Diploma – Thesis

Male reproductive strategies in the south african striped mouse (*Rhabdomys pumilio*)

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1. Abstract

In mammals a high variation in mating strategies occurs between species and sometimes eve within species. But reports of social flexibility in natural populations are rare. So the key aspect of this study was to receive more information about the interesting intraspecific variation in reproductive strategies of males of one population of the south African striped mouse (*Rhabdomys pumilio*) in the succulent karoo. To study the reproductive strategies of *R. pumilio* three different approaches were followed. (1) To receive data of free living males in the field animals were trapped, radio-tracked and observed directly in the field. (2) Experiments were made in an aggression area with males trapped in the field during different seasons. (3) To receive data about sexual suppression in young males experiments were made in captivity. Field studies showed that intraspecific variation in reproductive strategies occurs in males of *R. pumilio* in the succulent karoo at a medium population density. Males can change their group-living strategy into a roaming strategy and vice versa within one breeding season. Males were not more aggressive during than before the onset of the breeding season. Thus, male aggression probably does not only function to increase immediate mating success. Experiments in captivity showed that factors like the protein content of the diet and encounters with strangers can have an influence on at which age males become potentially reproductively active (i.e. scrotal). In conclusion it can be said that the males of *R. pumilio* in the succulent karoo shows a high social flexibility and are not fixed to one reproductive strategy.

Bei Säugetieren gibt es eine große Variation in Bezug auf die Fortpflanzungsstrategie zwischen den Arten und manchmal auch innerhalb einer Art. Jedoch sind Berichte über die soziale Flexibilität in natürlichen Populationen rar. So war der zentrale Aspekt meiner Arbeit, mehr Informationen über diese interessante intrasepzifische Variation in Bezug auf die männlichen Fortpflanzungsstrategie innerhalb einer Population bei der südafrikanischen Striemengrasmaus (*Rhabdomys pumilio*) in der Sukkulenten Karoo zu erhalten. Zur Untersuchung der Fortpflanzungsstrategie von *R. pumilio* wurden 3 verschiedene Wege verfolgt. (1) Um Daten von freilebenden Mäusen zu erhalten wurden diese im Freiland gefangen, telemetriert und direkt beobachtet. (2) Es wurden Experimente mit Mäusen aus dem Freiland in einer Aggressionsarena durchgeführt, die im Freiland gefangen wurden während

verschiedener Jahreszeiten. (3) Um Daten über die sexuelle Unterdrückung bei jungen Männchen zu erhalten wurden Experimente mit Mäusen aus der Gefangenschaft durchgeführt. Die Studien im Freiland zeigten, dass bei einer mittleren Populationsdichte bei Männchen der Art *R. pumilio* aus der Sukkulentenkaroo eine intraspezifische Variation in der Fortpflanzungsstrategie vorkommt. Die Männchen sind in der Lage innerhalb einer Fortpflanzungssaison ihre gruppenlebende Strategie in eine umherstreunende Strategie und umgekehrt zu ändern. Während der Fortpflanzungszeit waren die Männchen nicht aggressiver als vor dem Beginn der Fortpflanzungszeit. Folglich hat das aggressive Verhalten bei den Männchen möglicherweise nicht nur die Funktion ihren Fortpflanzungserfolg zu erhöhen. Die Experimente in Gefangenschaft zeigten, dass Faktoren wie der Proteingehalt der Nahrung und Begegnungen mit fremden Männchen einen Einfluss auf das Alter in welchem die Männchen fortpflanzungsaktiv werden haben kann. Zusammenfassend kann man sagen, das die Männchen von *R. pumilio* in der Sukkulentenkaroo eine hohe soziale Flexibilität zeigen und nicht auf eine Fortpflanzungsstrategie festgelegt sind.

2. Introduction

The dominant principle of biology is evolution by natural selection. Natural selection, operating on inherited random variation has shaped animals over generations to match the environments in which they live (Manning & Dawkins, 1998). Behaviour patterns which bring higher fitness benefits are supported by natural selection (Franck, 1997). Through behavioural adaptation to the environment animals can improve their chances to survive and to increase their fitness (e.g. black-headed gull, Tinbergen 1962; kittiwake, Cullen 1957).
Hamilton (1964) introduced the idea of "inclusive fitness". Inclusive fitness means the direct and the indirect fitness of an individual. The direct fitness is measured as the reproductive contribution from an individual to the gene pool of the population. The indirect fitness means the increase of the reproductive success of close relatives, e.g. by helping closer relatives to survive and to reproduce (e.g. termites, Wilson 1971; alpine marmots, Hackländer, Möstl & Arnold 2003; naked mole-rat, Lacey and Sherman 1991, Jarvis 1981).

The inclusive fitness of an animal depends on different environmental factors and is determined by survival, reproduction and social behaviour. To increase the inclusive fitness it is important to search for food resources and defend them, to avoid predators and to compete for mates. But benefits have to outweigh the costs associated with different strategies, e.g. of foraging or searching for mates, to maximise individual fitness. For this reason natural selection favoured reproductive strategies with low costs and high benefits.

To increase direct fitness, the right strategy of reproduction is very important. For example the choice of the right mating partner influences the reproductive success because the mating partner participates in half of the genetic outfit of the offspring. Moreover, in some species the mating partner contributes to the survival of the offspring by providing resources and helping to rear them (Franck, 1997). Who to mate with is determined by the mating system, which can be understood as a combination of male and female reproductive strategies.

Mating systems can be divided into four main categories: Monogamy (one male, one female), polygyny (one male, several females), polyandry (several males, one female) and promiscuity (several males, several females; Clutton-Brock, 1989). Beside, there are several alternative mating strategies, for instance the sneaker or the satellite strategy, which is followed by small males to compete with bigger males to increase their reproductive success. For example in the

North American big horn sheep (*Ovis Canadensis*) small males stay close to the dominant males as satellites. From time to time they try to copulate with the female when the dominant male is not guarding the female, which takes only a few seconds. The satellite strategy is known from insects, fishes, birds and mammals. The sneaker strategy occurs in the North American sun perch (*Lepomis macrochirus*). In this species two types of males occur: big males which are dark coloured defend a territory and small males, called sneakers which look like females. While the female is spawning in the territory of a big male, the sneakers jostle themselves between the dominant male and the female and release their sperm, fertilizing some of the eggs (Franck, 1997). Often different alternative reproductive strategies are available for males of one species. In most of the cases males can change their strategy during life. Which strategy is followed depends on which strategy yields the highest reproductive success for them in the present situation.

The more offspring an individual can produce, the more it increases its direct and by this inclusive fitness. Thus, the fitness of males is mainly determined by the number of females whose offspring they can sire (Trivers, 1972). Hence males seek to get access to as many females as possible. However, the strategies used to reach this aim can differ. When males of one species follow different reproductive strategies in different habitats, one might expect the strategy adopted to maximize fitness payoffs under particular ecological conditions (Schradin and Pillay, 2004).

For males, the most important resource is the access to receptive females (Trivers, 1972). One strategy to gain access to resources is aggressive behaviour. Aggression is always a sign for a competitive situation. Aggression can serve to get access to females by either defending territories that are important for females, or by defending females themselves. In side-blotched lizards (*Uta stansburiana*) males exist as morphs of three colours which show different levels of aggressive behaviour. Orange-throated males are aggressive and defend large territories with many females. Blue-throated males defend smaller territories with fewer females. Yellow-throated males do not defend a territory, but patrol a large home range. They obtain secretive copulations from females on the territories of dominant males (Sinervo, 2000).

Through territorial behaviour animals can defend resources and increase their reproductive success. It also influences the distribution of individuals that compete for space. So the most

common definition of a territory is a defended space with boundaries (Maher, 1995). For male reproductive success, it is especially important to defend space used by females. However, the energetic costs of defending a territory are very high and territorial aggression always includes the risk of being injured. Thus, any mechanism to reduce these costs would be of advantage. One strategy to reduce costs of territory defence is to be territorial only during the time of year the defence of resources yields a benefit. With regards as receptive females being an important resource for males, this means territorial aggression is mainly important during the breeding season. Thus, no or reduced male territoriality during the non-breeding season could save energy.

Another strategy to reduce costs of territoriality is the dear enemy phenomenon. Territorial neighbours fight to establish their mutual border (Olendorf, 1999). Through future respect of boundaries and reduced aggression towards neighbours (in comparison to strangers) the energetic costs of territorial defence and the risk of injury from escalated contest are reduced (Ydenberg et al. 1988). Olendorf hypothesized that the dear-enemy phenomenon is an expression of reciprocal condition cooperation (Getty 1987; Langen et al. 2000). He described it as a beneficial outcome which is a reduction in time, energy and possibly health costs of continued vigilance and aggression along the border. The potential cost is the risk of being cheated on by a neighbour that takes advantages of this trust and does not refrain from trespassing (Olendorf, 1999). In the cordylid lizard *Platysaurus broadleyi* residents were more tolerant towards immediate neighbours and showed less aggressive behaviour them than towards distant territory holders. Besides they allowed neighbours to approach more closely than non-neighbours before challenging them (Whiting 1999).

Territoriality can also influence dispersal, i.e. that animals move away from their natal area or their group. In contrast, in some other cases parents become territorial towards their adult young to avoid inbreeding, driving them away from their natal territory.
Dispersal movements have been studied in many species of mammals (Greenwood, 1980) and they are important for the longevity and composition of animal populations (Gese and Mech 1991). In most species, individuals disperse from their natal area before or by the age of sexual maturity (Krebs and Davis, 1997), but dispersal patterns vary greatly across taxa and also between individuals of the same species (Waser, 1996). In mammals dispersal is commonly recognized to be male biased while in birds it is female biased (Greenwood 1980,1983; Dobson 1982; Anderson 1989). One reason for dispersal is to avoid inbreeding

because inbreeding depression leads to reduced reproductive success (Krebs and Davies, 1996). Another reason could be social because younger males have often no chance to compete with the dominant older males for mates (Ribble 1992). Examples for male biased dispersal in mammals are *Papio anubis* (Packer, 1979) or *Peromyscus californicus* (Ribble, 1992). Both territoriality and dispersal influence the distribution of individuals and thus the social organisation of populations.

Social systems in mammals can be divided into two main categories, the solitary life and living in groups. Group-living can be organized in several different ways (see below) and lead to different mating systems. An example for a solitary lifestyle is the tiger who lives always solitary and meet only for mating (Sunquist, 1981; Schaller, 1967). In cheetahs only the females lives solitary while related males often built coalitions (Caro, 1986,1987). An example for group living animals are the hamadryas baboons who live in harems (Kummer, 1968) or the red deer who are organised as materialineal clans (Clutton-Brock, 1982), while silverbacked and golden jackals lives in family groups (Moehlmann, 1983).

A high variety in social organisation is represented in the most numerous of all mammalian taxa, the rodents. For instance the giant kangaroo rat (*Dipodomys ingens*) is a solitary rodent (Randall, 2001) while the gerbil *Gerbillurus vallinus* lives in colonies (Stuart, 1999). An example for a monogamous rodent is the California mouse (*Peromyscus californicus*; Ribble, 1991). In contrast naked mole-rats live in an eusocial system, i.e. a colony where only one female reproduces with up to 3 males while infertile female and male offspring are helpers at the nest (Lacey & Sherman, 1991).

Variety in social organisation cannot only be found between different rodent species, but in some cases even within a single species. The striped mouse (*Rhabdomys pumilio*, see picture 1) demonstrates a high level of intraspecific variability of its social system from solitarity to group-living (Schradin & Pillay, 2005b). *R. pumilio* is a muroid rodent with a wide distribution in southern Africa that includes many different habitats, such as grassland, marsh, forest, succulent karoo (a semi-desert with dwarf succulent shrubs being the dominant plant form) and deserts (Kingdon, 1974).

Picture 1: The striped mouse (*Rhabdomys pumilio*)

Whereas *R. pumilio* is solitary in grasslands (Brooks,1974; Perrin, 1980; Schradin and Pillay, 2005b; Willan and Meester,1989), it forms social groups in desert habitats (Schradin and Pillay, 2004). Males in the moist grasslands follow a roaming strategy, visiting several receptive females, and do not participate in parental care. In contrast, males in the arid succulent karoo are permanent members of social groups and help in care for young (Schradin and Pillay, 2003, 2004). Individuals of a group share the same nest, use the same group territory, and interact amicably with each other, but react aggressively towards individuals from other groups or against other roaming mice (Schradin, 2004). Home range size is also different between mice in grasslands and in the succulent karoo. Home ranges of males in the moist grasslands are 10 times larger than their counterparts in the succulent karoo (Schradin & Pillay, 2005b).

Intraspecific variation in the social system of one population of *R. pumilio* is also found. In the years 2001-2002 *R. pumilio* of the succulent karoo showed group-living behaviour. The winter of 2003 was the driest winters in the last 44 years, so survival probability was low resulting in a low population density. This situation was equal to the one found in the grasslands of southern Africa (Schradin, 2005b). Rainfall occurred in August and enabled a late breeding season. However, the social system changed and males were no longer associated with groups of communally-breeding females because females changed from communal to solitary-breeding. Males adopted a roaming strategy and visited several single breeding females (Schradin, 2005b). It seems that *R. pumilio* of the succulent karoo can change its mating strategy regarding to the current environmental conditions, showing a group living strategy under conditions of high population density, but a solitary strategy when

population density is low (Schradin & Pillay, subm.). The reason for this differentiate behaviour might be caused by the distribution of the females. If males want to maximise reproductive success, they have to adapt their strategy to the distribution of females. Under high population densities, males can defend groups of communally nesting females, while under low population densities, males might better roam and visit several solitary nesting females (Schradin & Pillay, 2005). This would predict that at mean population density both the roaming and the group-living strategy should be found because also solitary and group-living females should be found.

