispersing individuals were born in August or in early September and left home at the age of approximately eight to twelve weeks. Additionally fourteen new males and two new females which immigrated into the study grid were trapped. All new individuals were born during this breeding season and were, with the exception of two males,

sexually mature. This indicates that dispersal occurs in the striped mouse and that more males emigrated than females.

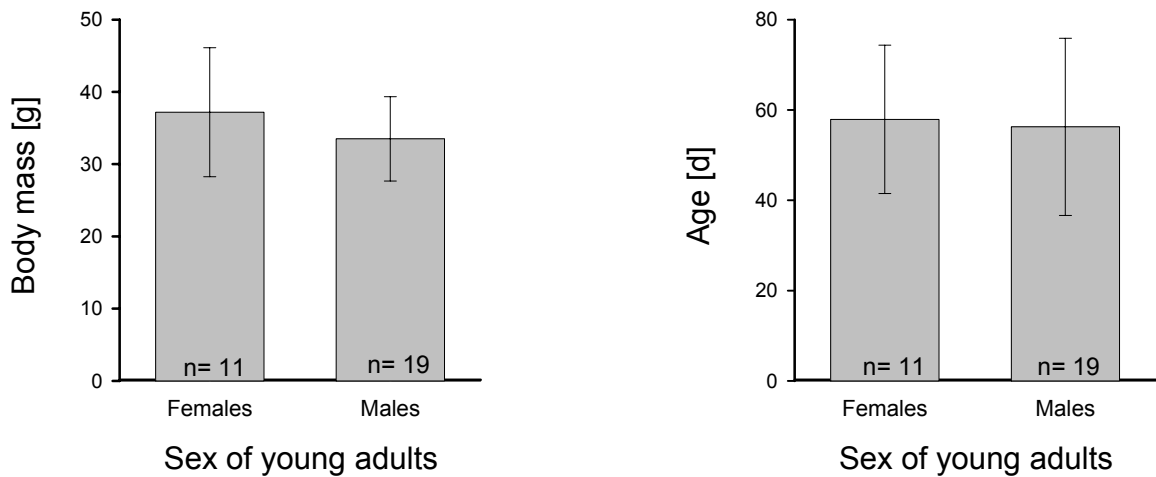


Fig. 9 Body mass and age of sexual maturity of females and males (mean \pm SD):

(a) Body mass: t – test for independent samples: $t= 1.226$, $df= 28$, $p= 0.239$;

(b) Age: t – test for independent samples: $t= 0.234$, $df= 28$, $p= 0.817$

There is no evident difference regarding age and body mass of sexual maturity between young males and females. Both sexes reached sexual maturity at an age of approximately eight weeks and with a body mass of 33 – 37g.

3.3.6. Home Range Size and Quality in two Seasons

Home range sizes were significantly greater during springtime (breeding season) than in winter (non-breeding season) (t – test for independent samples: $t = 2.073$, $df = 26$, $p = 0.048$, Fig. 10). In winter home range sizes were on average 0.27 ± 0.15 ha, whereas in springtime 0.4 ± 0.2 ha. In addition home range sizes of seven females could be determined in winter and in spring. Females significantly increased their home ranges during breeding season (Wilcoxon test: $n = 7$, $Z = -2.028$, $p = 0.043$, Fig. 11).

Fig.10 Home range size in breeding and non – breeding season (mean \pm SD)

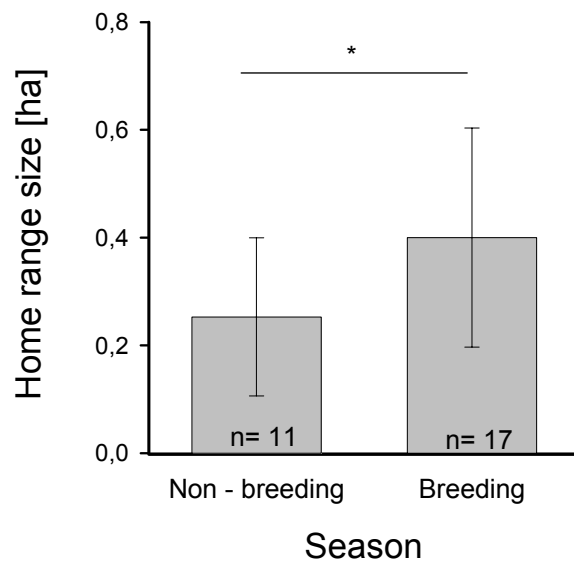


Fig. 11 Home range sizes of seven females in breeding and non – breeding season. Mean and raw data are presented in the figure. Raw data of each female are connected by a stroke.

Furthermore significantly more food was available during breeding season than in non – breeding season (t – test for independent samples: $t = 6.135$, $df = 23$, $p \leq 0.001$, Fig. 12). Again, data of seven females was available regarding their food supply in the breeding and in the non–breeding season. Food availability significantly increased during breeding season (Wilcoxon test: $n = 7$, $Z = -2.366$, $p = 0.018$, Fig. 13).

However food availability increased as a consequence of home range enlargements. No difference between winter and spring occurred when determining the percentage of food per ha (Wilcoxon test: $n = 7$, $Z = -0.507$, $p = 0.612$).

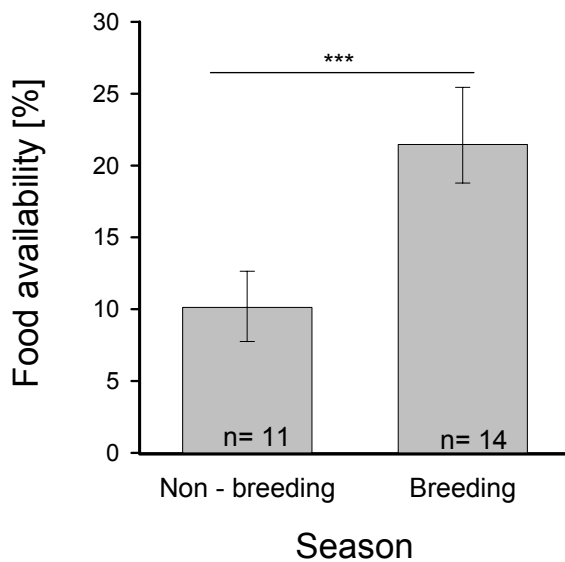
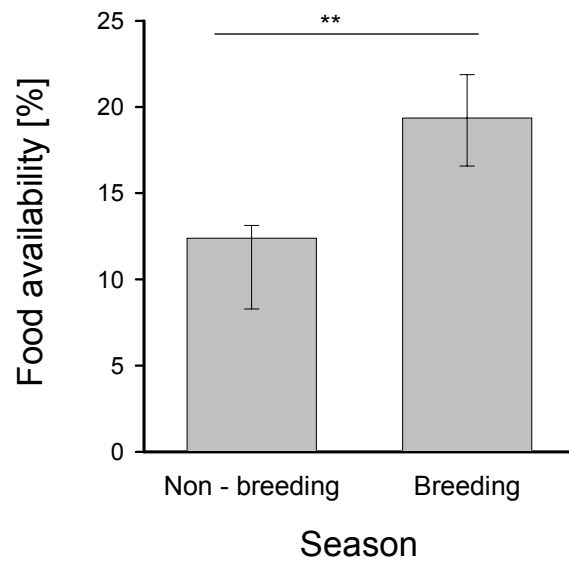


Fig. 12 Food availability in winter (non – breeding season) and spring (breeding season) (median \pm percentiles)

Fig. 13 Food availability (median \pm percentiles) of seven females in breeding and non - breeding season



There was no difference in regard to food dissemination and home range size in winter (Spearman - rank - correlation: $n = 11$, $r_s = -0.424$, $p = 0.194$, Fig. 14a) and spring (Spearman - rank - correlation: $n = 14$, $r_s = -0.51$, $p = 0.864$, Fig. 14b).

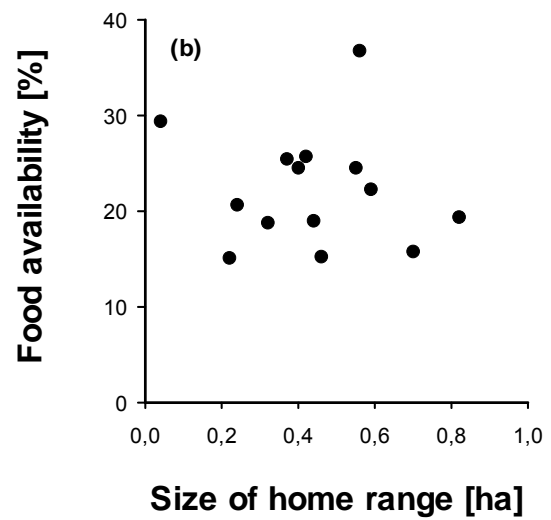
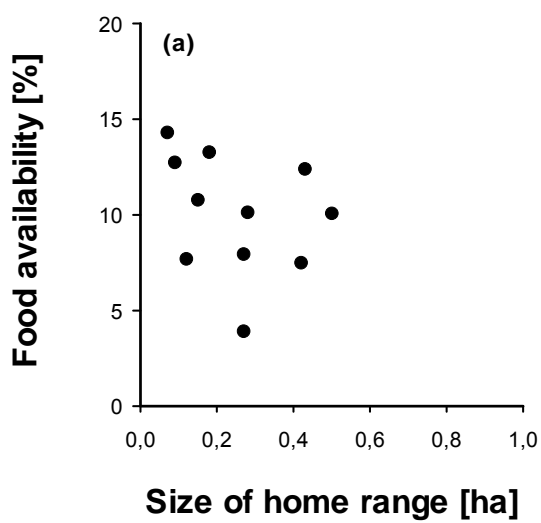


Fig. 14 Comparison of home range size and food availability
(a) in **winter** (non – breeding season) **(b)** in **spring** (breeding season)

3.4. Reproduction – Captivity Study

3.4.1. Time Lag between Births within Communal Nests in Comparison to Singular Breeders

The time lag of births within a communal nest (one average for each communal group) and for each singular breeder was compared with the population average. In captivity the population average was ten days. The average time lag of births was eleven days (range: 9.5 – 13.5 days) for singular breeders and for communal breeders seven days (range: 0.5 – 13 days). No difference between singular and plural breeding females concerning the synchronization of births occurred (Fisher's exact test: $p= 0.206$, Tab. 9). In 62.5% the delivery of pups was synchronized within the communal nest; in 46.15% births of singular breeders occurred synchronized in regard to the population average.

