Adaptations of the four-striped field mouse (*Rhabdomys pumilio*, Sparman 1784) to the Namib Desert

Dissertation

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V. Discussion

i. Demographic Structure

i.) Ecological Correlates

Weather and Climate

Weather experienced during the study period follows the long-term climate pattern of the Namib Desert, although the period is drier and hotter than the long-term average. As expected for a hyper-arid area, rainfall is very low and highly unpredictable in both space and time. Rain can therefore not be regarded as a reliable water source for *Rhabdomys*. In contrast, advective fog is experienced throughout the winter, spring and summer months. This makes fog a much more reliable source of moisture for animals inhabiting the Namib than rain. If water is a limiting factor for four-striped fieldmice inhabiting the Namib, critical processes, like reproduction, should be restricted to those months with sufficient fog precipitation or high humidity. Climate also has an influence on the food availability of *Rhabdomys*. Nara flower buds and nara flowers on both female and male plants are only available in seasons with lower temperatures, regular fog events and higher atmospheric humidity, while more nara shoots are available during the hot and dry season. Klopatek & Stock (1994) observed that the flowering of *A. horridus* does coincide with rain events, but the opposite is found to be true in this study. After the rain events (2.5mm each in October, November and December 1998), the number of buds and flowers in both female and male nara plants actually decreased.

Food and water resource availability

Food and water resources are closely linked for most rodents inhabiting arid areas (MacMillen & Christopher 1975). Desert rodents can obtain the necessary water from either from food sources, e.g. succulent plants, or through metabolic water (Christian 1980b). As the nara plant, which is the main food source for the population studied, has long tap roots that reach the water table (Kutschera et al. 1997), all green parts of the plant contain more than 80% water (Table V-1). Nara shoots, which contain the most water, are available all year round on both female and male plants. Nara flower buds are available on male plants for most of the year in large quantities, and nara melons are a source of water for animals inhabiting females plants. Four-striped fieldmice are therefore able meet their water needs nearly exclusively from nara plants.

	Water (%)	Nitrogen (mg / g)	Phosphorus (mg / g)	Carbohydrate (mg / g)	Ash (mg / g)	Carboh. / Nitrogen Ratio
fresh shoots	84.20	38.89	3.60	56.70	81.60	1.46
female flowers	83.14	40.72	3.68	105.67	97.87	2.60
male flowers	81.59	27.49	2.87	109.74	93.86	3.99
melon pulp	84.02	17.98	1.58	214.83	67.28	11.95
melon seeds	/	55.63	4.48	11.61	30.79	0.21

Table V-1: Nutritional value of *Acanthosicyos horridus* shoots, female and male flowers, and melon pulp and seeds. Modified table and data from Klopatek & Stock 1994.

The nara plant has an endomycorrhizal system that enhances nitrogen fixation in nutrient limited ecosystems, thus leading to a C/N ratio in the plant tissue that is higher than usual for desert environments (Klopatek & Stock 1994). As the flow of nutrients is mainly into flowers, fruits and new growth (Klopatek & Stock 1994), these can be very valuable and nutrient rich food sources for *Rhabdomys* living in the Namib Desert (Table V-1). This is reflected in the preference for nara flowers which animals of all hummocks display. Juveniles inhabiting hummock V-4 show a preference for nara melons, which are a substantial source of carbohydrates. The seeds of the nara melon are a good source of protein, fat and micronutrients (Table V-2) for animals having access to the melons.

	Macro Nutrients			**Micro Nutrients**	
mg / g	**Pulp**	**Seeds**	µg / g	**Pulp**	**Seeds**
Moisture	840.00	53.00	Ca	214.0	1000.0
Ash	160.00	34.00	Mg	190.0	3630.0
Protein	140.00	307.00	Fe	5.0	40.0
Fat	3.00	57.00	Na	141.0	30.0
Fibre	10.00	13.00	K	6540.0	4000.0
Carbohydrate	117.00	23.00	Cu	3.0	39.0
			Zn	6.0	55.0
			P	224.0	81.1
			B1 (Thiamin)	0.1	0.0
kj / 100 g			B2 (Riboflavin)	0.2	0.0
energy value	231.00	2709.00	B7 (nicotinc acid)	7.5	21.7

Table V-2: Nutritional value of *Acanthosicyos horridus* melon pulp and seeds. Table modified, data from (Arnold et al. 1985).