Reproduction of *R. pumilio* is limited by the availability of a protein rich diet (insects and seeds, Nel, 2003), which is why the breeding season in the succulent karoo is limited to spring, when plant growth is at its maximum, after the rain in winter and before the dry season in summer (Schradin and Pillay, Mamal Biol 2005). Nutrition and energy are essential for reproduction in mammals (Sadleir,1984; Loudon and Racey,1987; Kunkele, 2000) and dietary protein is paramount for reproduction in mammals (Nel, 2003). For example, sex ratios (Lamb and van Aarde, 2001), growth (Sinclair *et al.,* 1999; Lamb and van Aarde, 2001), growth rate (Massaro *et al*., 1977b; Sinclair *et al.,* 1999) and age at sexual maturity (Nakagawa and Masana, 1971) are influenced by the availability of dietary protein (Nel, 2003). Thus, low levels of dietary protein could negatively influence reproductive success (Nel, 2003).

Population density might also influences reproductive behaviour because at high population density living space and nutrition are rare and younger males are could be suppressed by dominant territory holders. In contrast at low population density space and food are available, so younger males have the possibility to disperse and should not be suppressed in reproduction. In the past it could be observed in the field that young *R. pumilio* males did not become reproductively active under conditions of high population density (Schradin & Pillay 2004), but when population density was low (Schradin & Pillay, 2005).

In the present study I investigated male reproductive strategies at intermediate population density in *R. pumilio* from the succulent karoo. While data were collected about male reproductive strategies during high and low population density, data during intermediate population density were so far not available. This information would enable it to test predictions on male reproductive strategies derived from studies under extreme (high or low)

population densities. The main aim was to test whether the intermediate population density had an influence on male strategy to live in groups or to roam. Another point was to obtain more information about the factors influencing at which age males become reproductively active. In detail, the following hypotheses were tested:

1. Females are a crucial resource for male reproductive success and the distribution of females influences male reproductive strategies (Ostfeld 1990). In particular, I predicted that when female striped mice are distributed in groups, the male strategy would also be a group living, i.e. males would defend groups of communal breeding females. In contrast, when females are solitary and dispersed, males were predicted to follow a roaming strategy, visiting several females.

Null hypothesis (H0): The distribution of females has no influence on male reproductive strategies.

First alternative hypothesis (A1): When females are group living, males are group living, too.

Second alternative hypothesis (A2): When females are group living, males follow a roaming strategy.

2. The home range size should correlate with the reproductive strategy, i.e. males who shows a roaming strategy should have a bigger home range than group living males because of the distribution of the females.

H0: The male reproductive strategy (roaming or group-living) has no influence on home range size.

A1: Roaming males have larger home ranges than group living males.

A2: Roaming males have smaller home ranges than group living males.

3. In mammals typically the males disperse from their natal area to avoid inbreeding and to get a chance of reproducing elsewhere. Thus I predicted that the males in *R. pumilio* disperse while the females stay in their natal area.

H0: There are no sex specific dispersal patterns.

A1: Males are the dispersing sex while females stay at their natal area.

A2: Females are the dispersing sex while males stay at their natal area.

4. Males can only reproduce when they copulate with oestrus females. So I predicted that roaming males visit predominantly females in oestrus.

H0: The oestrus of females has no influence on the presence of males.

A1: Males visit more females in oestrus than females in non oestrus.

A2: Males visit more females in non oestrus than females in oestrus.

5. Reproduction is restricted to the breeding season and male aggression might function to defend the access to fertile females. Thus I predicted that males show more aggressive behaviour during breeding season than outside the breeding season.

H0: The breeding season has no influence on aggressive behaviour of males.

A1: Males show more aggressive behaviour during the breeding season than during non-breeding season.

A2: Males show more aggressive behaviour during the non-breeding season than during breeding season.

6. Adult male and female of *R. pumilio* show aggressive behaviour against mice from other groups (Schradin 2004) but there are no investigations about the difference in territorial response towards neighbours and strangers. Reduced territorial behaviour against neighbours could decrease the costs of territoriality.

H0: There is no difference in aggressive behaviour towards neighbours and strangers.

A1: Neighbours show more aggressive behaviour towards each other than towards strangers.

A2: Neighbours show less aggressive behaviour towards each other than towards strangers.

7. Males with higher body weight might be stronger than males with lower body weight and thus have a better chances to win aggressive encounters.

H0:: Difference of body weight has no influence on aggressive behaviour.

A1: Heavier males show more aggressive behaviour.

A2: Lighter males show more aggressive behaviour.

8. Scrotality is a sign for potential male reproductive activity which could have an influence on aggressive behaviour.

H0: There is no difference in aggressive behaviour between scrotal males and non-scrotal males.

A1: Scrotal males show more aggressive behaviour than non scrotal males.

A2: Scrotal males show less aggressive behaviour than non scrotal males.

9. Male *R. pumilio* are scrotal only during specific periods, but which factors influence scrotality is so far unknown. As scrotality is associated with the breeding season, and breeding is restricted by the amount of available protein in diet, I predicted that the protein content of food might influence this process.

H0: Protein content of food has no influence on scrotality.

A1: Males with protein rich food are more likely to become scrotal than males with protein low food.

A2: Males with protein rich food are less likely to become scrotal than males with protein low food.

10. Another factor that could influence whether males become scrotal or not is population density, as males living under high population density are more likely to meet strange males during the day, which typically react aggressively towards other males (Schradin 2004). Thus, frequency of encounters with strange larger males might influence whether young males become scrotal or not.

H0: Meetings with strange males has no influence on scrotality.

A1: Frequent encounters with aggressive strange males influences scrotality positively.

A2: Frequent encounters with aggressive strange males influences scrotality negatively.

3. Methods

3.1 Study area and period

This study was conducted in Goegap Nature Reserve in Namaqualand, South Africa. Goegap is 20 km away from Springbok, the main town of Namaqualand and situated in the Northern Cape Province. Data were collected from end of June until middle of December 2004.

3.2 Field Studies

3.2.1 Field site

The field site was close to the research station and had a size of 9.5 ha. The study area was a semi-desert with shrubs, bushes and succulents. In spring wildflowers occur. A dry riverbed is passing through the field site. In this area the most common plants are shrubs like *Zygophyllum retrofractum, Lycium cinerum* and succulents like *Mesembryanthemum guerichianum* which are important as food plants for the mice. The vegetation is characterised as succulent karoo (Cowling et al., 1999).

3.2.2 Nest observations

Nine groups of *R. pumilio* were under investigation. To obtain information about the group composition, nest observation were done in the morning and the evening. Observations of the occupants of nests during this time revealed the identities of individual mice (Schradin, accept.). Nest observations started five to 10 minutes before mouse activity occurred and ended after mice had left the nest (in the morning) or after mice entered the nest. Mice activity started in the morning approximately when the sun began shining on the nest. In the evening mice came back to the nests approximately 15 minutes before sun went down. Nest observations were performed with the help of 2-3 field assistants (B. Brietz, P. Wiedmann, M. Scriba, A. Wiedon and E. Krause) and 2-3 co-workers (C. Keller, C. Schradin and M. Schubert), such that 5 – 7 groups were observed daily.

3.2.3 Trapping and marking

Mice were trapped with live traps (26 x 9 x 9 cm, like Sherman traps) baited with a mixture of raisins, bran flakes, salt, oil and peanut butter. Trapping was done in the morning and afternoon. Traps were made ready before nest observation and placed in the shade of bushes. After nest observation in the morning traps were checked twice every hour. In the evening they were checked once before nest observation and twice after nest observation. During the hottest time traps were turned upside down. Trapped mice were weighted, sexed and their reproductive status was determined: males were either scrotal (means the scrotum is visible) or not, for females it was recorded whether their vagina was perforated or not. For individual recognition, mice were marked with numbered ear tags (National Band and Tag Co., USA) and black hair dye (Inecto rapid, Rapido, South Africa). To differentiate females and males, females got hair dye at the head, males at the back. Numbers were written down with a brush and hair dye at the side such that individual recognition during nest observation was possible.

3.2.4 Radio tracking and determination of home ranges

Between June and December 2004, a total of 25 Females and 18 Males were equipped with radio collars (Holohil, Canada, MD-2C weighting 2.5g and PD-2C radio-collars weighting 4.5g). Mice which weighed less then 45g became small radio collars (2.5g), mice which weighed more then 45g became big radio collars (4.5g). Radio tracking was done with an AOR 8000 wide range receiver and a Telonics RA-14K antenna. Data were collected with a GPS (eTrex Venture, GARMIN International, USA). Radio tracking was done once during the day to determine the position of the mice in the field to ensure that the transmitter was moving, indicating that the mouse was still present and alive and had not lost the transmitter (control tracking). All mice were additionally radio-tracked in the late evening after nest observation to determine the sleeping sites and composition of sleeping groups. Home ranges were determined during the non breeding season (June and July) by the field assistant B. Britz and myself and during the breeding season by field assistants, M. Schubert and myself (middle of August-September). For this, each mouse was radio-tracked six times a day at two hours intervals, for a total of nine days (54 fixes; for validation see Schradin & Pillay 2005b). The position was recorded with a GPS (see other methods section). After collecting the data they were saved in the program Map Source. To determine the home range sizes data were converted into Excel and then imported into the program Ranges6.

A total of 21 males were radio-tracked during the entire study, and home ranges before the breeding season were determined for 14 males, during the breeding season for 10 males. During the study, 5 males with transmitters died (N = 4; eaten by a raptor or a snake, N = 1; removing the transmitter) and four males disappeared.

3.2.5 Determination of reproductive strategies

To determine the reproductive strategies of males it is important to differentiate between the group-living and roaming strategy: Group-living means that the male shares a nest with up to 4 breeding females and their non reproducing adult offspring of both sexes (Schradin and Pillay 2004). Roaming strategy means that the male visits several receptive females during different nights (home ranges of females can overlap). I defined a male as group living when he spent 90-100% of nights in the same nest as one group of females and their offspring or one single female and her offspring. I defined a male as a roamer when he spent less than 90% of nights in the nests of one female group.

With data from sleeping sites and nest observations it was possible to determine the reproductive strategy for 16 males. Data for sleeping sites were collected 6 days a week from June to December. Data for nest observation were collected over the whole time 6 days a week. The reproductive strategy for each males was determined monthly from July until November, because males could change their strategy.

3.2.6 Sex specific dispersal data

For determination of sex specific dispersal data of radio-tracked males (N=11) and females (N=15) from September 2004 were used. Data from the natal nests of each individual, which were all born in 2003, was provided by C. Schradin. In the program Map Source the distance between the natal nests and the sleeping sites from September 2004 were measured in meters. About 2 males and 7 females from 9 males and 15 females it was not possible to make a statement because the distance or the nests could not determine exactly in Map Source. Here the problem was one the one hand that the distance was less than 10 meters, so distance could not determine (N=4). One the other hand the nests could not determine exactly because sleeping sites were in the grass fields and exact determination wasn’t possible (N=5).

3.2.7 Influence of females` estrus on males` presence

To investigate if females `estrus had an influence on whether they were visited by males, data from 5 radio-tracked females who had given birth between August and November were used. For this first of all time had to be determined when postpartum estrus, estrus and birth interval occurred. Postpartum estrus occurres 1.1 day after parturition and duration of estrus is 4.6 days (Desbury et al 1984). Birth interval is between 23 –26 days. So postpartum estrus + estrus was defined with 6 days and the birth interval with 25 days. To get information about the day of birth, females were weighted with a scale in front of their nests during nest observation. The scale was prepared with peanut butter as bait. If a female had give birth it could be easily determined with the data of the body weight, because after given birth the body weight decreased by 10g (20%) or more. With data of the radio tracked sleeping sites, male's presence in female's nests could be determined. The number of males visiting females during the period of 19 days before parturition could be compared with the number of males visited females during 6 days after parturition and thus during post-partum oestrus to make a statement if the female's estrus had an influence on the male's presence. Here only solitary females and roaming males were considered.

3.2.8 Statistics

All tests performed were non-parametric and two-tailed (Siegel and Castellan 1988). The Mann Whitney U-Test was abbreviated as U-Test and the Fisher exact test as Fisher-Test. The Fisher Test was used to determine the reproductive strategy of the males. Additionally I used this test for getting information about the influence of oestrus females on males. For comparison of the home range size between males in non-breeding season and breeding season I used the U-test. Additionally I used this test to analyse the sex specific dispersal data. To format, analyse and present the data the following software were used: Microsoft Excel, Microsoft Word and Sigmaplot.

3.3 Variation in male aggression

3.3.1 Animals

For these experiments free-ranging males of *R. pumilio* from the field site were used. Mice were trapped during the non-breeding and breeding-season in the morning between 8 and 10 am in front of their nests at the main field site and in the dry riverbed adjacent to the main field site (see methods before).

3.3.2 Presentation arena and experimental design

To measure aggressive behaviour, trapped males were tested in a neutral presentation arena (see picture 1). Mice were tested in pairs and for each experiment each male was used in only one pair. The 100 x 80 x 65 cm arena was built from 10mm thick chipboard veneered white, lined out with plastic foil on which a 2-3 cm layer of sand was provided to make the arena as natural as possible.

Picture 2: Aggression area

To avoid influence from olfactory cues from previous experiments, e.g. faeces or urine, the sand in the arena was changed between experiments and the arena was cleaned with 90% alcohol (for a similar procedure see Perrin 2001). The sand was obtained from the dry riverbed going through the field site. A partition (79 x 47 x 1.5 cm chipboard) in the middle of

the arena separated the two males to avoid that they could see each other before testing. This habituation phase lasted 5 min before the partition was removed and the experiment started. Seven Sunflower seeds were given to each male during the 5min habituation phase as it is know from experience that this calms down captured wild mice (Schradin, pers. commun). Observation took place in a room in the research station and where made with naked-eye. Duration of observation was 15 minutes. After 15 minutes the experiment was terminated. If the males showed damaging fights (biting), the experiment was immediately terminated before the 15 minutes had vanished. Time from beginning until the first aggressive behaviour occurred was measured as latency time. Time from beginning until males showed biting behaviour was measured as whole time. If the males showed no aggressive behaviour during the 15 minutes whole time was determined as 900 sec = 15 min.
In addition following behaviour patterns were recorded as state:

- Sociopositive: males have body contact, grooming each other
- Neutral: no interactions
- Submissive: sitting far away from each other
- Aggressive: one male chases the other male, fighting (standing on their hind legs and kicking each other with their forelegs), biting

3.3.3 Aggressive behaviour between strangers during non-breeding season and breeding season

To compare aggressive behaviour between the non-breeding (N=9 pairs) and the breeding season (N=10 pairs), males were trapped and tested like described under presentation area. Males of one pair were trapped far away from each other such that they could not have been acquainted with each other.