Tab. 9 Births that occurred more synchronized concerning the population average

	Birth interval > PA (births were not synchronized)	Birth interval < PA (births occur synchronized)
Within groups	n = 3	n = 5
Singular breeders	n = 13	n = 6

Trios were housed in two terrariums, which were connected by a plastic tube. The background for this experimental housing was, that females should have the opportunity to nest and rear their offspring alone (one tank of each female), if they wanted to. Pregnant females never “dispersed” to the other tank not containing the communal nest to give birth. Furthermore communal breeding females mixed their offspring together in one nest, even if the young had a different age. From time to time the whole group participated in the construction of a new nest. Then the old nest was left and the whole group settled down in the new one.

3.4.2. Communal versus Singular Breeding: Reproductive Success

Primiparous females are known to have smaller litters. However litter sizes of first and second litters of females did not differ concerning their sizes (t – test for independent samples: $t = -0.577$, $df = 46$, $p = 0.567$). Therefore both litters were included in the analysis. Pairs trios and females of a communal nest not producing any offspring were excluded in the analyses (females nesting communally: $n = 2$, trios: $n = 2$, pairs: $n = 7$). Reproductive success of females was defined as pup survival from day 0 – 10 (see data analyses).

Litter sizes of females breeding communally did not differ from females housed under singular breeding conditions (Mann Whitney U – test: $Z = -1.173$,

$p = 0.241$, Fig. 15). The mean score of litter sizes in pairs was 5.9 ± 2.1 pups and 5.39 ± 1.82 young mice in communal nests.

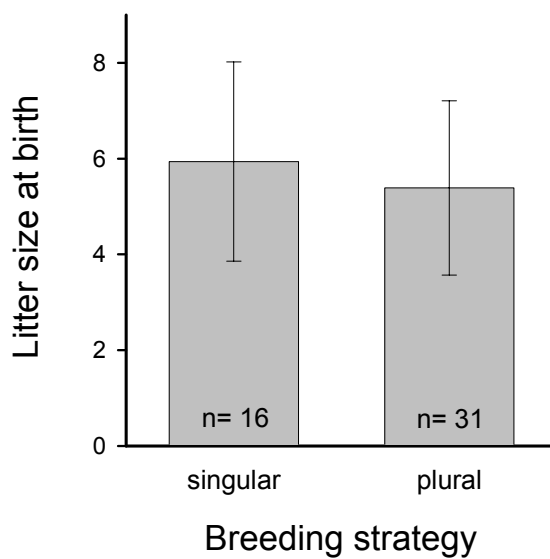


Fig. 15 Litter sizes (mean \pm SD) at birth of communal and singular breeders ($p = 0.241$)

The number of pups surviving the first ten days of life did not differ between singular and communal breeding females (t – test for independent samples: $t = 1.471$, $df = 26$, $p = 0.153$, Fig. 16).

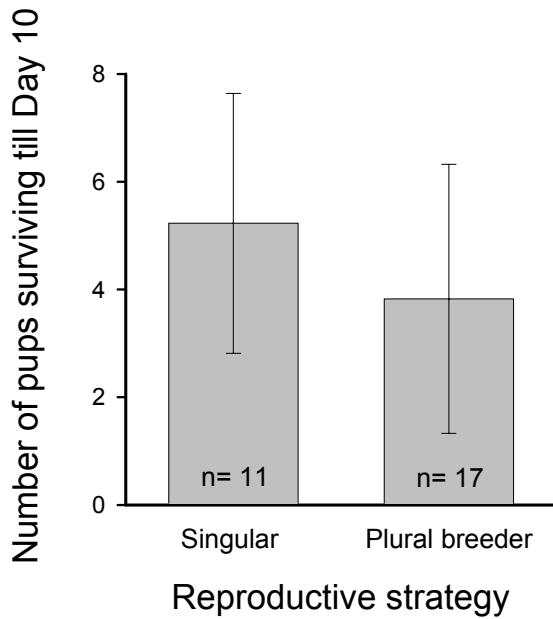
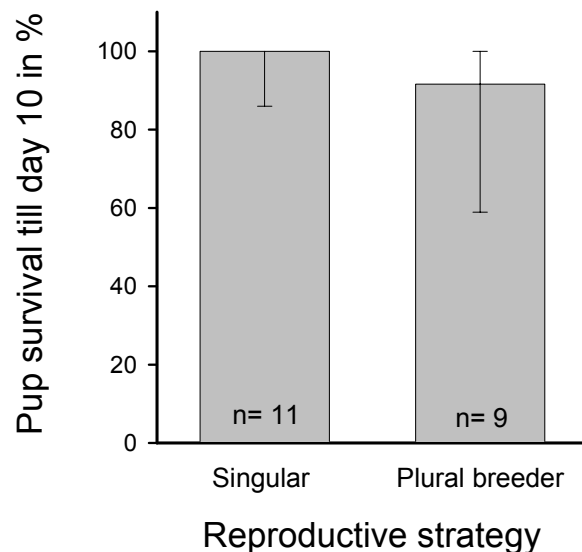


Fig. 16 Number of surviving pups in regard to the breeding strategy of the mother
An average for each female was calculated. Mean \pm SD are presented in the figure

Pup survival probabilities during the first ten days did not differ between communal and singular nests (one mean value per communal nest; Mann Whitney U – test: $Z = -1.218, p = 0.223$, Fig. 17). In singular nests on average 100% (range: 50 – 100%) of pups survived the first ten days, whereas 90% (range: 0 – 100%) of offspring survived in communal nests.

Fig. 17 Pup survival probabilities in communal and singular breeder nests ($p = 0.223$)
For communal nests one average was calculated
Median \pm percentiles are presented in this figure



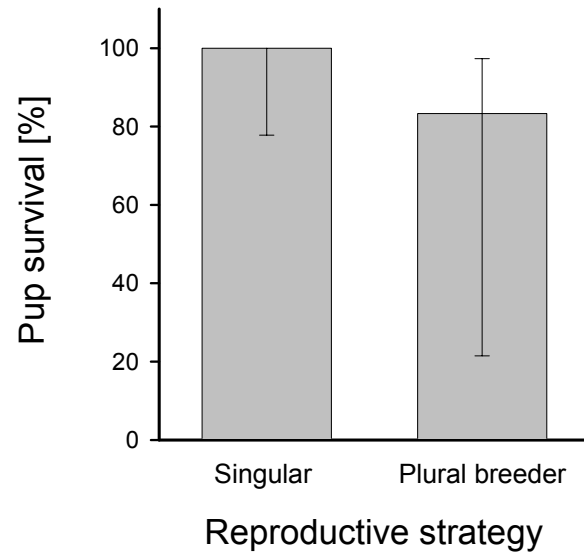
In several cases pups were found death in the terrarium. The death was often caused through biting in the head. This indicates infanticidal behaviour. Pups were eaten or half eaten or laid death inside or outside the nest. In two cases communal nesting females, which were both mothers at this time, killed a pup. After the killing, the young was eaten by both of them and other offspring. However infanticidal behaviour was not only restricted to communal breeding societies; it also occurred in pairs. Although infanticide was more common in communal breeding societies no significant difference was noticed (Fisher's exact test: $p = 0.072$, Tab. 10). When infanticide took place in singular breeding nests all pups of one litter were killed. In contrast, in communal nests the whole litter was killed in only 3 cases; in the other 6 cases 1 – 4 pups (2 ± 1.4) were victimized by perpetrators.

Tab. 10 Occurrence of infanticide from pups of singular and plural breeders ($p = 0.072$)

	Infanticide occurred	No infanticide was noticed
Singular breeder	n = 3	n = 11
Plural breeder	n = 9	n = 7

In addition five females housed under communal conditions in the beginning were separated from their sisters after the experiment and housed with the male under singular breeder conditions. These females did not have a greater reproductive success when housed only with their male (Wilcoxon test: $n = 5$, $Z = -0.730$, $p = 0.465$, Fig. 20).

Fig. 20 Pup survival probabilities (till Day 10) under singular and plural breeding conditions (median

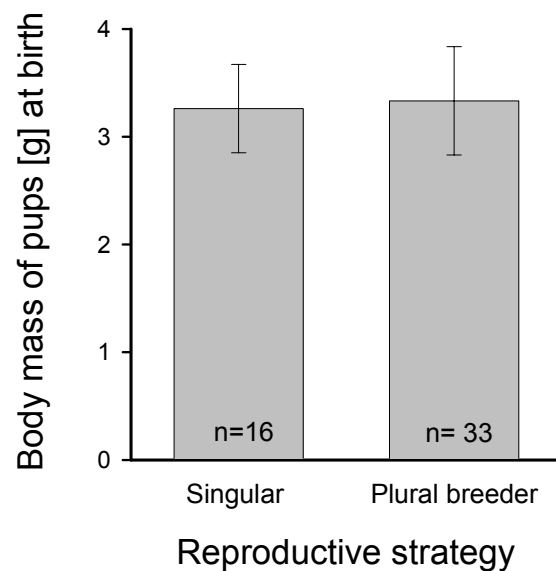


3.4.3. Body Mass of Pups

There was no difference concerning the body mass at birth between pups of singular and plural breeding females (t – test for independent samples: $t = -0.496$; $df = 47$; $p = 0.622$, Fig. 21). Pups from communal nests weighted on average $3.3 \pm 0.5g$, offspring from singular breeders $3.2 \pm 0.4g$. Moreover body

mass at birth was negatively correlated with litter size (Pearson correlation: $n = 46$, $r = -0.382$, $p = 0.009$, Fig. 22): Pups from small litters were heavier than those born in larger ones. Weight gain of pups from larger litters and in regard to the breeding strategy of their mothers did not differ during the first 16 days of pups' lives (Tab. 11). Nevertheless litter size and not breeding strategy of juveniles' mothers influenced body mass significantly at Day 16 (Tab. 12). Body mass of offspring was negatively correlated with litter size at weaning age (Pearson correlation: $n = 31$, $r = -0.386$, $p = 0.032$).