Another possible source of protein available to *Rhabdomys* at the study site are seedpods of the camelthorn tree (Table V-3). Seedpods are found on and below the trees throughout the year, with fresh seedpods being produced during the winter months (C. Krug, pers.obs.). Acacia seedpods are the main food source for four-striped fieldmice inhabiting hummock V-1, but play a minor role in the diet of animals inhabiting the other hummocks.

mg / g	seed pods [a]
Dry Matter	938.00
Ash	47.30
Organic Matter	952.70
Crude Protein	124.10
Neutral Detergent Fibre	477.00
Acid Detergent Fibre	335.20
Hemicellulose	141.80

%	seed pods [b]	SD (%)	Range (%)
Crude Protein	27.00	2.00	23 - 31
Carbohydrate	5.70	1.00	3 - 9
Starch	26.00	6.00	15 - 35
Fibre (neutral detergent)	32.00	7.00	21 - 47

Table V-3: Nutritional value of *Acacia erioloba* seedpods. Data from [a] (Ngwa et al. 2000) and [b] (Barnes et al. 1997).

In hummock V-1, protein-rich acacia seedpods are consumed during the moister parts of the study period, while nara shoots, which contain a high proportion of water, are eaten during the hotter and drier months. As acacia seedpods are available all year round, the use of nara shoots indicates that the individuals inhabiting this hummock are using the nara shoots to meet their water demands during the hot season. Nara flower buds are rich in protein and have a high water content. Animals inhabiting hummocks V-2 and V-3 are therefore able to meet their water and protein needs by using this type of food. During the hot and dry period, the number of nara flower buds decreases, and animals primarily use nara shoots, which are also high in water and protein. Animals inhabiting hummock V-4 rely on nara shoots and nara melons to meet their water demands throughout the year. These food types are also rich in protein, as are the seeds of the nara melon. In addition, adult females also feed on acacia seedpods as a source of protein.

By relying mainly on the nara plant, which is a source of both water, protein and other nutrients, *Rhabdomys pumilio* is able to meet both its water and protein needs in an environment that is otherwise water and nutrient limited. As changes in the nutritional status of an animal have implications for the survival of the individual, its fertility and fecunditiy, and ultimately, the population dynamics of the species in a habitat (Perrin 1980b), populations in the hummocks studied will differ in regard to their dynamics, longevity of individuals, sexual maturity, timing of reproductive activity as well as juvenile recruitment.

ii.) Population Demography

Body size

Both adult female and male *Rhabdomys* captured in the Namib Desert are heavier than four-striped field mice caught at other locations, but their head-body length is shorter compared to the animals found in other areas (females: Table V-4, males: Table V-5). Therefore the surface:body mass ratio of the animals in the Namib desert is reduced, which in turn decreases thermal conductance. With that, heat uptake from the environment throughout hot days is reduced, and less heat is lost during cool nights. It is also interesting to note that the specimens caught in arid areas (Gabarone, Kalahari and Namib) have larger hindfeet than animals from more mesic areas. Larger hindfeet, or generally larger feet, are an advantage for locomotion in sandy desert areas.

Locale	Mass	HB (mm)	T (mm)	TL (mm)	HF (mm)	Author
Highveld	35.7	104.3	86.7	191.0	21.2	Rautenbach (1981)
Kwazulu-Natal	40.9	106.2	83.5	191.1	20.0	Taylor (1998)
Gabarone		108.0	113.0	221.0	24.0	Smithers (1971)
Kalahari	45.7	109.0	105.0	214.0	24.0	Smithers (1971)
Namib	44.9	81.7	98.4	180.4	24.4	Krug (2002)

Table V-4: Size comparison between female *Rhabdomys pumilio* captured a various locations.