3.3.4 Aggressive behaviour between strangers and neighbours during breeding season

To test aggressive behaviour between strangers and neighbours, males were trapped during the breeding season and 7 males were tested both with a stranger and with a neighbour as described under aggression area. Neighbours were males who had their home ranges side by

side, as revealed by radio-tracking. Strangers had at least one home range of another male between each other, such that they could not know each other.

3.3.5 Influence of body weight on aggressive behaviour

To test the influence of body weight on aggressive behaviour on males, data from dyads collected during the non-breeding season (N=9) and the breeding season (N=10; see above) were used. Males were weighted before tested in the presentation area. The difference of the body weight was correlated with the time until termination of experiment due to damaging fights (whole time, see above).

3.3.6 Influence of scrotality on aggressive behaviour

To test the influence of scrotality on aggressive behaviour, all males who were tested in the aggression area during non-breeding and breeding season were checked before experiment whether they were scrotal (N=7) or not (N=11). The latency time and whole time was compared between non scrotal and scrotal males.

3.3.7 Statistics

All tests performed were non-parametric and two-tailed (Siegel and Castellan 1988). The Mann Whitney U-Test was abbreviated as U-Test and the Wilcoxon matched pair rank sign test as Wilcoxon-Test. The U-Test was used to compare aggressive behaviour of males between non-breeding and breeding season. It was also used to compare the aggressive behaviour between scrotal and non-scrotal males. For the comparison between strangers and neighbours regarding aggressive behaviour the Wilcoxon –Test was used. To test whether body weight influences aggressive behaviour I made a correlation between the whole time (means time when the experiment starts until the experiment finished) and the difference of body weight. For this correlation the Spearman rank correlation (r_s) was used. Data are presented as medians ± 25% and 75% percentiles. To format, analyse and present the data the following software were used: Microsoft Excel, Microsoft Word and Sigmaplot.

3.4 Experiments in captivity: Factors influencing scrotality

To find out which factors plays a role in male mice becoming scrotal, captive males were separated from the family groups after weaning at the age of 16 days (Brooks 1982; day of birth = day 0) and kept solitary in 26.0 x 15.5 x 20.5 cm (l x h x w) Lab-o-tec^{R} cages. Cages were kept at the veranda of the research station protected from rain under natural weather conditions. Hay was provided as litter material and cotton wool and tissue paper as nesting material. Mice were fed every morning between 7 and 9 am (for details see below). Water was provided ad libitum in the form of cotton wool balls dipped in water. Starting on day 21 mice were weighted and checked weekly until they were scrotal. Experiments were terminated when a male became scrotal.

3.4.1 The influence of protein on scrotality

Males were tested in pairs consisting of siblings from ten different litters (N=10; paired data design) in two experimental groups. Every pair consisted of one solitary male fed with high protein food and one solitary male fed with low protein food. Protein high food consisted of sunflower seeds (peeled sunflowers 22.5g proteins per 100g; DAK nutrition table), low protein food consisted of apples and carrots (apples 0.3g proteins per 100g, carrots 1.1g proteins per 100g; DAK nutrition table).

3.4.2 The influence of encounters with strange males on scrotality

In experiment two all males (N=10 sibling pairs) were fed with high protein food. In each pair, one male functioned as control while the other male was stressed to resemble high population density in the field. To resemble high population density, hay with urine and faeces from strange scrotal males was laid into the cages 5 days a week between 11 am and 13 pm. In addition, scrotal males (stimulus males) were presented 5 days a week for 5 minutes per day between 14 and 17 pm to resemble territorial encounters, which are common in the field in periods of high population density (Schradin, 2004, Schradin and Pillay, 2004, Schradin accep.), but not in season of low population densities (Schradin and Pillay, submit.). During these 5 minutes the same behaviour patterns were recorded as described under the

experiments with the aggression area. If the scrotal male attacked the young male before the 5 minutes were passed, the experiment was stopped. Stimulus males were captive males from the colony kept at the research station (kept solitary in 42 x 15,5 x 26,5 cm (l x h x w) Lab-o-tec^{R} cages and fed as described before) or wild males who lived around the research station and were trapped before starting the presentation. After my departure 4 extra pairs were tested in the station. These data are described separately in the results.

3.4.3 Statistics

All tests performed were non-parametric and two-tailed (Siegel and Castellan 1988). The Wilcoxon matched pair rank sign test was abbreviated as Wilcoxon-Test and used for the experiments in captivity. Data are presented as medians ± 25% and 75% percentiles. To format, analyse and present the data the following software were used: Microsoft Excel, Microsoft Word and Sigmaplot.

4. Results

4.1 Field Studies

4.1.1 Determination of reproductive strategies

In July and August both strategies (roaming strategy and group-living strategy) could be observed. Significantly more males were group-living males than roaming in July (n=10, $p<0.01$, Fisher Test) and August (n=12, $p<0.01$, Fisher Test). In September nearly the same number of group-living and roaming males occurred (n=9, $p<0.01$, Fisher Test). In contrast in October (n=8, $p<0.05$, Fisher Test) significantly more males were roaming than group living. In November (n=6, $p>0.05$, Fisher Test) no signifcance difference could be found. However there was a trend in this month. The results shown in Figure1.

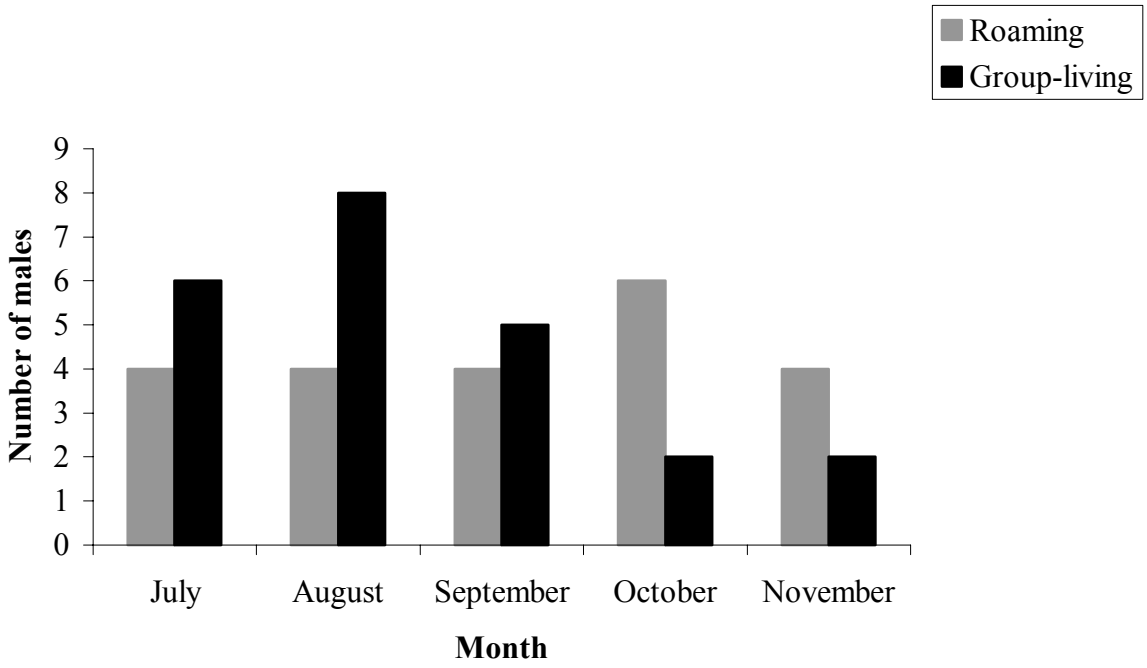

Fig 1: Reproductive strategies of males showed monthly [July $p<0.01$, August $p<0.01$, September $p<0.01$, October $p<0.05$, November $p>0.05$, Fisher Test].

4.1.2 Determination and comparison of home range size

The home range size from roaming males was not significant bigger than the home range size from group living males (n roaming=6, n group=7, p>0.05, U=18, U`=24, U-Test). Median for roaming males was 1.26 ha, 1st/3rd quartile were 1.01/1.34 ha. Median for group-living males was 0.83 ha, 1st/3rd quartile were 0.59/1.44 ha. Results shown in Figure 2.

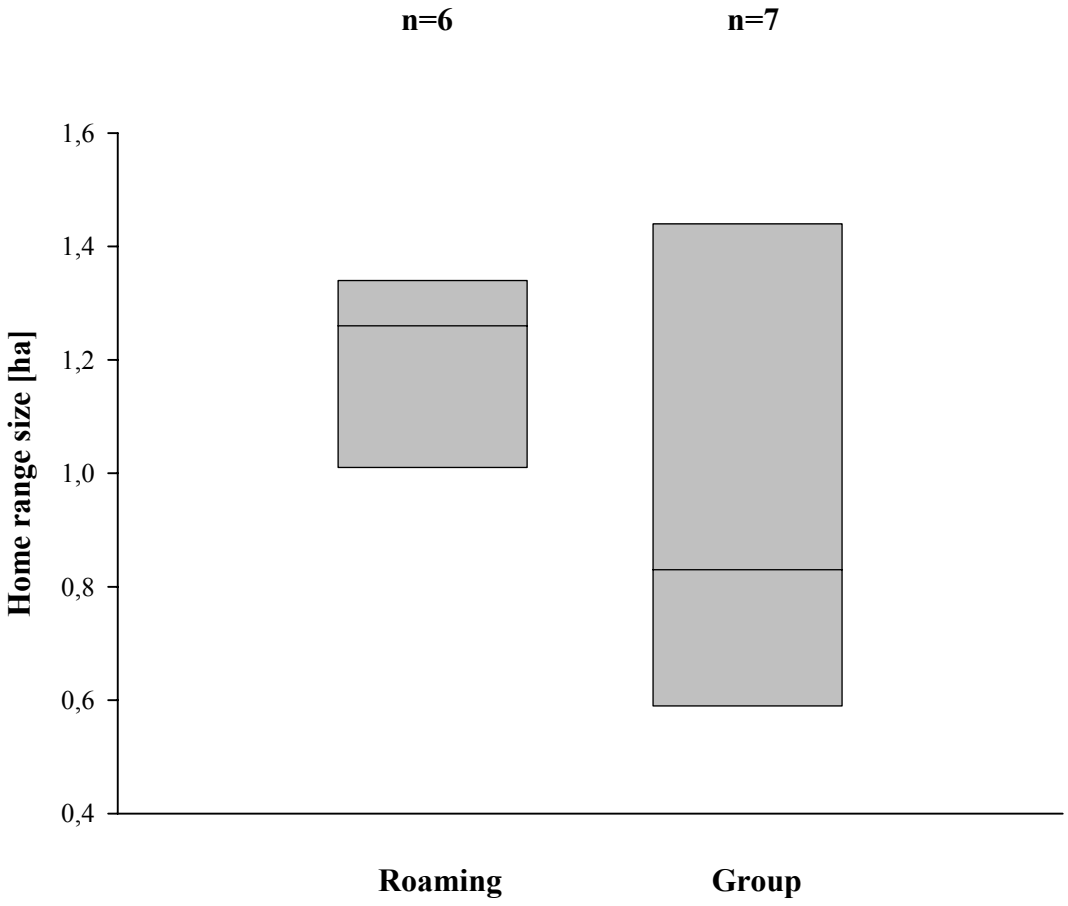

Fig 2: Home range size in [ha] of roaming males (roaming) and group-living males (group) are shown [p>0.05, U-Test].

4.1.3 Sex specific dispersal data

Figure 3 shows that males dispersed significantly farther away from their natal nests than females (n males=9, n females=10 ,$p<0.05$, U=19, U`=71, U-Test). Males dispersed 140.6 m (median, $1^{st}/3^{rd}$ quartile: 96.2/257.3 m), females dispersed 27 m (median, $1^{st}/3^{rd}$ quartile: 11.1/131.8 m).