Fig. 21 Body mass of pups at birth from singular and plural breeding females ($p = 0.622$) Mean and standard deviation are presented in this figure



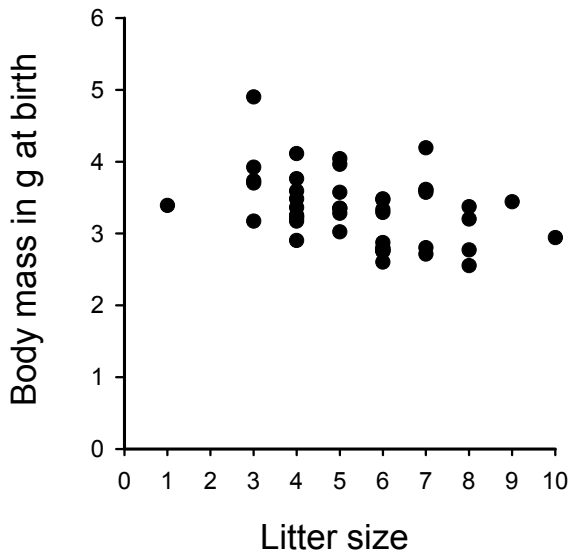


Fig. 22 Correlation of litter size (number of pups) and body mass at birth ($p = 0.009$)

Tab. 11 Comparison of weight gain in various categories (Day 0–3, Day 4–10, Day 11–16) between singular ($n = 11$) and plural breeders ($n = 16$) considering litter size (*two – way ANOVA for repeated measurements*)

Factor	<i>df</i>	Mean Square	<i>F</i>	<i>p</i>
Weight gain	1.564	6.409	6.685	0.006
Weight gain * breeding strategy	1.564	0.203	0.212	0.755
Weight gain * litter size	1.564	0.365	0.381	0.634
Litter size	1	2.589	2.519	0.126
Breeding strategy	1	3.441	3.349	0.080

Tab. 12 Body mass of juveniles at Day 16 concerning the breeding strategy of mothers (covariate litter size) (*two – way ANOVA* ($n_{\text{singular}} = 11$, $n_{\text{plural}} = 16$))

Factor	<i>df</i>	Mean Square	<i>F</i>	<i>p</i>
Body mass * litter size	1	24.748	5.199	0.030
Body mass * breeding strategy	1	4,76	0.75	0.394

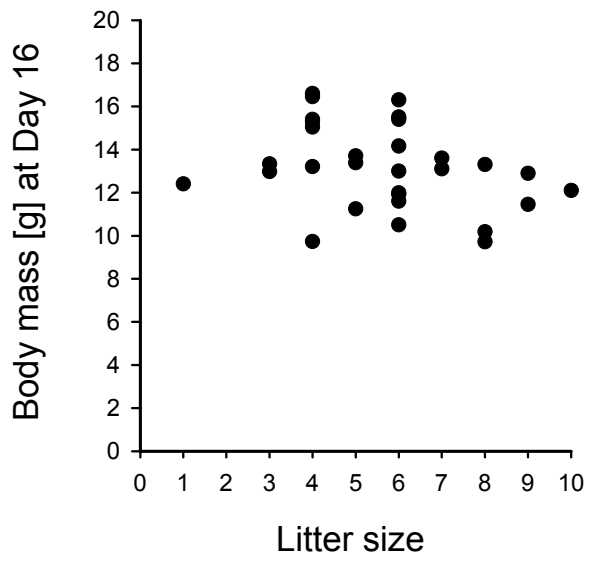
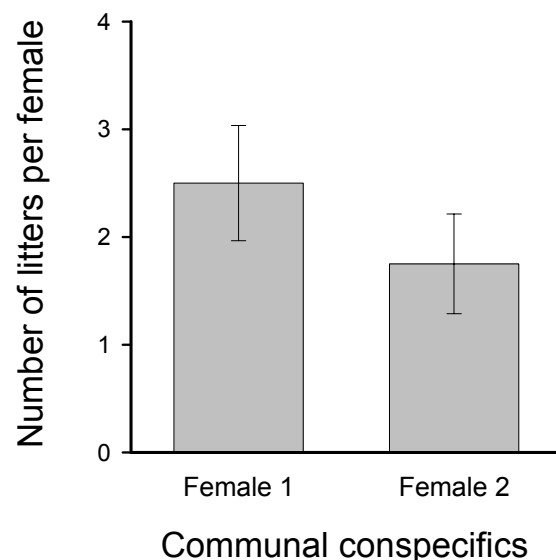


Fig. 23 Body mass of juveniles in g in correlation to litter size ($p = 0.032$)

3.4.4. Reproduction of Littermates

Mothers having offspring first, in comparison to their sibling, produced more litters (Wilcoxon test: $n = 8$, $Z = -1.857$, $p = 0.063$, Fig. 23). Females reproducing first had a mean score of 2.5 ± 0.5 litters. In contrast female mice which became reproductively active after their sister had on average only 1.75 ± 0.5 litters. Furthermore a tendency of greater survival probabilities of pups born to first mothers was obvious in comparison to pups of females producing later (Wilcoxon test: $Z = -1.604$, $p = 0.103$, $n = 7$, Fig. 24). The mean score for survival probabilities of young mice from mothers reproducing first was 97% (range: 0 – 100%) and 65% (0 – 100%) for pups from second mothers. The number of killed pups by infanticide did not significantly differ between females reproducing first and females reproducing second (Wilcoxon test: $Z = -1.633$, $p = 0.102$, $n = 6$, Fig. 25). However a tendency is noticeable. On average 1.7 ± 3.2 pups of females delivering first were victimized by adult individuals. In contrary 3 ± 3.5 pups of the second female were killed.

Fig. 23 Number of litters (mean \pm SD) of females giving birth first (female 1) within a communal nest and those delivering their offspring later (female 2) ($p = 0.063$)



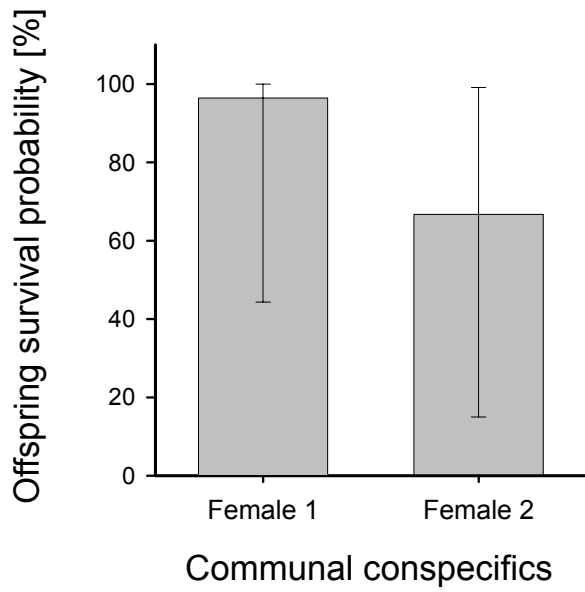
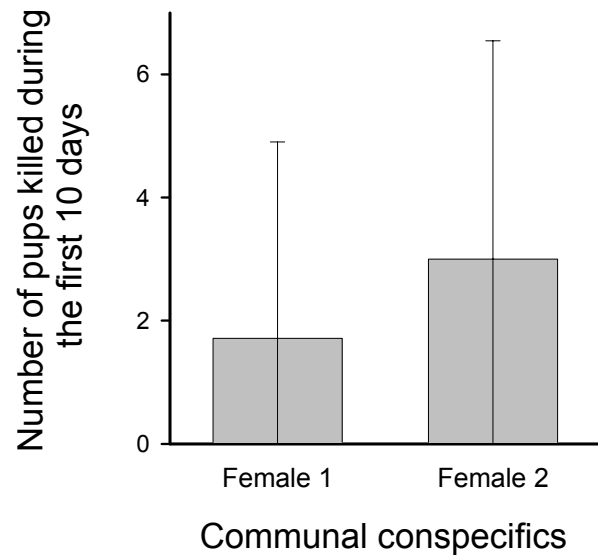


Fig. 24 Pup survival probabilities of mothers that delivered their offspring first (female 1) and in comparison to her sister (female 2) (median \pm percentiles) ($p = 0.103$)

Fig. 25 Number of killed pups of females reproducing first and their siblings ($p = 0.102$) Mean \pm SD are presented in this figure



3.4.5. Parental and Allo – parental Care in Communal Nests



All members of a communal nest participated in the care of the offspring. However females exhibited significant more amicable behaviour towards pups (t – test for independent samples: $t = 2.109$, $df = 19$, $p = 0.048$, Fig. 26). Females participated on average 41% (range: 31.58

– 68.67%) during behavioural observation in the care of young. The mean score of amicable behaviour during observation was 26.5% (range: 14.27 – 56.27%) for males. Although no significant difference regarding amicable behaviour towards pups between mothers and aunts was noticed, females which had pups participated more in the care of the offspring (Wilcoxon test: $n = 7$, $Z = -1.859$, $p = 0.063$, Fig. 27) The mean score for mothers was 28.1% (range: 19.1 – 39.6%) and 20.8% (range: 17.2 – 30.8%) for aunts.