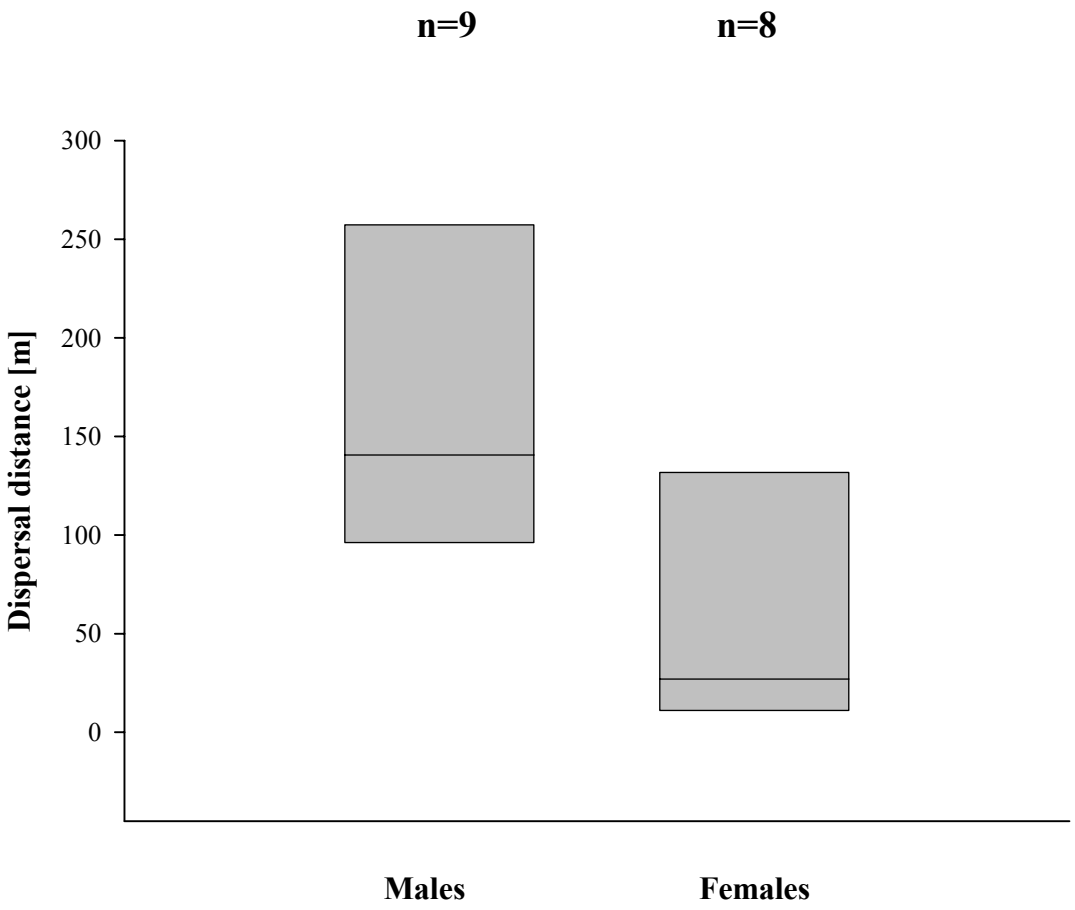

Fig 3: Distance between natal nest from 2003 and sleeping nest in September 2004 [$p<0.05$, U-Test].

4.1.4 Influence of females`estrus on males`presence

Males visited females significantly more often during 19 days before parturition than during 6 days after parturition (n solitary females=5, n roaming males=32, $p<0.05$, Fisher Test).

Table 1: Solitary females and the number of males during 6 days after/ 19 days before parturition [$p<0.05$, Fisher Test].

Females	**Number of males during 6 days after birth**	**Number of males during 19 days before birth**
174	0	0
194	2	4
129	0	10
116	0	15
414	0	1
Σ	**2**	**30**

4.2 Variation in male aggression

4.2.1 Aggressive behaviour between strangers during non-breeding season and breeding season

Latency time (time until first aggression was shown) was not different between the breeding season (BS) and the non-breeding season (NBS; n NBS=9, n BS=10, $p>0.05$, U=30.5, U`=59.5, U-Test; Fig. 4). Median for NBS was 196 s, $1^{st}/3^{rd}$ quartile were 62/402 s. For BS median was 69.5 s and $1^{st}/3^{rd}$ quartile were 6.5/ 311.3 s.

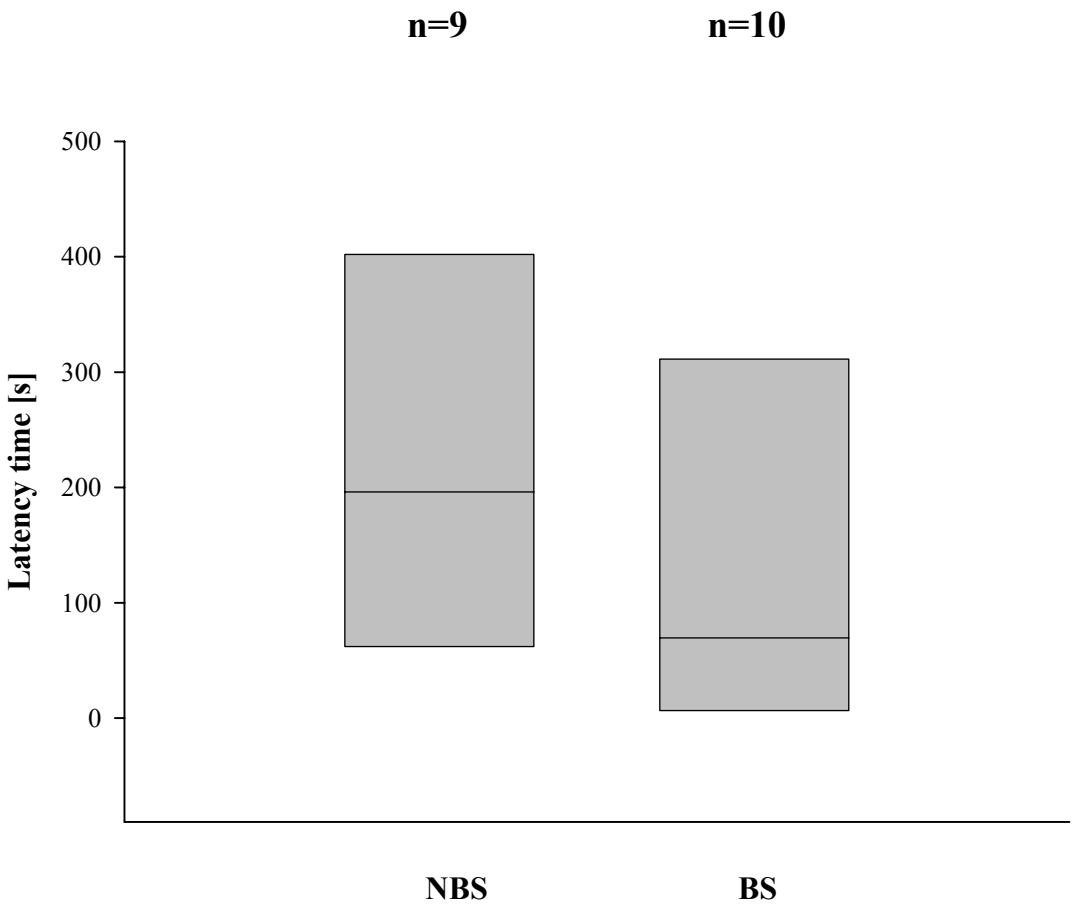

Fig. 4: Latency time until onset of aggression for males during the non-breeding season (NBS) and the breeding season (BS) [$p>0.05$, U-Test].

Whole time (time until damaging fights occurred) did not differ between the breeding season (BS) and the non-breeding season (NBS; n NBS=9, n BS=10, p>0.05, U=37, U`=53, U-Test; Fig. 5). Median for NBS was 565 s, 1st/3rd quartile were 170/900 s. For BS median was 226 s and 1st/3rd quartile were 105.3/610.3 s.

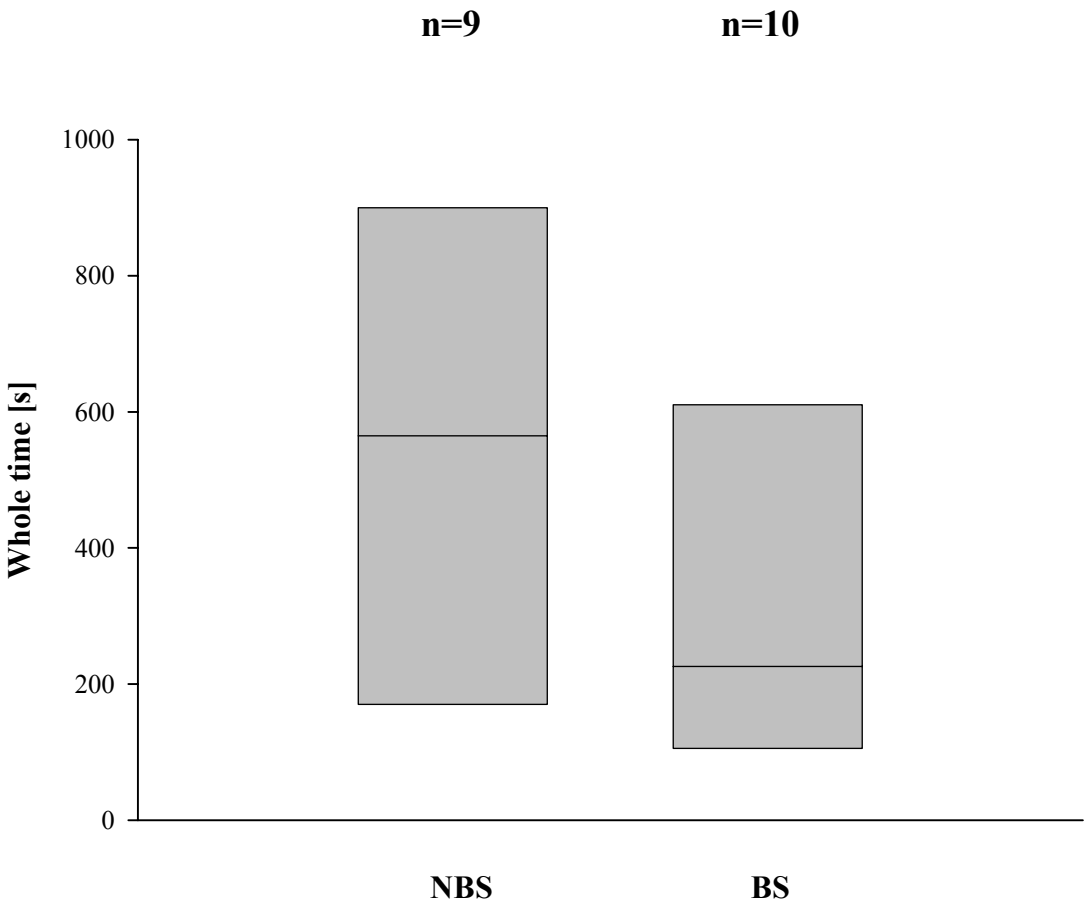

Fig. 5: Duration of experiments before occurrence of damaging fights or end after 900s during the non-breeding season (NBS) and the breeding season (BS) [p>0.05, U-Test].

4.2.2 Aggressive behaviour between strangers and neighbours during breeding season

Latency time was significantly shorter in encounters between neighbours than between strangers (n = 7, $p<0.05$, T=1, Wilcoxon-Test, Fig. 6).Median for neighbours was 43 s, $1^{st}/3^{rd}$ quartile were 15/93 s. For strangers median was 156 s and $1^{st}/3^{rd}$ quartile were 70/342.5 s.

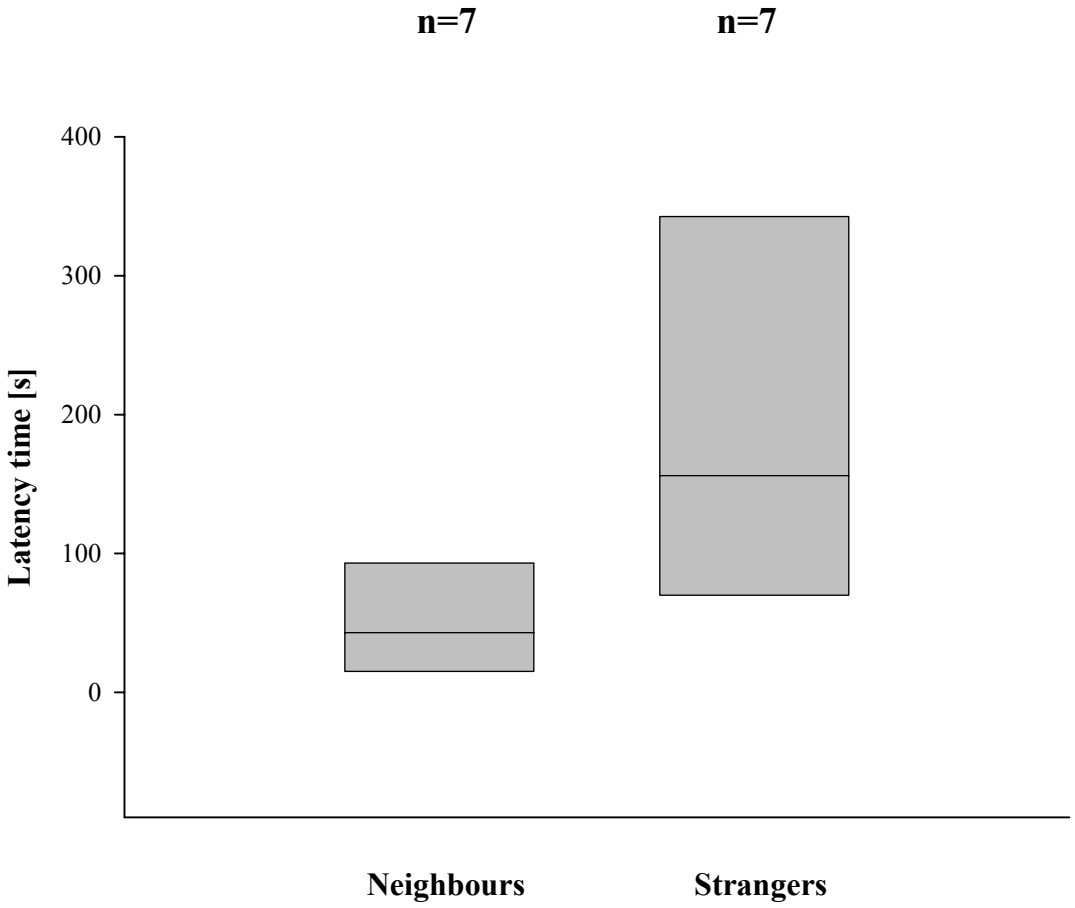

Fig. 6: Latency time until onset of aggressive behaviour between neighbours and strangers [$p<0.05$, Wilcoxon-Test].

Whole time did not differ between neighbours and strangers (n=7, p>0.05, T=4, Wilcoxon-Test, Fig. 7). Median for neighbours was 103 s, 1st/3rd quartile were 84.5/245.5 s. For strangers median was 288 s and 1st/3rd quartile were 134/678 s.