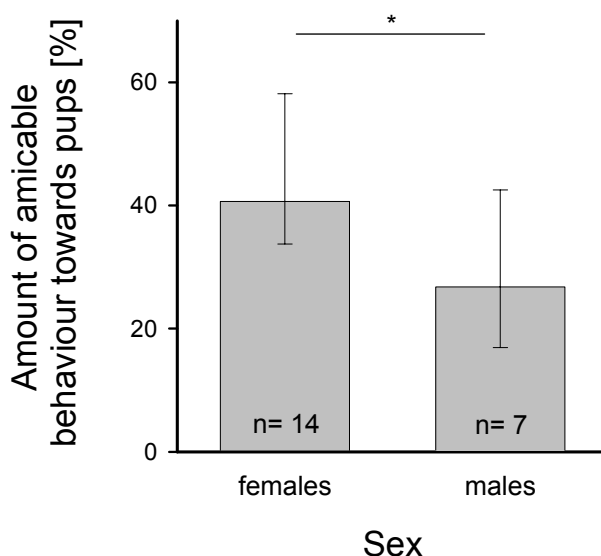
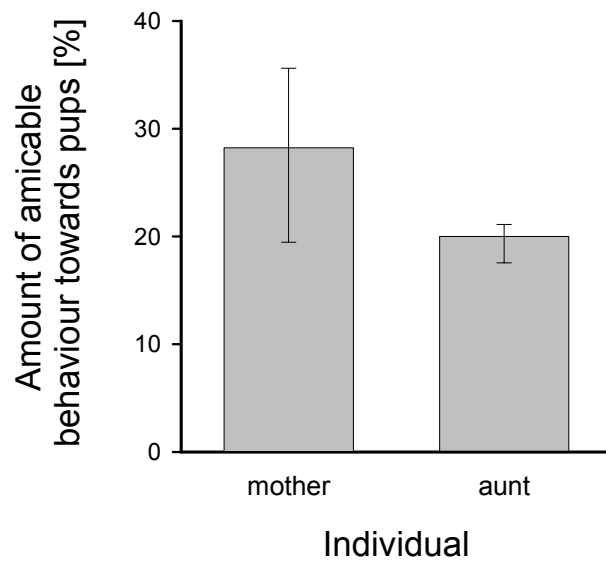


Fig. 26 Care of care during behavioural observation in regard to the sex of the caregiver (median \pm percentiles)

Fig. 27 Amicable behaviour towards pups exhibited by mothers and aunts ($p = 0.063$)
Median \pm percentiles are presented in this figure



3.4.6. Care of Adults concerning different Ages of Pups

Communal care was defined as any behaviour, which was beneficial for the



offspring, e.g. licking, huddling, nursing, grooming, retrieving to the nest, spending time in the nest, sitting in body contact or proximity (see methods Tab.2). Some mothers were observed to nurse own and offspring of her sister. However in several cases it was impossible to distinguish between huddling

and nursing of pups in females, because pups were mostly hidden under the belly. Thus the observer classified this behaviour as huddling/nursing. For this reason all care giving behaviour towards pups was summarized and then evaluated.

Mothers participated significantly more in the care of the offspring and during the first three days in comparison to Day 4 – 6 ($p = 0.013$, Fig. 28). The mean score of amicable behaviour shown by mothers during behavioural observation was 32.81% (range: 17.17 – 52.0%) in the first three days. Mothers exhibited on average 15.58% (range: 0.25 – 33.0%) in the care of the offspring during Day 4 – 6. During Day 7 – 10 the mean score of parental behaviour by mothers in behavioural observations was 24.25% (range: 3.25 – 40.38%) and 30.47% (range: 11.0 – 61.75%) during Day 11–16.

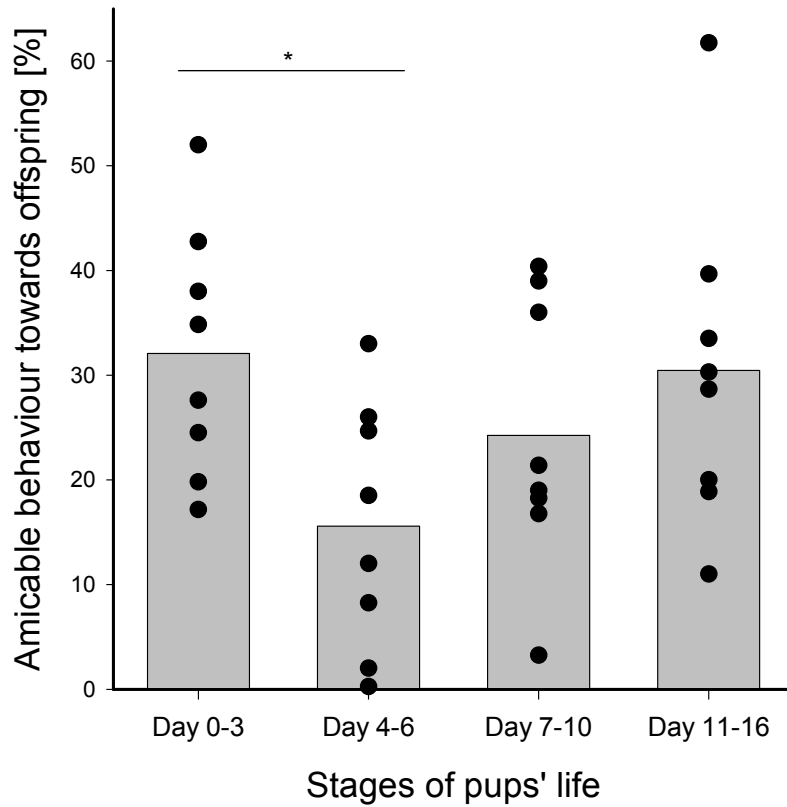


Fig. 28 Parental care of **mothers** concerning different ages of the offspring (ANOVA for repeated measurements: $n = 8$, $df = 3$, $\chi^2 = 10.8$, $p = 0.013$, post hoc: Tukey Kramer test) Mean and raw data of females are presented in this figure.

There was no difference regarding amicable behaviour towards the sister's offspring exhibited by aunts in various life stages of the pups' life (Friedman test: $n = 6$, $\chi^2 = 5$, $df = 3$, $p = 0.172$, Fig. 29). But a great individual variation is obvious.

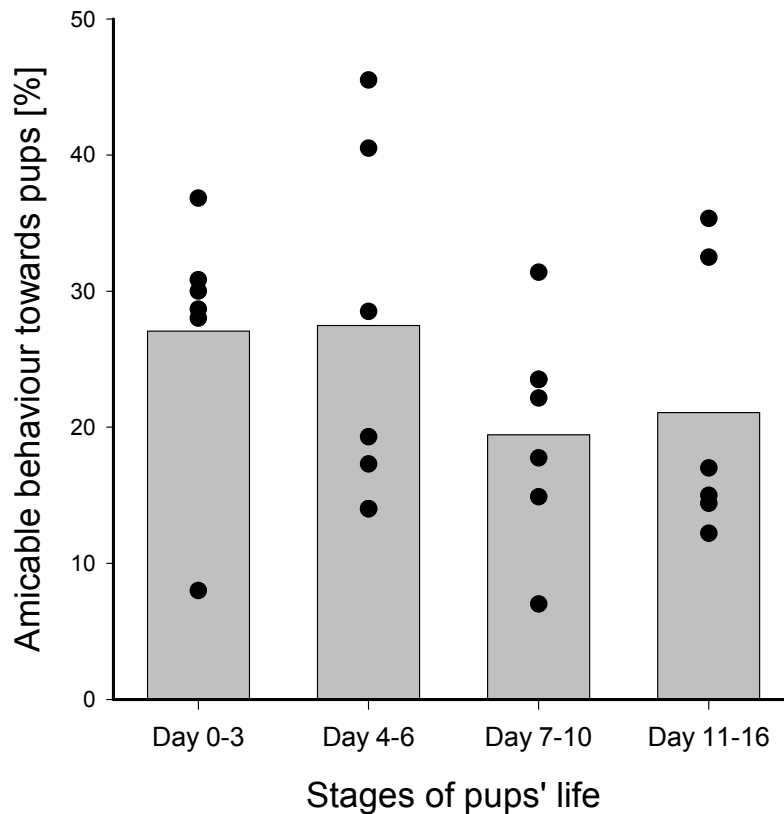


Fig. 29 Allo – parental care of **aunts** regarding different ages of offspring Mean and raw data of six aunts are presented in this figure

Paternal care did not differ concerning different ages of offspring (Friedman test: $n = 7$, $\chi^2 = 2.3$, $df = 3$, $p = 0.495$, Fig. 30). However some fathers participated in the care of offspring to a great extent while others exhibited less amicable behaviour towards their offspring.

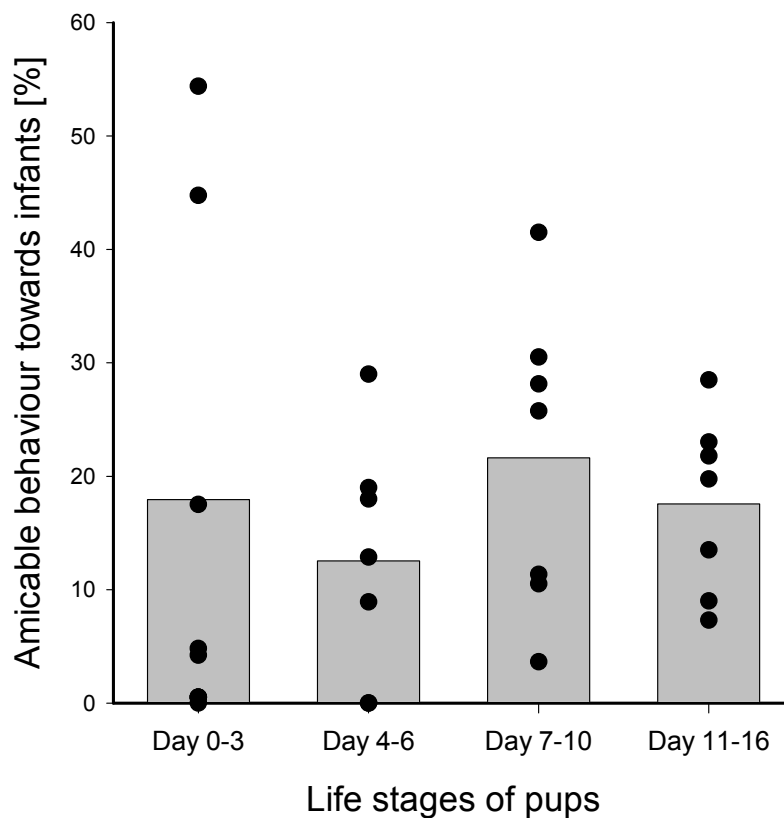


Fig. 30 Paternal care of **fathers** in regard to various ages of his young
Mean and raw data of seven fathers are presented in the figure

3.4.7. Care in the Morning and Afternoon

All adults of a communal nest participated more in the care of the offspring in the mornings than in the afternoon. Mothers and aunts exhibited significantly more care in the mornings (Fig. 31, Fig. 32). A tendency for males was recognizable (Fig. 33).

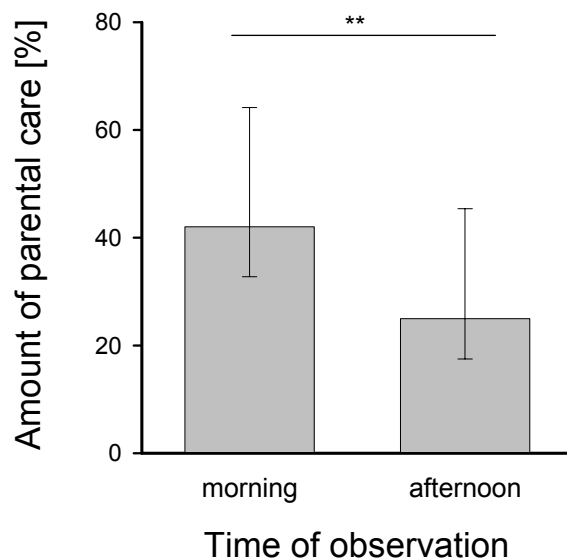


Fig. 31 Behaviour of mothers towards pups in the morning and afternoon (median \pm percentiles) (paired t -test: $n = 10$, $t = 3.820$, $df = 9$, $p = 0.004$)

Fig. 32 Behaviour of aunts towards the young in the morning and afternoon (paired t - test: $n = 8$, $t = 3.102$, $df = 7$, $p = 0.017$)
Median \pm percentile are presented in this figure

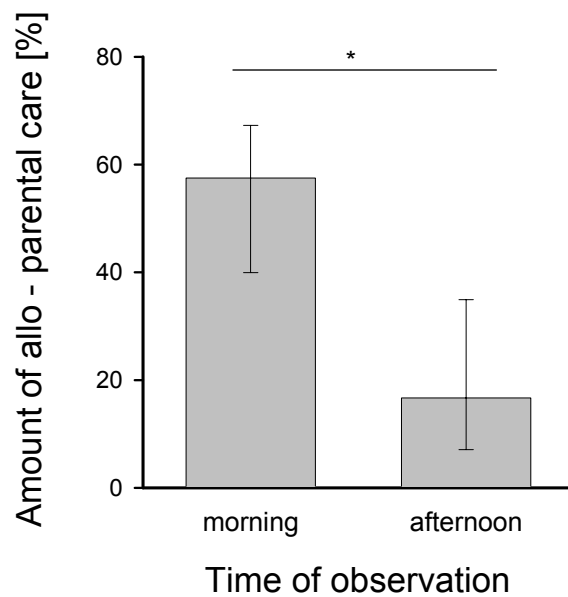
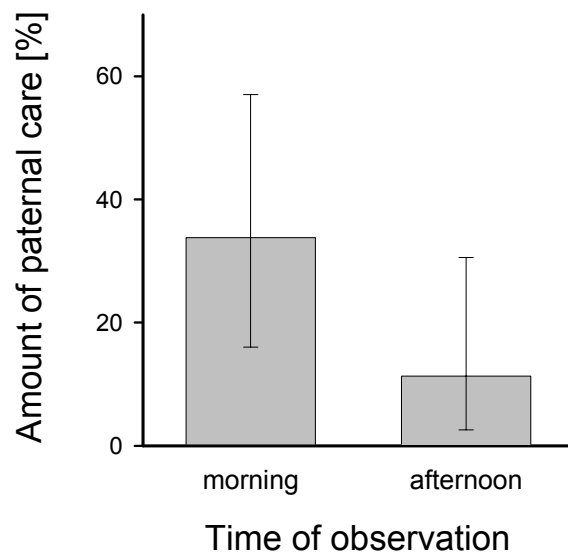


Fig. 33 Paternal care (median \pm percentile) in the morning and afternoon (paired t - test: $n = 7$, $t = 2.238$, $df = 6$, $p = 0.067$)

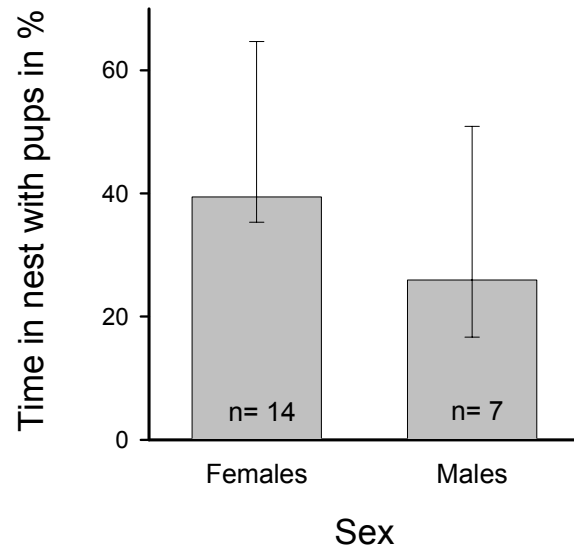


3.4.8. Males: Paternal Care or Mating Strategy?

There was no significant difference in regard to the time spent alone in the nest between females and males (t – test for independent samples: $t = 1.332$, $df = 9$, $p = 0.199$, Fig. 34). The mean score for females staying alone in the nest was 39% (range: 11.9 – 72.69%). Males spent on average 25.5% (range: 4.76 – 62.25%) alone in the nest relating to the total time of nesting behaviour.

By comparing the time spending alone with the time spent with other adults in the nest, it turned out that males predominantly spent their time with females in the nest ($p = 0.068$, Fig. 36). In contrast nesting behaviour of females did not differ concerning the number of adults in the nest (alone versus with others).

Fig. 34 Time in nest with pups without other adults
Median \pm percentiles are presented in this figure
($p = 0.199$)



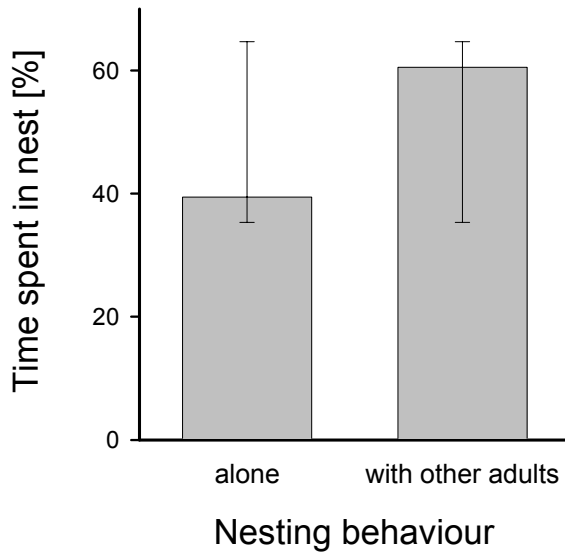
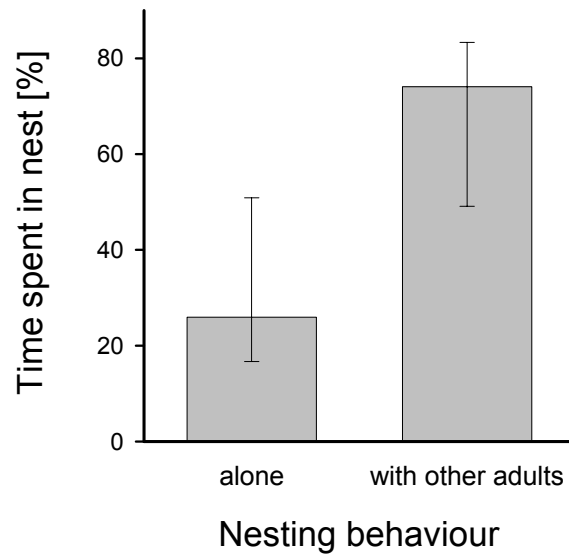


Fig. 35 Nesting behaviour of **females** in regard to the time spent alone or with other individuals in the nest (median \pm percentiles) (paired t – test: $n = 14$, $t = -1.187$, $df = 13$, $p = 0.257$)

Fig. 36 Nesting behaviour of **males** (alone versus with females) (paired t – test: $n = 7$, $t = -2.220$, $df = 6$, $p = 0.068$)



3.4.9. Retrieval Experiment

More females retrieved pups back to their nest than fathers (Fisher's exact test: $p = 0.004$, Tab. 13). Sixteen of twenty females and only two of ten males



participated in the retrieving of the offspring. Female retrieved significantly more pups than males (Mann Whitney U – test: $n_{\text{females}} = 16$, $n_{\text{males}} = 2$, $Z = -1.975$, $p = 0.049$, Fig. 37). The mean score for the retrieval behaviour of fathers was 24% (range: 16.7 – 29.7%). Females retrieved on average 56% (range:

22.2 – 100%). Moreover there was no significant difference regarding retrieving behaviour of aunts and mothers (paired t -test: $n = 8$, $t = 0.340$, $df = 7$, $p = 0.744$, Fig. 38). The mean score for the retrieval behaviour of mothers was 42.5% (range: 0 – 100%) and 45.5% (range: 0 – 100%) of aunts. Aunts, which had young themselves during the experiment did not retrieve more pups than those without own offspring (Mann Whitney U – test: $Z = -1.055$, $p = 0.292$, Fig. 39). However this result has to be interpreted with caution: There was less data available for aunts with and without offspring (same individuals, $n = 3$). Thus a test with related samples could not be conducted. Aunts having pups themselves retrieved on average 50% (range: 40 – 100%) of young. In contrast the mean score of the amount of retrieved pups was 16.5% (0 – 100%) for aunts without own offspring during the experiment.

In two cases it was observed that females built a new nest in the tank where the pups were placed.