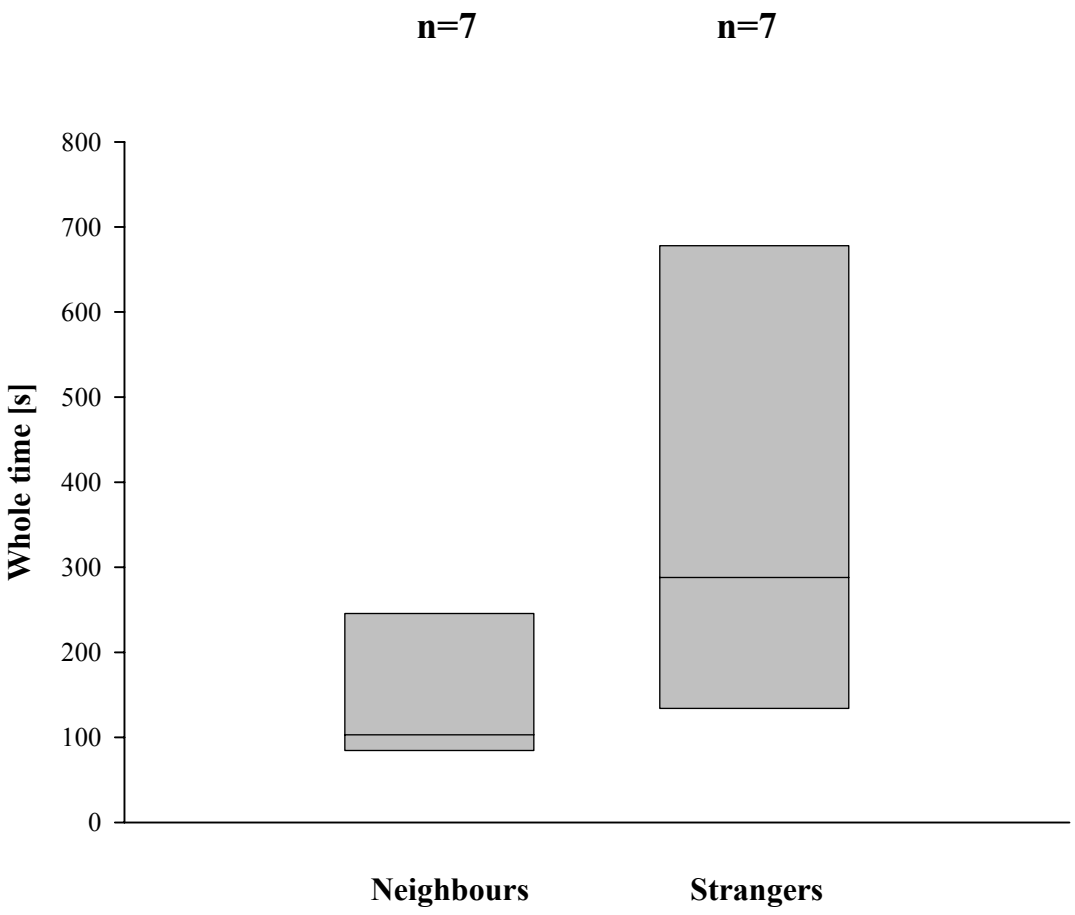

Fig. 7: Whole time until onset of aggressive behaviour between neighbours and strangers [p>0.05, Wilcoxon-Test].

4.2.3 Influence of body weight on aggressive behaviour

During the non-breeding season tested pairs with high difference in body mass did not show significantly faster damaging fights (whole time) than pairs with small difference in body mass. This means that there was no correlation found between the intensity of aggressive behaviour and the body weight (n=9, p=0.64, r_s = -0.18,Spearman rank correlation, Fig. 8).

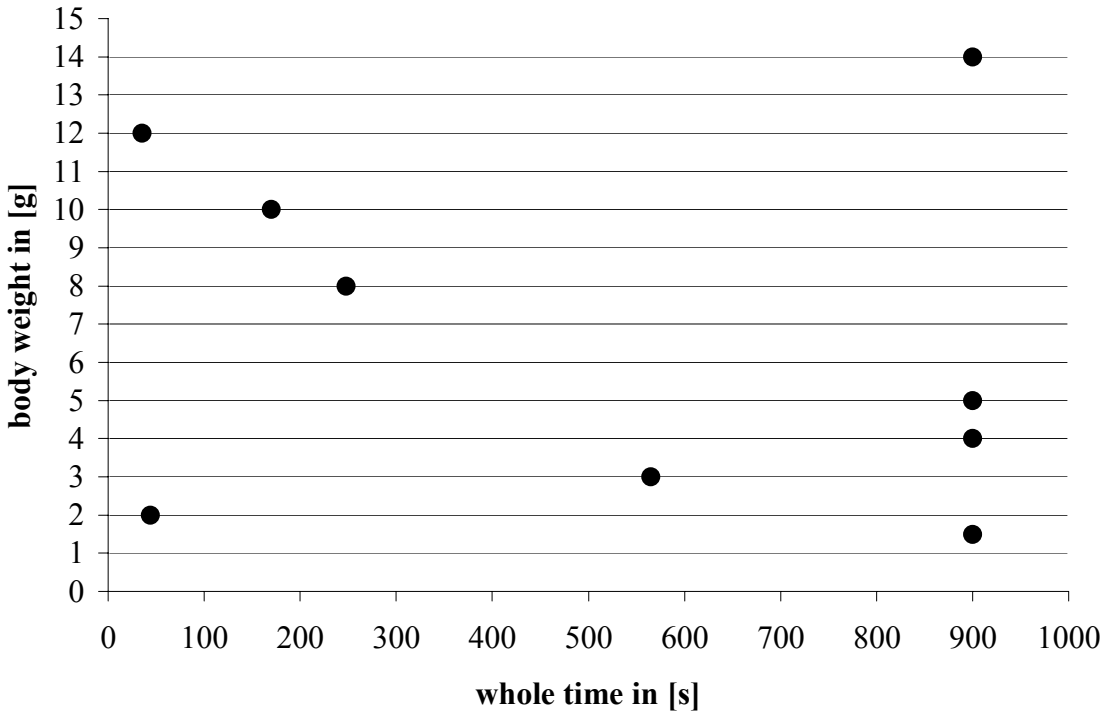

Fig. 8: shows body weight in [g] and whole time in [s] from males during non-breeding season [p=0.64, Spearman rank correlation].

During the breeding season tested pairs with high difference in body mass did not show significantly faster damaging fights (whole time) than pairs with small difference in body mass. This means that there was no correlation found between the intensity of aggressive behaviour and the body weight (n=10, p=0.68, r_s=0.15, Spearman rank correlation, Fig 9).

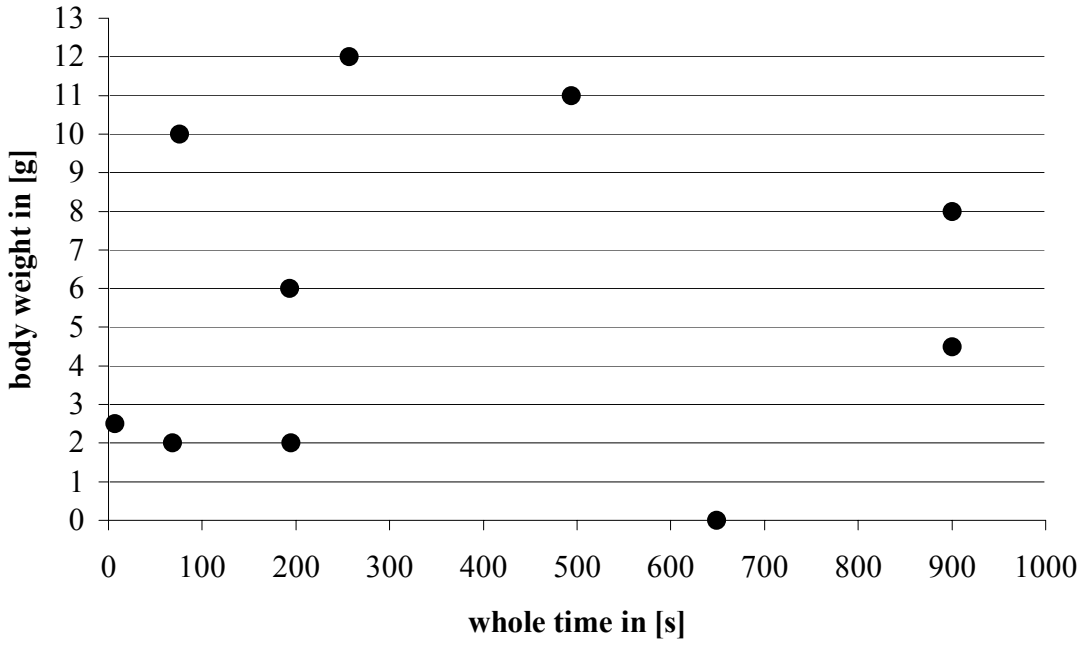

Fig 9: shows body weight in [g] and whole time in [s] during breeding season [p=0.68, Spearman rank correlation].

4.2.4 Influence of scrotality on aggressive behaviour

Latency time of scrotal males was not shorter than that of non-scrotal males (n scrotal=7, n non-scrotal=11, p>0.05, U=22.5, U`=54.5, U-Test, Fig 10). Median for non-scrotal males was 203 s, $1^{st}/3^{rd}$ quartile were 129/538.5 s. For scrotal males median was 102 s and $1^{st}/3^{rd}$ quartile were 7/272.5 s.

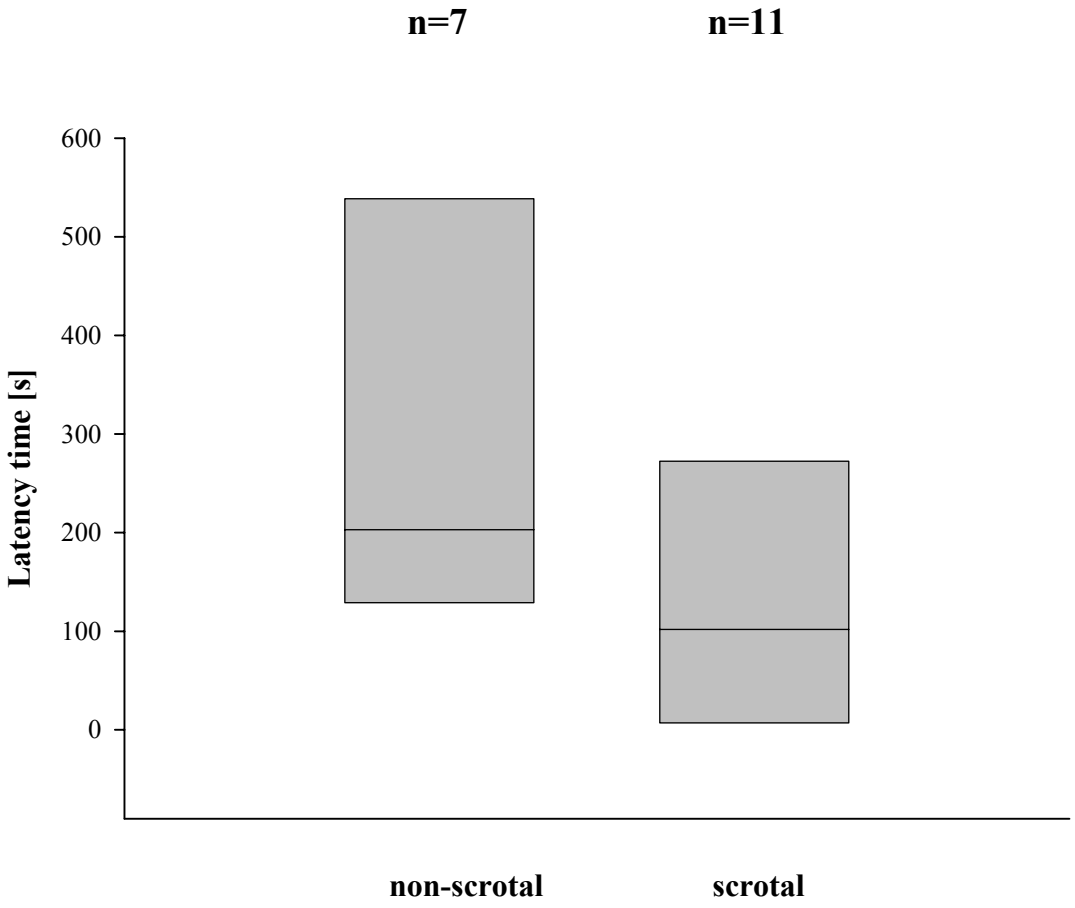

Fig. 10: Latency time until onset of aggression of non scrotal and scrotal males [p>0.05, U-Test].

Whole time did not differ between scrotal and non-scrotal males (n scrotal=7, n non-scrotal=11, p>0.05, U=28, U`=49, U-Test, Fig. 11). Median for non-scrotal males was 900 s, $1^{st}/3^{rd}$ quartile were 209/900 s. For scrotal males median was 257 s and $1^{st}/3^{rd}$ quartile were 134.5/607 s.