Tab. 13 Individuals participated in the retrieving of pups ($p = 0.004$)

	Retriever	Non – retriever
Females	$n = 16$	$n = 4$
Males	$n = 2$	$n = 8$

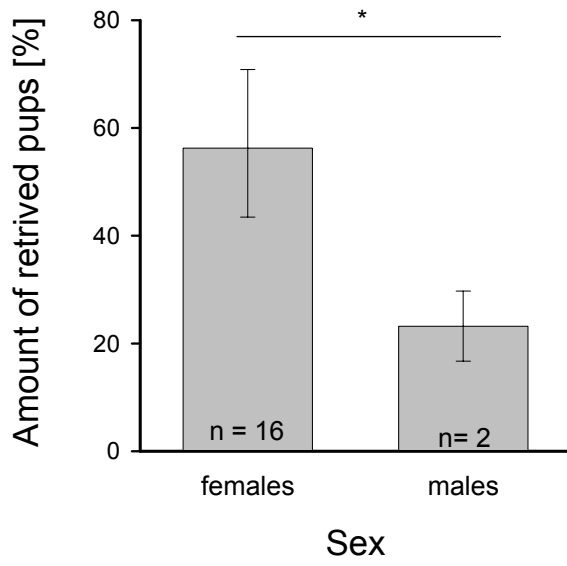


Fig. 37 Retrieval behaviour of females and males in % Median \pm percentiles are presented in this figure

Fig. 38 Retrievals of pups back to the nest of mothers and aunts (median, percentiles) ($p = 0.744$)

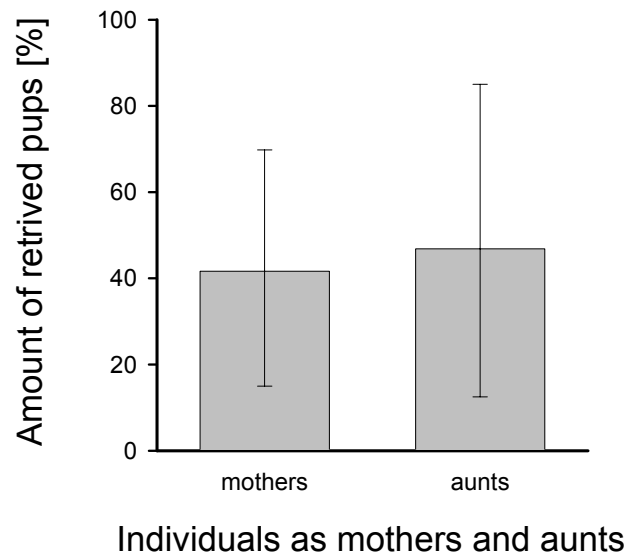
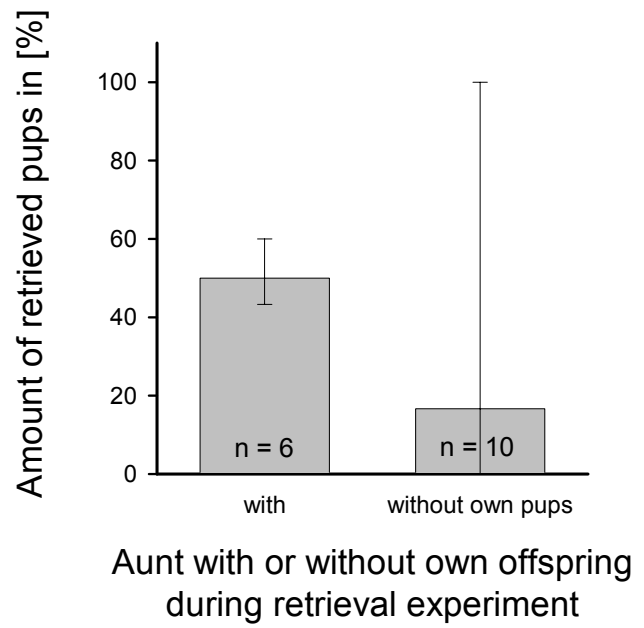


Fig. 39 Comparison of retrieval behaviour between aunts having offspring themselves and aunts without pups. during the experiment Median and percentiles are presented in this figure ($p = 0.292$)



4 Discussion

The striped mouse from the succulent karoo lives in groups; several breeding females share one nest. Thus communal breeding and nesting seemed to characterize these animals (SCHRADIN & PILLAY, 2004). However, detailed studies on communal breeding in the striped mouse were missing so far. The results of this study presented, revealed that the picture is much more complex than anticipated. Females sharing a communal nest had no advantage concerning their direct fitness benefits. Pup survival in communal nests did not differ from the one of offspring reared in singular nests. Moreover reproductive success was asymmetrical distributed among the group members and under natural conditions pregnant females “dispersed” from the communal nest to a temporary nesting site to give birth.

4.1. Over – winter Survival Probabilities

I suggested that more mice would share a nest during cold nights for thermoregulatory benefits. This hypothesis was based on the situation in winter 2003. There huddling group affiliation changed in coherence with outside temperatures (SCHRADIN & PILLAY, subm). Studies on other muroid rodents highlighted the thermoregulatory benefit gains through huddling (CANALS *et al.*, 1989, 1997, 1998). HAIM and FAIRALL (1986) demonstrated in their experiments that *Rhabdomys* from desert areas have higher oxygen consumptions and higher thermal conductance rates compared to striped mice from mesic areas. For this reason desert living *Rhabdomys* have higher metabolic rates under low temperatures. Huddling can reduce energy, which is required to maintain body temperature at a constant level. So it was expected that more individuals share a nest during cold nights in wintertime.

However the situation in winter 2004 was a different one from the year before. In 2003 population density was very low, as most mice had died during a severe

drought. The winter was with 5 mm of rain the driest in the recorded history (SCHRADIN & PILLAY, *subm*). Accordingly a food shortage arose and survival probability was low. Only 2% of mice survived, and of nine focal groups, only one had more than one survivor. Thus, no

family groups existed in the winter 2003. Food supply was higher in the winter of 2004 than in 2003 and a higher percentage of mice had survived (ca. 30%, SCHRADIN *pers commun*). In the winter of 2004 stable family groups existed and mice did not form huddling groups with unrelated individuals. Since forming huddling groups with unfamiliar mice could be associated with risks, e.g. increased competition or taking over of nesting sites, mice must outweigh costs and benefits and find compromises increasing own survival probabilities. It seems that mice chose to sleep in huddling groups of unrelated individuals to avoid heat loss during nights only when no relatives were available.

But nest sharing might be only one possible explanation for the survival probability of an individual. There might be other important factors such as home range quality and individual body mass, which were investigated in this research. In wintertime individuals are particularly confronted with high costs of thermoregulation. Moreover winter is typically characterized by lower food availability and food quality, which results in the loss of body mass (SCHRADIN & PILLAY, *accept 2005b*). Over – winter survival probabilities of individuals are known to be influenced by ecological factors such as temperature, food availability and population density (RÖDEL *et al.*, 2004). Group living might influence an individual's over – winter survival probability but can be associated with positive and negative effects, e.g. increased competition for food, a greater conspicuousness to predators and a greater risk of parasite transfer and diseases (POOLE, 1985). Besides physiological conditions are decisive to an individual's survival (RÖDEL *et al*, 2004).

The food availability, the home range size, the body mass of individuals and their group affiliation did not significantly differ between females that survived and those, which died during winter. However, sample sizes were small so that it is not possible to accept the null hypothesis. Furthermore, other factors are likely to influence survivorship, e.g. differing individual abilities and predation.

4.2. Reproduction

4.2.1. *Synchronous Breeding within the Group (Field and Captivity Study)*

Births occurred synchronized within communal nesting females in the field study ($p = 0.015$). In this research females gave birth of on average 2.5 days apart from each other. Striped mouse mothers are not able to distinguish between own and strange pups (PILLAY, 2000). Thus the risk of infanticide by female members of the communal nest is decreased when giving birth synchronized. During breeding season mothers have high costs of lactation and pregnancy. A lactating mammal has to increase her nutritional intake up to two times, just to maintain her normal body mass (RANDOLPH *et al.*, 1977). Thus synchronisation of births could result in various benefits for females and their offspring. Mothers could share nest guarding and care taking responsibilities. This could increase the individual fitness by improved heat retention, lowering of predation risks for pups and increased milk production (WILKINSON & BAKER, 1988). Since females of a communal nest were close kin they gain indirect fitness benefits by raising pups of their nest mates. Furthermore mothers can invest more time in foraging entailed with own physiological demands and future reproduction.

The results found in the field study could not be confirmed in captivity. Here synchronously breeding was only noticed in a few communal nests. However, mice were housed under semi - natural conditions and in close proximity at the research station, which could have caused changes regarding their physiological and behavioural status. Furthermore social determinants could have had a crucial influence on birth intervals (HILL *et al.*, 2000).

4.2.2. "Dispersing" of Pregnant Females (Field Study)

The most unexpected discovery was that nearly all pregnant females left their communal nest for giving birth. However a lot of them returned with the pups to their original nest around eight days later. In contrast, 45.5% of females left their communal nest permanently and founded new groups. This indicates that female *Rhabdomys* pursue a communal nesting, but not a communal breeding strategy.

But why do females take upon those strains of finding a new nest, giving birth and returning to their communal nest? One possible explanation for this phenomenon is to prevent infanticide by nest mates. Infanticide can be defined as any behaviour resulting in the immediate death of pups of the perpetrators own species (HAUSFATER & HRDY, 1984) and can be explained by: (1) exploitation (infant presents a resource, (cannibalism)), (2) competition for resources, (3) sexual selection, (4) parental manipulation and (5) social pathology. In rodents infanticide occurs regular and several studies where conducted with the aim of understanding this behaviour. VOM SAAL & HOWARD (1982) demonstrated in their experiments that infanticidal behaviour of male house mice (*Mus musculus*) results in a reduction of gestation period of subsequent litters for female mice whose newborn pups had been killed. Furthermore house mouse males are less likely to kill offspring of females with whom they have copulated (BROOKS, 1984). In the striped mouse it was observed that breeding males were displaced by new once in several cases. So this might have caused females to leave their original nest for giving birth and

thus reducing pup mortality risks due to new breeding males (There was too less data available to be evaluated). However, this statement can only partly explain the observed phenomenon, because females still left the communal nest when the “old” breeding male was not displaced by a new one. BOONSTRA (1977) demonstrated that pup survival was improved by removal of adjacent females in *Microtus townsendii*. He concluded that females compete with other females for resources and nesting sites. So infanticide can be defined as one form of reproductive competition (HAUSFATER & HRDY, 1984). Most researches studying infanticidal behaviour in rodents indicate that when intraspecific killing took place, they were more likely to be perpetrated by adult females than by adult males (BROOKS, 1984). In the striped mouse up to four breeding females shared a nest. Thus females might increase the probability of infanticide by giving birth in their original nest. If births are synchronized and females leave their communal nest to give birth elsewhere before returning with their pups several days later to pool them with the offspring of their closely related nest mates, they will develop a kind of protection mechanism for their young. Now infanticidal behaviour between mothers should be reduced since

female striped mouse are not able to distinguish between own and alien offspring (PILLAY, 2000).