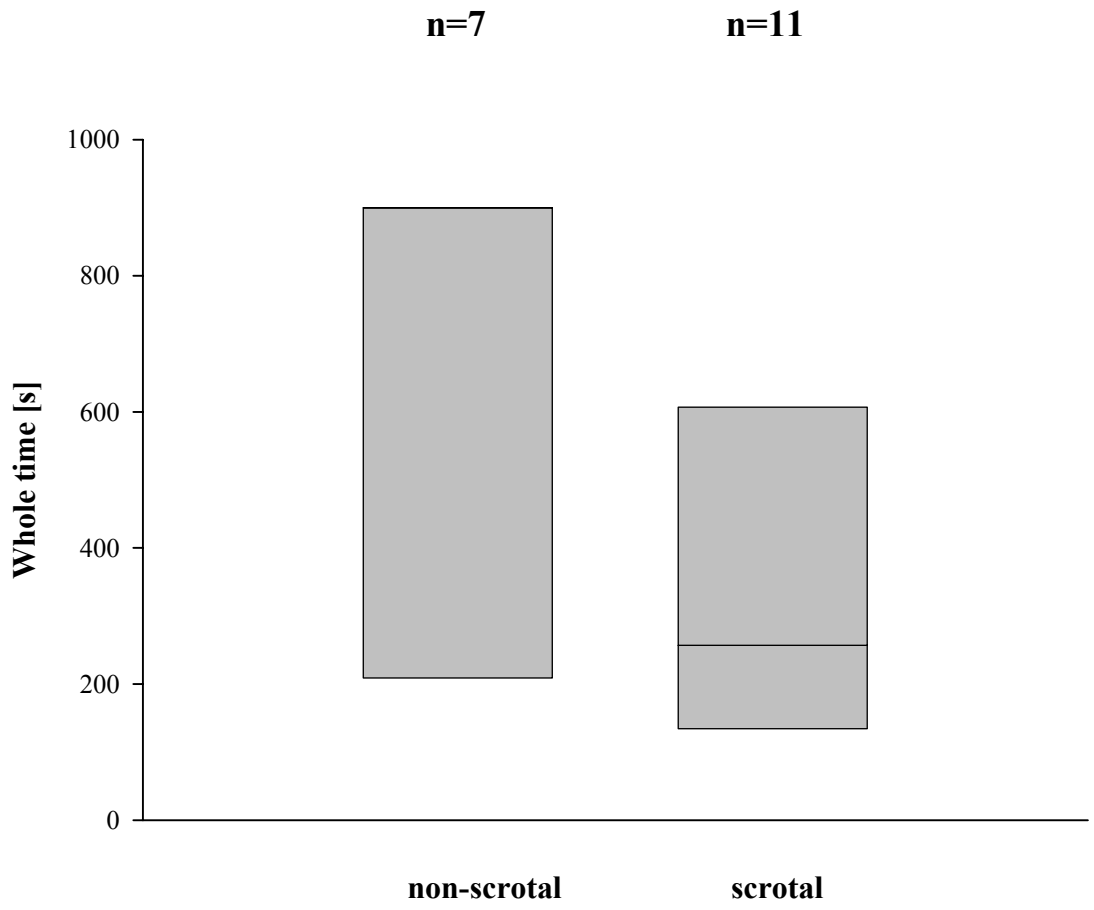

Fig. 11: Whole time until onset of aggression of non scrotal and scrotal males [p>0.05, U-Test].

4.3 Experiments in captivity: Factors influencing scrotality

4.3.1 Influence of protein on scrotality

All males became scrotal in this experiment. Males with high protein diet became scrotal at a significantly younger age than males with low protein diet ($n = 10$, $p < 0.005$, $T=0$, Wilcoxon-Test; Fig. 12). However, males did not differ in body weight when becoming scrotal ($n=10$, $p>0.05$, $T=32.5$, Wilcoxon-Test, Fig. 13). Median for males with high protein diet was 4 weeks, $1^{st}/3^{rd}$ quartile were 4/4 weeks. For males with low protein diet median was 6 weeks and $1^{st}/3^{rd}$ quartile were 6/6.75 weeks.

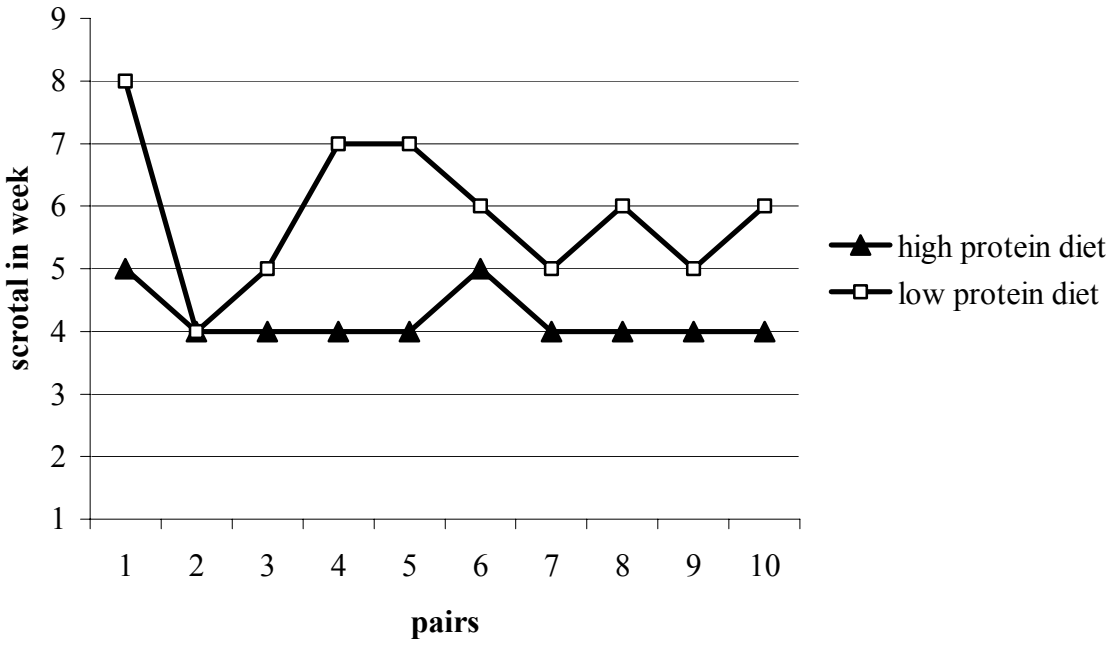

Fig 12: Week of life in which males became scrotal [$p<0.005$, Wilcoxon-Test].

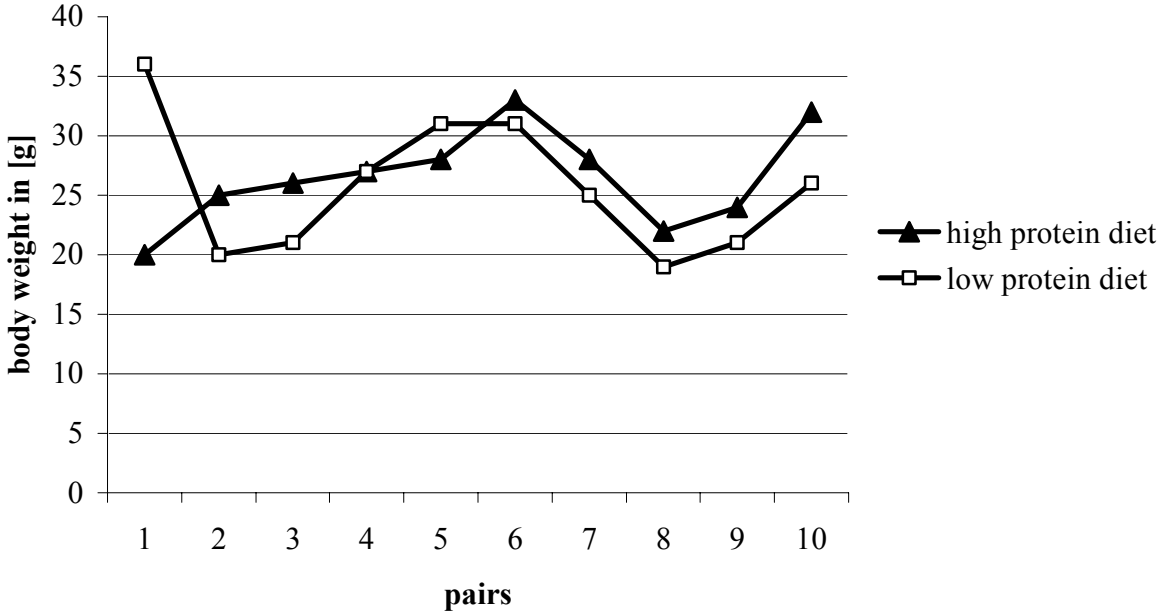

Fig 13: Body weight in [g] when males became scrotal [p>0.05, Wilcoxon-Test].

4.3.2 Influence of encounters with strange males on scrotality

All males became scrotal in this experiment. Males who lived solitary did not become scrotal at a significantly younger age than males who had encounters with strange males (n=10, p>0.05, T=0, Wilcoxon-Test, Fig. 14). However, there was a trend and median for solitary males was 5 weeks, 1st/3rd quartile were 4/6weeks. For males who had encounters median was 5 weeks and 1st/3rd quartile were 5.5/6weeks.There was also a trend in difference of body weight when males became scrotal (n=10, p=0.05, T=4, Wilcoxon-Test, Fig. 15)

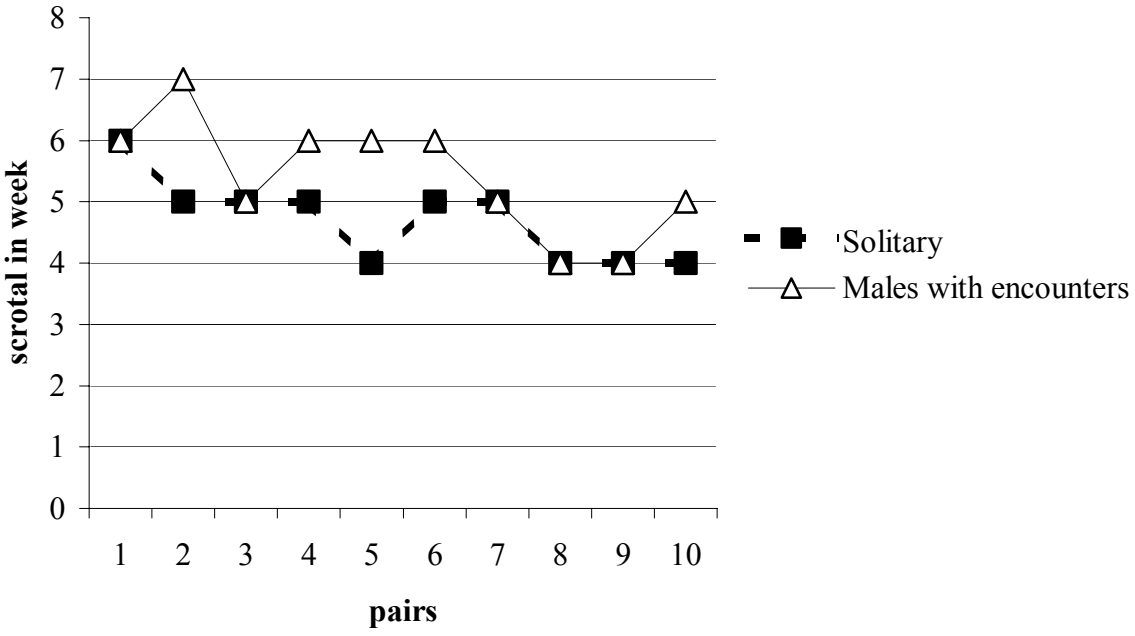

Fig 14: Week of life in which males became scrotal [p>0.05, Wilcoxon-Test].

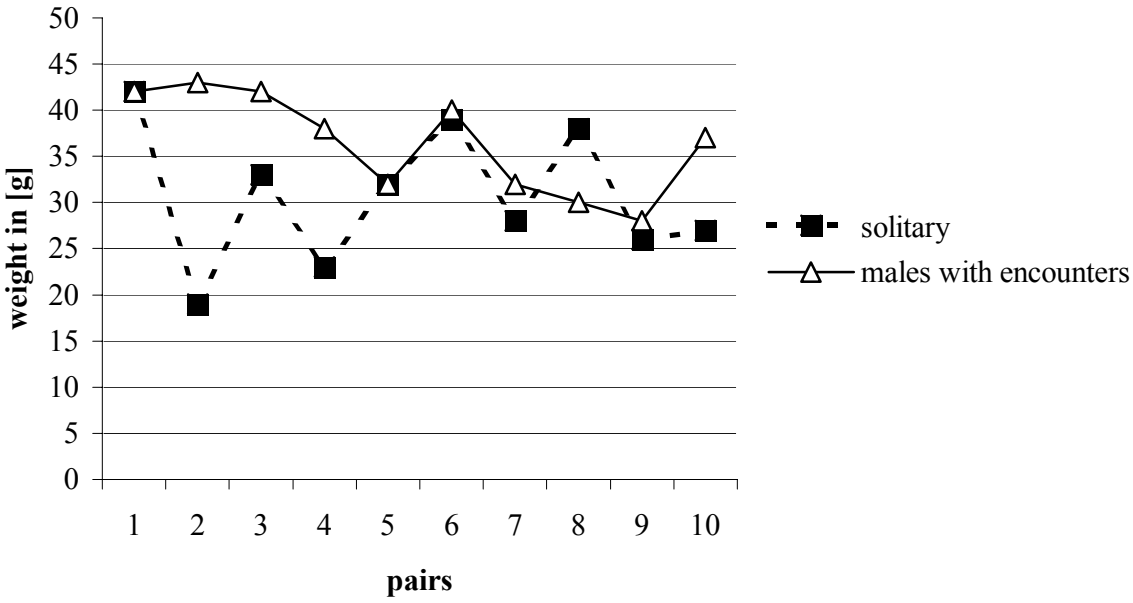

Fig 15: Body weight in [g] when males became scrotal [p=0.05, Wilcoxon-Test].

Data high population density with extra pairs showed that solitary males became very significant faster scrotal than males who had encounters with strange males (n=14, p <0.01 very significant, T=0, Wilcoxon-Test, Fig 16). Median for solitary males was 4.5 weeks, $1^{st}/3^{rd}$ quartile were 4/5 weeks. For males who had encounters median was 5.5 weeks and $1^{st}/3^{rd}$ quartile were 5/6 weeks. Solitary males had significantly more body weight when becoming scrotal than males who had encounters with strange males (n=14, p=0.01, T=6, Wilcoxon-Test, Fig 17).