Now the question arises why some females founded new groups while most females returned to their communal nest. In 2003, female mice left their winter huddling communities to found new groups in spring (SCHRADIN, subm). The population density was low and all mice were able to find a suitable nesting site. In 2004 the population density was higher in comparison with 2003. So females founding new groups have managed to find and to establish suitable territories, whereas the other females only gave birth in temporary nesting sites, which were situated in the same territory as the communal nest. In addition a trend of dispersing farther away by female striped mice which founded new groups was recognizable ($p = 0.91$).

4.2.3. Reproductive Success: Plural versus Singular Breeders (Field and Captivity Study)

Results of the field and the captivity study demonstrated that the reproductive success did not differ between singular and plural breeding females. In the field a great variation was observed regarding reproductive success of females living in a communal nest. Some females had a high reproductive success, whereas others did not give birth at all (which did not occur in any solitary living females). Females not reproducing might have suffered from suppression by other female mice sharing the communal nest (KÖNIG, 1993). However field mice were not sacrificed for the purpose of uterine scars, abnormalities, etc, so a plausible explanation for not reproducing can not be given here.

In the field five of eleven females left their nest permanently and founded new groups. These female mice did not dispersed into an area which was unknown to them. They chose habitats in which they used to forage in former

times. So dispersal risks were minimized. Nevertheless, these opportunities were restricted since most suitable areas were already occupied. Population density was higher in 2004 than in 2003. Thus, less free nesting sites and territories were available. Social behaviour is known to be affected by population density (EMLEN, 1982). An increase of population density leads to habitat saturation, i.e. suitable unoccupied habitats become limited (HAYES, 2000). So many female striped mice had to find a compromise: Staying and producing offspring within a communal nest, which might be associated with a lowered reproductive success, or wandering around and searching for new good quality nesting sites. The second strategy would probably be associated with high risks: the risk of predation, the uncertainty of successful establishment in a suitable habitat, the uncertainty of finding a mate and the uncertainty of successful independent reproduction. Thus females might favour to nest communally under higher population densities, when ecological circumstances prevent solitary breeding.

Discussing advantages of communal breeding and nesting under natural conditions one might think that females or rather their offspring might profit from adoption by other communal females of the nest in cases of the death of the mother. In my point of view this explanation should only receive little attention: Pups are especially vulnerable during the first days of life. Nevertheless nearly all pregnant females "dispersed" to deliver their offspring alone outside their communal nest. Furthermore these females stayed on average eight days (exception: females founding new groups) away from their communal group, i.e. pups were alone during foraging excursions. Moreover predation risks are particularly high in the breeding season. So females took

the risk of their own death associated with the starvation of the young instead of rearing their offspring communally during the first days of pups' lives. Additionally one should consider that 45,5% of the females left their communal nest permanently.

In captivity the reproductive success did not differ between communal and singular breeding females. Pregnant females were never observed to "disperse" to the tank not containing the communal nest to give birth. Furthermore females mixed their offspring communally in one nest, even if the

young were of different age. Resources are known to increase competition between females (BROONSTA, 1977). In captivity all mice were provided with sufficient and highly nutritious food. This might have decreased the competition among sisters, so that it was not necessary to “disperse” from the communal nest. However there might be other factors influencing this aspect, e.g. restriction of movement in captivity.

No difference regarding the body mass and the weight gain of pups between these two categories occurred. Moreover the body mass of pups was influenced by litter size.

Infanticidal behaviour occurred more often in communal nests than in singular breeding groups ($p = 0.072$). Females nursing own and alien offspring in communal nests might be confronted with increased cost of lactation. This increase of costs and the own physiological demands might have caused females to kill some of their offspring to secure own survival and that of the remaining pups. Moreover in some communal nests births occurred synchronized, here the nursing of pups might have been distributed asymmetrical. Thus one female might have nursed more offspring in comparison to her sibling resulting in higher lactation costs. Another explanation for infanticidal behaviour in communal nests might be reproductive competition between females or abnormal aggression caused by laboratory conditions.

Additionally one experiment, where females were housed in a communal nest in the beginning and then separated from her sibling was conducted. Pup survival probabilities did not differ when these females were only housed with their male ($p = 0.465$). Nevertheless these females had a different life history background than singular breeders. Moreover behavioural and physiological changes caused by communal nesting could have had long term effects.

In captivity females giving birth first produced more litters ($p = 0.063$) than females giving birth second. Furthermore pups of female mice reproducing first had higher survival probabilities in comparison to offspring born to the second females. Timing and intensity of reproduction are crucial factors concerning the fitness of individuals. These factors depend on individual physiological conditions. That is why heavier females might reproduce earlier than smaller ones (FUCHS, 1981) and give birth to larger litters (KÖNIG, 1993).

The strategy of giving birth first might play an important role under natural circumstances, where the breeding season is restricted to three months and followed by a dry and hot summer, which is characterized by a high mortality rate. Here females should gain a greater benefit in regard to their lifetime reproductive success, when they breed as early as possible. However females reproducing later in comparison to their siblings may have suffered from a reduced fecundity, which could have been caused by stress. In two cases one female of a communal nest did not reproduce at all and might have been suppressed by the other female (despotic society, KÖNIG, 1993). Aggression rarely occurred under normal circumstances. However one communal nest containing a reproducing and a non – reproducing female had to be separated for the reason of highly agonistic behaviour: The mother exhibited aggression after her delivery of the second litter towards the “infertile” one. The defensive female was not allowed in the terrarium containing the nest (with pups) anymore. It is not clear what caused this changes of behaviour, because the mother was not aggressive towards her sister when she had pups for the first time then and infanticide was never noticed in this trio.

There are other important factors influencing pup survival probabilities, i.e. ecological conditions like quality of the environment, temperature and rain (REID, 2003). Food quality is decisive for a females’ reproduction, i.e. regarding poor quality food, lactating females are forced to forage longer to gain the same nutritional intake (DUNBAR et al., 2002) or she and her offspring suffer from increased mortality rates. However the results of this study indicated that pup survival probabilities are not correlated with habitat quality or territory size. Nearly all studied mice lived close to a dry riverbed, which is distinguished by luxuriant vegetation in comparison to other habitats in the nature reserve, which included more sandy patches and less vegetation (SCHRADIN & PILLAY, in prep). The area around the riverbed was characterized by a high abundance of shrubs and ephemerals. Thus all mice were provided with sufficient food making a differentiation regarding pup survival probabilities difficult. Furthermore individual abilities and skills might play a major role in own survival probabilities and random effects.

4.2.4. Parental and Allo – parental Care in Communal Nests (Captivity Study)

The results of the behavioural observations demonstrate that all individuals participated in the care of the offspring. Females participated significantly more in the care of the offspring than males ($p = 0.048$). Furthermore, mothers exhibited more amicable behaviour towards pups than aunts ($p = 0.063$).

Paternal care is rare in mammals, where it occurs in only approximately 7 % of all species (KLEIMAN & MALCOLM, 1981). SCHRADIN & PILLAY (2005b) tested the influence of fathers on pup development in the striped mouse. The presence or absence of fathers had no direct effect on the offspring's survival rates. However, they found that litters grew faster in the presence of fathers and suggested that huddling behaviour shown by males reduced heat and energy loss suffered by pups. So the offspring could invest energy efficiently in growth. Males showing parental care can improve their fitness under specific environmental circumstances (SCHRADIN & PILLAY, 2005b). During this study, males exhibited in several cases highly aggressive behaviour towards intruders (my hand) in order to protect their dependent young. In contrast, females (mothers and aunts) were less likely to attack intruders, but tried to protect the pups by hiding them under their belly or by retrieving them into another corner of the tank. Parental aggression could be an interesting topic for a future study.

Aunts may participate in communal care for increasing their indirect fitness benefits (Hamilton, 1964) and to cultivate their relationships within a group. However, most aunts had offspring themselves during some part of the study. So behavioural changes caused by pregnancy could have resulted in a higher amount of care giving later.

Mothers exhibited significantly more parental care during the first three days of the pups' life than during Day 4 – 6 ($p = 0.013$). Mothers should participate more in offspring care during early life stages of their pups since

these are much more vulnerable at this age. In the neonatal period (birth to 4 days) pups are still very small, the fur is not fully developed yet and the eyes are still closed (BROOKS, 1982). In these days pups might require more care, especially huddling in order to minimize energetic losses. Since mothers experience high costs of lactation they have to compromise between parental care and foraging, which might explain why mothers showed less care of the offspring during Day 4 – 10. The costs of lactation increase as offspring grows (MARTIN, 1984), so mothers might have spent more time in foraging to cover energetic deficits. Pups tended to emerge from the nest at Day 10, so they could follow

their mothers or any other adult animal. Here the young mice explored their environment under the care of adults for the first time. Since pups left the nest they were able to initiate interactions with other individuals. This might explain why mothers spent more time with their offspring during Day 11 – 16. The amount of behaviour shown towards the pups by aunts and males did not differ during various life stages. But the results pointed out that care giving behaviour varied very much among individuals.

Mothers and aunts participated significantly more in parental care in the mornings than in the afternoons (A tendency was evident for males). The reason for this are temperature differences: Morning temperatures were always lower in comparison to afternoon temperatures. So pups could experience higher energetic and heat losses in the morning, when adults would not show the required amount of parental care, especially huddling.