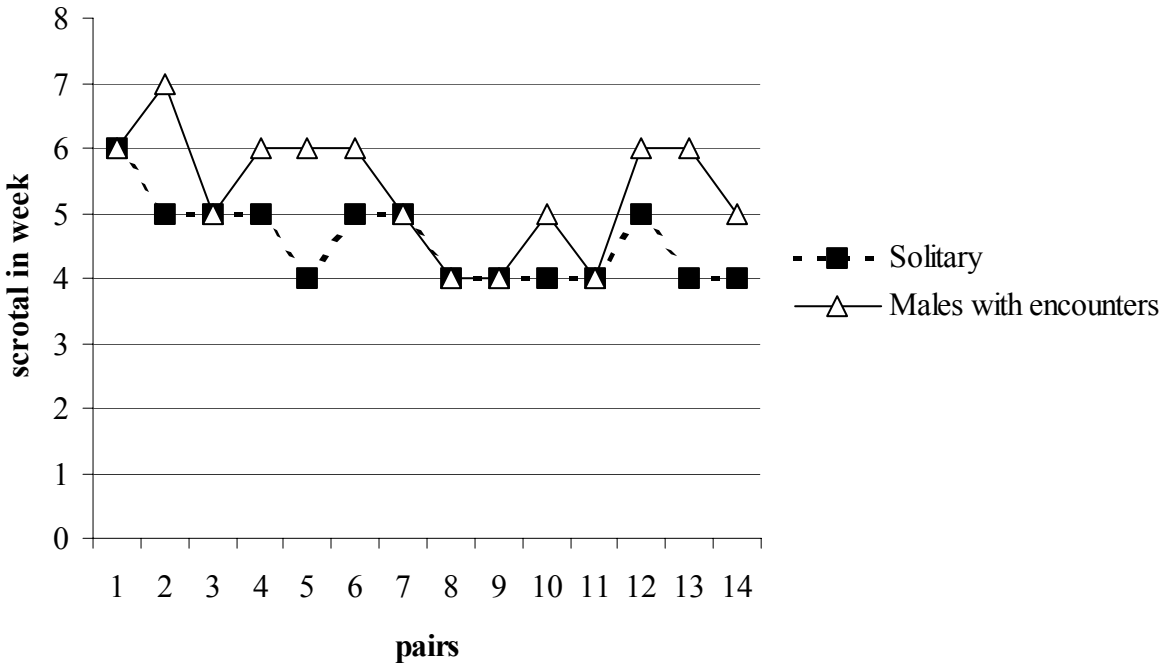

Fig 16: Week of life in which males became scrotal [p<0.01, Wilcoxon-Test].

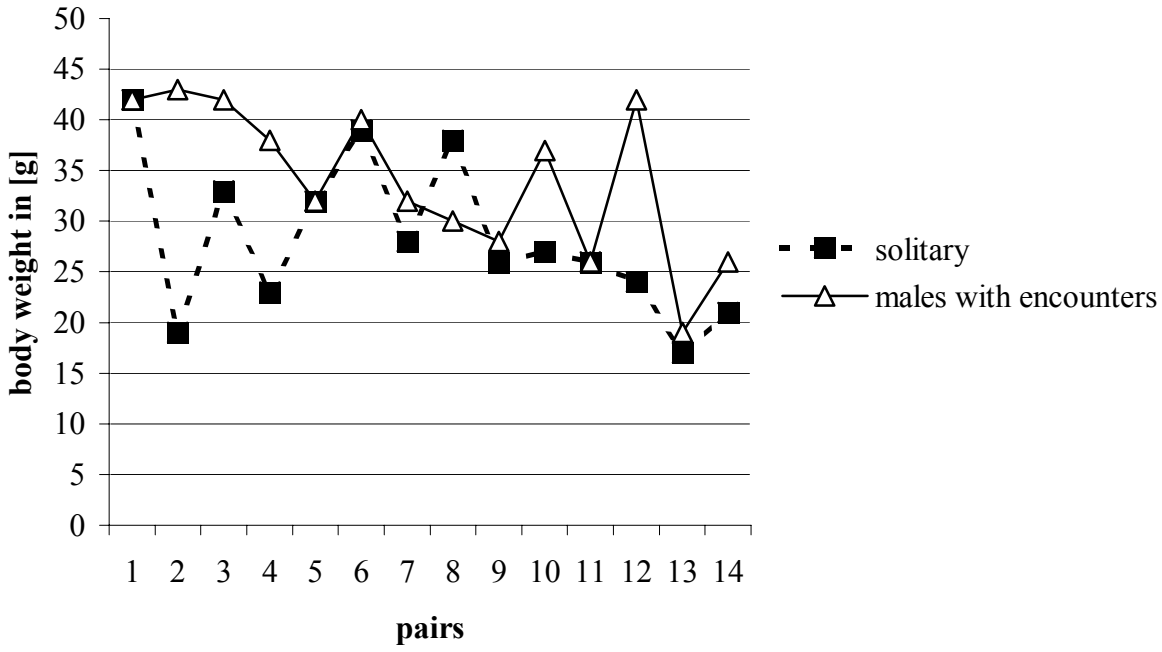

Fig 17: shows body weight in [g] of males in time became scrotal [p=0.01, Wilcoxon-Test].

5. Discussion

5.1 Field Studies

5.1.1 Determination of reproductive strategies

It was predicted that the roaming strategy is used if females are solitary and dispersed in a home range of one male. In contrast, if females live in one group, the males were predicted to be also group-living. Males and females are solitary foraging during the day. While foraging they can meet each other and possibly copulate. In this study only data from sleeping sites and nest observation were used to determinate the reproductive strategies. To obtain foraging data it would have been necessary to follow and observe mice for the entire day. During the entire study from July until November males showed both strategies, the roaming strategy as well as group-living. In the month July and August (during non breeding season) significantly more males were group-living than roaming. In September breeding season started and the situation changed. Nearly the same number of males showed roaming and group-living behaviour. During September several females gave birth for the first time. It could be observed that some pregnant females leaved their group a few days before parturition and changed to a solitary lifestyle. So the males had to change their behaviour as well to become a chance to mate with the females. In October there were significant more roaming males than group-living males. October was the month with the highest birth rate. Most of the females who gave birth in October were solitary living, so this matched with the results of the males. In November also more roaming males than group living males occurred. In this month only one female was group living, all other females showed a solitary lifestyle. Like in October this matched with the results of the males. To determinate the reproductive strategies a limit had to be fixed between roaming and group living. It was not easy to determinate this limit because no exactly definition could be found. So in this case I determinate the limit for group living between 90% to 100% because it was easier to differentiate between roaming males and group living males. However it needs to be mentioned that some roaming males showed group living behaviour for a very short time. For further investigations it could be helpful to differentiate these limits in a more detailed way. In conclusion it can be said that the present study shows during a mean population density the strategy of the males is adapted to the distribution of the females.

5.1.2 Determination and comparison of home range size

In this part of the study the consideration was that the home range size should correlate with the reproductive strategy, i.e. home range size of roaming males should be bigger than home range size of group-living males because of the distribution of the females. But results showed that the home range size from roaming males were not significant bigger than the home range size from group living males. One reason for this might be that the solitary females were not distributed so far away from each other, so the males had not to roam widely. The results showed that generally the home range size of group-living males was smaller than one ha while in roaming males the home range size was bigger than one ha. Here it should be mentioned that the sample size was very small. Further work is needed to get more information in detail. It would be interesting also to compare the home range size from the same males during non-breeding season and breeding season to get information about if males change their home range size during seasons. Here it can be said that the reproductive strategy had no influence on the home range size.

5.1.3 Sex specific dispersal data

I predicted that the males in *R.pumilio* disperse from their natal area while the females stay in their natal area. Here the results confirmed the prediction. Males dispersed significantly farther away from their natal nests than females. Causes for this could be possibly to avoid inbreeding and to get a chance of reproduction out of the natal area. Males showed only distances more than 50 meters while most of the females dispersed less than 50 meters.
This could be due to the fact that females' home ranges can overlap while males' home ranges don't overlap. So males had to dispersed more than females to get a chance of reproduction elsewhere. For further investigations it would be interesting to compare this data with the data during small and high population densitiy to get information in detail if differences exist during difference poulation densities.

5.1.4 Influence of females`estrus on males`presence

Females`estrus had no influence on males present. In contrast to the prediction males were presence more often before parturition than after parturition. One causation for this might be that mating occurs possibly during the day when mice are foraging and not staying at the nest. Some females stayed close to the group until a few days before parturition and were solitary living during parturition and after parturition. This could due to avoid infanticide. Another reason for this results could be maybe that females are more aggressive after parturition for defending their offspring. A strategy to avoid infanticide (given birth at a solitary nest and maternal aggression after parturition) avoid possibly that females will be pregnant after parturition. More information in detail (e.g. follows of mice during the entire day) will be necessary to get a better insight in this question. For this maybe it would be helpful to increase the sample size. In conclusion it can be said that in this study the present of the males at the nest of the females was not influenced by the estrus of the females.

5.2 Variation in male aggression

5.2.1 Aggressive behaviour between strangers during non-breeding season and breeding season

Strange males showed not significant more aggressive behaviour during breeding season then during non-breeding season. So breeding season had no influence on aggressive behaviour on strange males. One causation for this behaviour could be that it serves not only for defending females but also for defending food resources. Another point which should consider that the time for collected data in non-breeding season was maybe to late. Field data showed, that some of the males roamed at this time, possibly searching for females. Males should begin to roam before breeding season to search for females and to get a chance to immigrate in a group. Otherwise it could be to late to find a mating partner. In addition the stress level during trapping and testing in the aggression area should not be ignored. Some males were sitting still during the whole 900 seconds and it seems as if they had fear in this unknown area. Other males like male 419 showed a very high level of aggressive behaviour in general. Regarding to the number of tested males it could be that it was to small. This point should maybe be considered in further investigations, as well as the fact that this study was only descriptive. The level of aggressive behaviour was only determined with direct observation. There were no experimental confirmation through hormonal analyses. This would complete further investigations. In conclusion it can be said that the level of aggressive behaviour in males is not only lead back to the breeding season but also to other factors in non-breeding season, like competition for food or to find a mating partner or a group premature.

5.2.2 Aggressive behaviour between strangers and neighbours during breeding season

Mice showed significantly more aggression towards neighbours in latency time but not in whole time. So males tolerate strangers more than neighbours. One explanation for this could be that males from neighbouring home ranges are competitors with regard to the females and this is the reason why they show more aggressive behaviour towards neighbours than towards strange males. *R. pumilio* is a solitary foraging rodent. During foraging males could possibly meet females from neighbouring groups. It is known that females copulate often only with known males (Ferkin, 1988; Parker et al., 2001). These known males are the male from the own group and maybe neighbouring males. In this case strange males were not regard as competitors. Another point of interest could be that roaming is spread widely, e.g. neighbouring males would be in direct competition for the same females, if they roam in the same area. Another explanation could be competition for food resources, especially in desert areas where rainfall is not regular. Here it can be said that in this study it did not seems as the dear enemy phenomenon does occure in *R. pumilio* in the succulent karoo.

5.2.3 Influence of body weight on aggressive behaviour

Tested pairs with high difference in body mass did not show significantly more aggression than pairs with small difference in body mass, neither during non-breeding season nor during breeding season. There was no correlation between the intensity of aggressive behaviour and body weight. It seems as the difference in body weight had no influence on aggressive behaviour of males. Males needs force for fight with competitors. So heavier males should have an advantage against males with less body weight. Normally the higher the difference in body weight the more males heavier body weight should be advanced. But in nature it could be observed that also males with less body weight were likely to attack strangers in front of their nests even those significantly heavier than themselves (Schradin, 2004). In the aggression area circumstances are different from nature. Here it should mentioned that trapping and testing the males in the aggression seemed to be influenced by the stress factor.
Here it can be said that the difference of the body weight had no influence on the aggressive behaviour.

5.2.4 Influence of scrotality on aggressive behaviour

Scrotal males showed not more aggression than non-scrotal males. Thus, scrotality had no effect on aggression in males. One reason for this might be that other factors than scrotality could have an influence on the level of aggressive behaviour, e.g. competition for food or other resources. Future work is needed to get more information in detail, e.g. it would be necessary to make hormone analyses to measure the testosteron level. It is known that testosteron has an influence on the aggressive behaviour (Sinervo, 2000). It would be interesting to get an insight how far hormones (like testosteron) influences the aggressive behaviour of the males in *R. pumilio*.

5.3 Experiments in captivity: Factors influencing scrotality

5.3.1 Influence of protein on scrotality

I predicted that quality of food had an influence on captivity males becoming scrotal because nutrition and energy are essential for reproduction in mammals (Sadleir,1984; Loudon and Racey,1987; Kunkele,2000). In this investigation all males in the experiment became scrotal which means a low protein diet could not prevent males from becoming scrotal. But it delayed the time until males became scrotal because males with high protein diet became significantly faster scrotal than males with low protein diet. Between pairs no difference in body weight could be found refer to the time when males became scrotal. This was due to the fact that low protein diet decreased the growth. Thus influenced the time becoming scrotal. So further investigations are needed to make a statement about which factors influencing suppression in young males of *R. pumilio*. In conclusion it can be said that the protein diet had only an influence on the time becoming scrotal. But it could not prevent scrotality.

5.3.2 Influence of encounters with strange males on scrotality

I predicted that encounters with strange males had an influence on young males becoming scrotal or not. Like in the experiment before all males became scrotal. The males who lived solitary became scrotal at a younger age than males who had encounters with strange males, but this result was not significant. However, the sample size for this experiment as enlarged from 10 to 14 after my absence, and with this higher statistical power males which encountered strange males were significantly older when getting scotal than control males.
Another point which could be discussed is that maybe it was not enough to presented only one scrotal strange male five times a week. It could be that presenting one strange scrotal male in the morning and another one in the afternoon could have a stronger effect on the young males. And represent the situation in the field under high population density could be maybe more adequately. So it can be said that this experiment had an influence on the time when males became scrotal but could not prevent scrotality.