An retrieval experiment was conducted to determine parental and allo – parental care. Females retrieved pups significantly more often than fathers. Sixteen of twenty females and only two of ten males participated in retrieving of the new born pups. However some males seemed to look after the displaced pups while females retrieved them back into the nest. In some cases males ran nervously around the terrariums and it seemed that they did not know how to respond to the situation.

There was no difference regarding the amount of retrieved pups between aunts and mothers. Retrieval behaviour of aunts might be influenced by hormonal

changes caused by pregnancies in the past or future or by the presence of her sister's pups. However aunts might participate as much in pup retrieving as mothers to decrease encounters within the communal nest or to gain social benefits.

4.2.5. Young Individuals and Reproduction (Field Study)

Individuals born during the first half of the breeding season were more likely to become reproductively active during the same breeding season than those which were born during the second half. Nevertheless, most of these sexually mature young animals stayed at their natal nest instead of dispersing. However dispersal occurred regularly, especially in males.

In 2002 all juveniles stayed at their natal nest even after they became sexually mature. Offspring participated in territorial defence and in nest construction (SCHRADIN & PILLAY, 2004). Thus their behaviour might have been beneficial for the pups in the nest and yielded an increase of reproductive success of the breeding individuals, so that they could be labelled as helpers at the nest (EMLEN, 1982). However data confirming helping activities by juveniles were not available in this study. In contrast, in the captivity study young mice were removed from their "natal terrarium" to prevent helping effects. SCHRADIN & PILLAY (2004) reported that adult offspring seemed to be sexually suppressed although they were physiologically capable of reproduction. Possible reasons might be that reproduction is always associated with costly gestation and

postnatal investment in the litter (CREEL & CREEL, 1991). Thus, young adults might not be capable of investing sufficiently in their offspring. In this semi – desert region the breeding season is followed by a dry summer, which is associated with a low food abundance resulting in a body mass loss of around 12% (SCHRADIN & PILLAY, accept 2005b). Almost 70 % of mice died during wintertime (SCHRADIN & PILLAY, subm). Therefore young individuals especially the once born late in the breeding season might favour a strategy which only contains own physiological demands resulting in an increased survival probability instead of investing into reproduction. On the other hand PILLAY (2002) demonstrated in a captivity study that the occurrence of reproductive inhibition in females was caused by incest avoidance, which could lead to inbreeding depression. However as I already mentioned most individuals born early in the breeding season became reproductively active during the presented study. Furthermore young females remained and reproduced communally with their mothers within their natal nest. EMLEN (1992) argued that dominant individuals (mothers) would share reproduction in order to induce subordinates (daughters) to remain at the nest, if they benefit from continued presence of them (fitness forfeiting). In contrast, FRENCH (1994) pointed in a study on Mongolian gerbils out that litters born to daughters two weeks after their mother's delivery suffered a significantly higher mortality than did litters born immediately after the mothers gave birth. As population density increases during the breeding season high quality habitats are filled. Thus mothers might accept

their daughters, who have no opportunities to breed solitarily (GERLACH & BARTMANN, 2002). Since mother – daughter units are close kin, females gain indirect fitness benefits (HAMILTON, 1964) by nesting communally.

Social behaviour is affected by population density (EMLEN, 1982) and sexual suppression is likely to occur when ecological and demographical conditions limit breeding opportunities (EMLEN, 1982, CREEL & CREEL, 1991). In 2002, 151 mice/ha were trapped at the study grid (SCHRADIN & PILLAY, subm). So population density was high leading to habitat saturation and territorial aggression. Thus young mice could not disperse and therefore stayed as infertile helper at the nest (SCHRADIN & PILLAY, 2004). In 2004, 11 mice/ha were

trapped at the field site. So population density was much lower in 2004 than compared to 2002. KOENIG *et al.* (1992) predicted in his delayed dispersal threshold model that within one population some individuals would remain philopatric, whereas others would disperse. This model can be transferred to the *Rhabdomys* population in 2004. Here some young individuals, especially males dispersed from their natal nest. Since most good quality territories and nesting sites were already occupied most of the studied animals remained philopatric enjoying the benefits of group living.

4.3.6.1. Home Range Size and Quality within two Seasons (Field Study)

Home range sizes increased during the breeding season. In spring females mostly enlarged their home ranges without vacating their winter home ranges. By increasing the home ranges females shifted from evergreen shrubs around the dry riverbed to sandy patches, which were covered with highly nutritious

annuals (SCHRADIN & PILLAY, in prep.). Food availability is of major importance for the reproduction in mammals (BRONSON, 1985). In spring, which is characterized by the abundance of ephemerals, striped mice started to breed. Since ephemerals are highly nutritious more energy was available to cover own physiological demands so that individuals could invest in reproduction. Furthermore annuals might play an important role concerning survival probabilities in summer, where food is only restricted to *Zygophyllum retrofractum* shrubs resulting in a body mass loss of around 12% (SCHRADIN & PILLAY, accept 2005b). So animals with a good access to ephemerals might be able to store more fat and thus to increase their probabilities of survival.

Therefore more food was available in spring. However food availability increased as a consequence of home range enlargements and was not correlated with the size of the habitat. Population density in 2002 was higher than in 2004. In 2002, animals sufficiently defended small areas and females mostly responded aggressively towards other female intruders (SCHRADIN & PILLAY, 2004). Thus it was difficult to enlarge home ranges since these habitats bordered to many neighbours from other groups. In contrast, population density was much lower in 2004. Thus females had the opportunity to explore surrounding areas and therefore to enlarge their home range.

5 Conclusion

Communal nesting and breeding have been reported for 35 species and from 9 families within the order Rodentia (SOLOMON & FRENCH, 1997). Most studies suggested advantages, which evolved from communal breeding, resulting in greater lifetime reproductive success for females and a decline of costs in regard to their own bodily condition. However these researches were mainly conducted in captivity (KÖNIG, 1993, 1994a, 1994b, HAYES & SOLOMON, 2004). Since conditions in nature are variable and energetically challenging for animals benefits of communal nesting might be greater in the wild. Furthermore under laboratory conditions individuals were paired compulsory and had no option to disperse leading to results, which might not apply under natural circumstances.

For this reason the present study investigated causes and consequences of communal breeding in the striped mouse, a group – living solitary forager (SCHRADIN & PILLAY, 2004), in the field and in captivity. Moreover in captivity females of a communal group were housed in two terrariums, which were connected through a PVC – tube. Background of this experimental design was that females should have the opportunity to disperse and breed independently, if they wanted to (one tank per female).

Surprisingly results from both, wild and captivity study indicate that females did not had advantages concerning their direct fitness by nesting communally. Pup survival probabilities did not differ between nests, which were shared by multiple females and singular breeders. Moreover reproductive success was subject to a great variation amongst individuals within one nesting site. Data from captivity revealed that females reproducing earlier gave birth to more litters and pup survival probabilities were improved in comparison to their littermates.

The most unexpected discovery was found in the wild: Here most females nesting communally left their original nest to give birth in temporary nesting sites and then returned to their group with the pups several days later. SCHRADIN & PILLAY (2004) investigated the social system in the striped mouse in 2002, which was characterized by a high population density. They observed

that communal nesting and breeding occurred regular during the breeding season. Nevertheless the “dispersing” behaviour of pregnant females was not noticed. Since population density was high temporary nesting sites of less quality might have been occupied by other mice as well. So females might not have had the opportunity to deliver their pups outside the communal nest. On the other hand SCHRADIN & PILLAY (2004) might have failed to notice this

phenomenon, because mice were only temporarily equipped with radio tags. Thus individual sleeping sites could not have been estimated accurately.

The social system of *Rhabdomys* was continuously investigated in the last three years. Within these years extreme differences concerning population density appeared. The first year (2002) was characterized by a high population density (SCHRADIN & PILLAY, 2004). In contrast, in the year 2003 most of animals died during a severe drought (SCHRADIN & PILLAY, subm); therefore population density was quite low. However the population recovered gradually in 2004. During these three years *Rhabdomys* exhibited different pattern to cope with natural circumstances. These mammals are known to be flexible in regard to their social system (SCHRADIN & PILLAY, 2005a). In 2002, all individuals lived in large family groups, which contained up to six adult members and their offspring. Females bred communally within their group. However in 2003 the social system changed from group living to a more solitary lifestyle. At the onset of the breeding season all females left over – winter huddling groups, which consisted of unrelated individuals (SCHRADIN & PILLAY, subm) to pursue a solitary breeding strategy. It was suggested that females did not form communal nests, because no close relatives survived (SCHRADIN & PILLAY, subm). Nevertheless at the end of the breeding season more individuals became social (SCHRADIN & PILLAY, subm), and mothers and daughters bred communally within one nest. In 2004 all individuals over – wintered in stable family groups. Furthermore at the start of the breeding season these units remained constant to a great extent. However most of the females breeding communally gave birth in temporary nesting sites and then returned several days later to mix their offspring with alien ones in the communal nest. So female mice sharing one nest pursued a communal nesting, but not a communal breeding strategy. As population density was higher in 2004 compared to 2003, most of females might not have been able to establish unoccupied territories of good quality. Dispersals into an unknown areas are always associated with high risks. Thus female mice might have had to come to the compromise of staying and sharing reproduction within one nest perhaps with reduced direct reproductive success instead of dealing with costs of dispersal.

Population density and reproductive competition between individuals sharing one nest seemed to be major determinants regarding breeding strategies of female *Rhabdomys*.

However during this research new questions evolved to understand costs and benefits of communal breeding and nesting in the wild:

- 1) Were dispersing female mice less related to females of the communal nest than those, which returned to their original nesting site after their delivery?
- 2) Does nest guarding exist in wild *Rhabdomys* populations?
- 3) Do mothers, aunts and fathers coordinate their forage behaviour towards newborn pups in the communal nest?
- 4) Do individuals of a communal nesting site spend more time in the nest during the neonatal period of the pups?
- 5) Do young mice follow adults to acquire personal skills? Does a preference towards mothers, aunts or fathers exist?
- 6) Do animals sharing one nest have different hormonal levels (corticosterone) compared to solitary and singular breeders?
- 7) What is the role of juveniles staying as helpers at the nest?

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