6. General conclusions

This study investigated the variation of male reproductive strategies in the south african striped mouse (*R.pumilio*) in the succulent karoo in a mean population densitiy.

In conclusion to the corresponding hypotheses the following results can be summarized:

The hypothesis that the distribution of females had an influence on the reproductive strategy could be verified. Males showed the roaming strategy as well as the group-living strategy during July and November. But the reproductive strategy had no influence on the home range size. No significant differences could be found between roaming males and group-living males. This could be due to the solitary females, who might not be distributed so far away from each other. The hypothesis that males disperse farther away from their natal nest than females was verified. The significant differences could be caused by the aim to avoid inbreeding and to get a chance of reproduction outside the natal area. The hypothesis that the females` estrus had an influence on males` presence could not be verified. In contrast it could be found that roaming males visited solitary females significantly more during 19 days before parturition. One reason for this might be that mating occurs during the day while mice are foraging. In this study it could be shown that males of *R.pumilio* obviously adapted their reproductive strategy to the distribution and behaviour of the females but further work is needed to assess the facts influencing the reproductive behaviour of the males in more detail.

The hypothesis that the breeding season has an influence on the aggressive behaviour could not be verified. No significant differences could be found between non-breeding and breeding season. This could be due to other factors which might have an influence on the level of aggressive behaviour independent of the breeding season. The hypothesis that neighbours tolerate each other more than strangers could not be verified. In contrast results showed that neighbours react significant more aggressive towards each other than towards strangers. Competition for females might be a reason for this unexpected behaviour. Body weight and scrotality had no significant influence on the level of aggressive behaviour. This could be due to other factors which could be important for the level of aggressive behaviour, e.g. defensible resources like females or food . For further investigations it would be interesting to measure the testosteron level additionally to get more information about factors influencing aggressive behaviour.

The captivity experiments showed that the quality of protein diet and encounters of strange males are not responsible for reproductive suppression in young males of *R.pumilio.* The protein diet as well as the encounters with strange males could delayed the age when males became scrotal, but could not prevent scrotality. So here it can be said that other factors are responsible for reproductive suppression in males.

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9. Appendix

Unabhängigkeitserklärung – Declaration of Independence

Hiermit erkläre ich, dass ich die vorliegende Diplomarbeit selbstständig verfasst und keine anderen als die aufgeführten Quellen und Hilfsmittel verwendet habe.

I herewith declare that this thesis was written independently by myself and no sources or aids were used other then those listed.

Ort, Datum

Determination of reproductive strategies

Table 2: Reproductive strategy for males showed monthly;
G=Group-living, R=Roaming

Individual	July	August	September	October	November
403	-	R	R	R	-
419	R	G	G	-	-
141	R	G	G	R	R
423	-	-	G	G	G
421	G	G	-	-	-
413	-	G	-	-	-
113	G	G	R	R	R
457	-	-	G	R	R
405	G	G	-	-	-
437	G	G	G	R	R
427	-	R	R	R	-
407	-	-	-	G	G
441	G	-	-	-	-
409	G	G	-	-	-
429	R	R	-	-	-
91	R	R	R	-	-

Table 3: p-values of reproductive strategy showed monthly

Month	July	August	September	October	November
p-value	0.0048	0.0020	0.008	0.0357	0.07

Table 4: Number of whole tested males, roaming males and group-living males are shown for every month from July until November.

	July	August	September	October	November
Number of males	10	12	9	8	6
Roaming males	4	4	4	6	4
Group living males	6	8	5	2	2

Determination and comparison of home range size

Table 5: shows home range size (HR size) of roaming males and group living males in [ha]

Male	HR size roaming [ha]	HR size group [ha]
91	1.60	
113	1.35	1.71
141		
403	0.95	
405		0.23
407		1.43
419		
421		0.83
423		1.45
427	1.32	
429	0.48	
437	1.20	0.78
441		0.40

Sex specific dispersal data

Table 6: row data from dispersal of males

Male ID	Natal nest	Year of birth	Sleeping site Sept 2004	Distance [m]
91	S16	2004	S148	140.6
141	S95	2003	S140	96.2
113	Gras2	2003	B18	104.2
437	S19	2003	S129	65.8
427	S19	2004	S145	144.8
403	S62	2003	S131	248.4
429	S23	2004	S136	55.6
459	S107	2003	S5	257.3
457	S16	2004	S5	361.1

Table 7: row data from dispersal of females

Female ID	Natal nest	Year of birth	Sleeping site Sept 2004	Distance [m]
102	N8	2003	S5	159.4
426	F16	2003	S131	268.1
412	S85	2003	S152	14.5
410	S85	2003	S152	14.5
174	S100	2003	S140	562.9
194	S19	2003	B18	39.5
406	S62	2003	S129	49.1
116	S76	2003	S153	204.2

Aggressive behaviour between strangers during NBS and BS

Table 8: Row data of latency time in [s] during NBS (non-breeding season) and BS (breeding season)

	NBS		BS	
Number of pairs	**ID males**	**Latency time [s]**	**ID males**	**Latency time [s]**
1	441/141	203	427/403	5
2	189/409	62	457/419	8
3	413/433	196	113/429	102
4	429/175	675	437/141	4
5	457/445	900	497/449	350
6	423/435	171	445/451	37
7	411/403	25	467/453	417
8	419/437	30	479/79	900
9	91/421	402	507/423	6
10			509/443	195

Table 9: Row data of whole time in [s] during NBS (non-breeding season) and BS (breeding season)

	NBS		BS	
Number of pairs	**ID males**	**Whole time [s]**	**ID males**	**Whole time [s]**
1	441/141	248	427/403	257
2	189/409	170	457/419	76
3	413/433	900	113/429	649
4	429/175	900	437/141	193
5	457/445	900	497/449	494
6	423/435	565	445/451	68
7	411/403	44	467/453	900
8	419/437	35	479/79	900
9	91/421	900	507/423	7
10			509/443	195

Table 10: p-values of latency and whole time and medians ± 25% and 75% percentiles of NBS (non-breeding season) and BS (breeding season)

	p-value	**median**		**25% percentile**		**75% percentile**	
		NBS	**BS**	**NBS**	**BS**	**NBS**	**BS**
Latency	0.25	196	69.5	62	6.5	402	311.25
Whole	0.54	565	226	170	105.25	900	610.25

Aggressive behaviour between neighbours and strangers

Table 11: Row data of latency time and whole time in [s] of neighbours and strangers

	Latency time			**Whole time**		
Number of pairs	**ID males**	**Neighbours [s]**	**Strangers [s]**	**ID**	**Neighbours [s]**	**Strangers [s]**
1	141/113	100	231	141/427	103	288
2	429/141	25	136	429/437	134	900
3	423/403	43	156	423/429	357	169
4	113/457	141	900	113/407	900	900
5	457/437	86	454	457/MW	98	456
6	437/427	5	4	437/403	71	72
7	403/113	2	4	403/407	4	99

Table 12: p-value of latency and whole time and medians ± 25% and 75% percentiles of Neighbours (N) and Strangers (S).

	p-value	Median		25% percentile		75% percentile	
		N	S	N	S	N	S
Latency	0.03	43	156	15	70	93	342.5
Whole	0.22	103	288	84.5	134	245.5	678

Differences of body weight

Table 13: Row data of body weight difference in [g] in comparison to latency time and whole time in [s]

	NBS				BS			
Number of pairs	**ID males**	**Latency time [s]**	**Whole time [s]**	**Difference of body weight [g]**	**ID males**	**Latency time [s]**	**Whole time [s]**	**Difference of body weight [g]**
1	441/141	203	248	8	427/403	5	257	12
2	189/409	62	170	10	457/419	8	76	10
3	413/433	196	900	4	113/429	102	649	0
4	429/175	675	900	5	437/141	4	193	6
5	457/445	900	900	1.5	497/449	350	494	11
6	423/435	171	565	3	445/451	37	68	2
7	411/403	25	44	2	467/453	417	900	4.5
8	419/437	30	35	12	479/79	900	900	8
9	91/421	402	900	14	507/423	6	7	2.5
10					509/443	195	195	2

Table 14: p-value of NBS (non-breeding season) and BS (breeding season) and median ± 25% and 75% percentiles

	NBS				BS			
	p-value	**Median**	**25% P**	**75%P**	**p-value**	**Median**	**25% P**	**75% P**
Latency	0.64	565	170	900	0.68	226	105.25	610.25
Whole	0.81	196	62	402	0.76	69.5	6.5	311.25

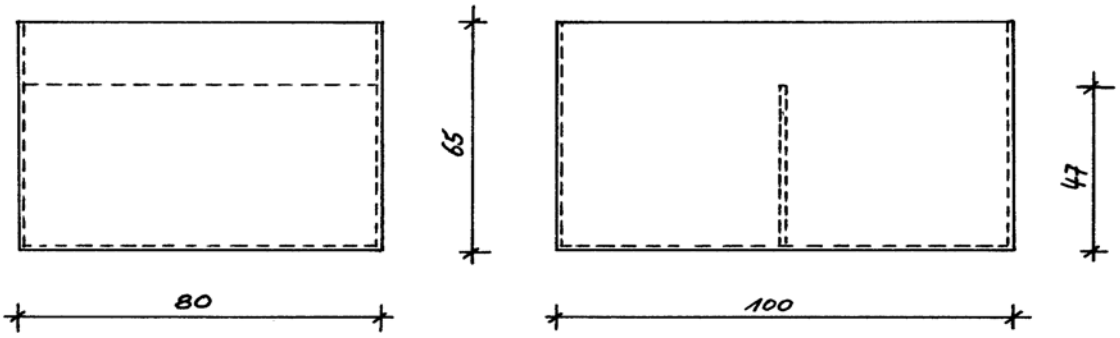
Aggressive behaviour in non-scrotal and scrotal males

Table 15: Row data of latency/whole time in [s] from non scrotal /scrotal males

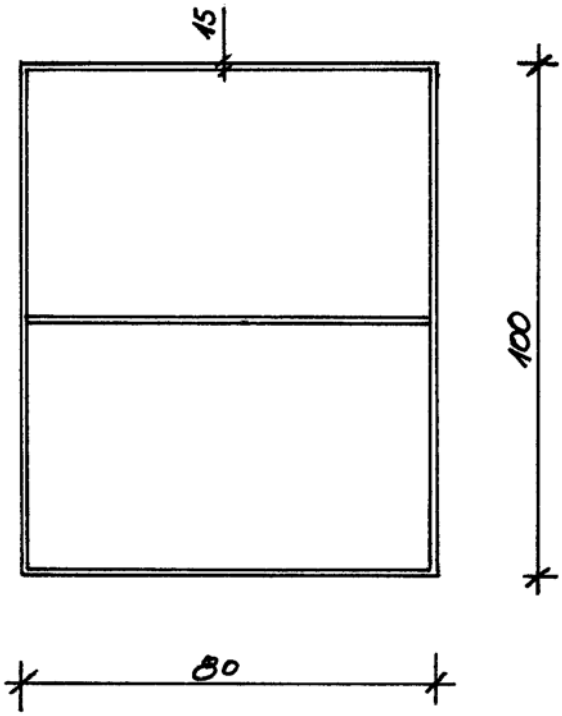
	Non scrotal			Scrotal		
Number of pairs	**ID males**	**Latency time [s]**	**Whole time [s]**	**ID males**	**Latency time [s]**	**Whole time [s]**
1	441/141	203	248	427/403	5	257
2	189/409	62	170	457/419	8	76
3	413/433	196	900	113/429	102	649
4	429/175	675	900	437/141	4	193
5	457/445	900	900	497/449	350	494
6	419/437	30	35	445/451	37	68
7	91/421	402	900	467/453	417	900
8				479/79	900	900
9				507/423	6	7
10				509/443	195	195
11				423/435	171	565

Aggression area

Side view



Over view



Experiments captivity

Table 16: Row data of quality of protein diet

Pair	high protein diet		low protein diet	
	Body weight [g]	Scrotal in week	Body weight [g]	Scrotal in week
1	20	5	36	8
2	25	4	20	4
3	26	4	21	5
4	27	4	27	7
5	28	4	31	7
6	33	5	31	6
7	28	4	25	5
8	22	4	19	6
9	24	4	21	5
10	32	4	26	6

Table 17: p-value and medians ± 25% and 75% percentiles of high protein diet (hpd) and low protein diet (lpd)

p-value	Median		25% percentile		75% percentile	
	hpd	lpd	hpd	lpd	hpd	lpd
0.004	4	6	4	5	4	6.75

Table 18: Row data of high population density

Pair	Solitar		High population density	
	Weight [g]	Scrotal in week	Weight [g]	Scrotal in week
1	42	6	42	6
2	19	5	43	7
3	33	5	42	5
4	23	4	38	6
5	32	4	32	4
6	39	5	40	6
7	28	5	32	5
8	38	4	30	4
9	26	4	28	4
10	27	4	37	5

Table 19: p-value and medians ± 25% and 75% percentiles of solitary (S) and high population density (HPD)

p-value	Median		25% percentile		75% percentile	
	S	HPD	S	HPD	S	HPD
0.06	5	5.5	4	5	6	6

Table 20: extra pairs high population density

Pair	Solitar		High population density	
	Weight [g]	Scrotal in week	Weight [g]	Scrotal in week
11	26	4		4
12	24	5		6
13	17	4		6
14	21	4		5

Table 21: p-value and medians ± 25% and 75% percentiles of solitary (S) and high population density (HPD) in extra pairs

p-value	Median		25% percentile		75% percentile	
	S	HPD	S	HPD	S	HPD
0.008	4.5	5.5	4	5	5	6