Locale	Mass	HB (mm)	T (mm)	TL (mm)	HF (mm)	Author
Highveld	36.8	103.4	86.6	190.9	21.4	Rautenbach (1981)
Kwazulu-Natal	42.9	106.1	85.5	192.0	20.0	Taylor (1998)
Gabarone		105.0	110.0	215.0	25.0	Smithers (1971)
Kalahari	42.2	105.0	106.0	211.0	24.0	Smithers (1971)
Namib	48.9	84.9	100.0	185.4	25.7	Krug (2002)

Table V-5: Size comparison between male *Rhabdomys pumilio* captured a various locations.

MNA and Population Structure

Populations of *Rhabdomys* in the Pronamib are stable, and population densities are low (Christian 1980a). As the vegetation in the Pronamib is classified as semi-desert and savanna transition (Giess 1970), vegetation is sparse, but evenly distributed, while the vegetation cover in the Namib is clumped. As *Rhabdomys* is dependend on cover, animals will aggregate in the nara hummocks. In combination with the resource availability in the nara hummocks, this will lead to localised populations with high densities, and high population fluctuations.

The hummocks with the greatest population density are the smallest hummocks V-1 and V-8, a female and male nara plant respectively. Both are of similar size ($37m^2$ vs $28m^2$), and have very dense plant cover. The population in V-1 declines very sharply during the hot, dry months, and stays low during winter. The first population peak in spring is due to immigration of young adult females. In October and November, one breeding male and three reproductively active females are found in the hummock, and juveniles are recruited into the population from December 1999. The spring population decline in hummock V-8 is also due to emigration, one breeding pair stays in the hummock. Juveniles are being recruited into the population from November.

Hummocks V-2 (♂), V-3(♂) and V-4(♀) support similar population densities, but these are considerably (one magnitude) lower than the population densities in the very small hummocks. In both hummocks, V-2 and V-3, populations peak in late summer and start declining in autumn, population density halves. With juvenile recruitment from November, population size in V-2 rises again, while population density in hummock V-3 stays at the low level. The population in hummock V-4 follows the pattern of hummocks V-2 and V-3, but the population decline starts a month later, and is not as pronounced as in the other hummocks. Population increase at the end of the study period is again due to juvenile recruitment.

The hummocks V-7(♀) and V-9(♂), which have the lowest population densities on the study site, are of similar size as hummock V-2 and V-4, but the plant cover is less dense, and both hummocks have large open sandy patches, which the mice generally avoid. In contrast to all other hummock, population in V-7 peaks during the winter months. This is due to juvenile recruitment, but these animals disperse again two months later, and the population crashes. As in the other hummocks, population increases at the end of the study period with juvenile recruitment. Population in hummock V-9 is very low during winter and spring, and the marked increase in population density is due to juvenile recruitment. All populations, with exception of the population in hummock V-7, decline over the winter months, when food availability and food quality decrease. The population increases in all populations are mainly due to juvenile recruitment, in some cases, adult animals immigrate into the hummocks. The population fluctuations are very similar to the population fluctuations of *Rhabdomys* in other areas. Both Brooks (1974) and David (1980) report high population fluctuations on the Highveld and the Cape Flats respectively. During one breeding season (six-month period) the population on the Cape Flats grew eleven fold, the lowest increase was a doubling of the population size over a similar period (1980). Wirminghaus & Perrin (1993) also report marked population fluctuations, with a peak after the breeding period in autumn, and decline and dip in spring. David (1980) reports population sizes between 4 and 20 individuals per 0.1ha, which is corresponds to the lowest population densities found in the Nara hummocks of the Namib Desert. The nara plant can therefore be regarded as an optimum habitat for *Rhabdomys* which sustains a high number of individuals.

Sex ratio in this study varies not only between hummocks, but also within hummocks. Females are favoured in hummocks V-2 and V-9, two larger male nara plants, while males are more common in hummock V- 7, a larger female nara plant. Sex ratio is 1:1 in the smallest hummock, V-8, a male plant. In hummock V-1, the other small nara hummock, sex ratio shifts halfway through the study. Males are more common during the first population peak and the population decline, while females are more common at the start of the second breeding period. In hummock V-3, the sex ratio shifts towards the favour of females during the breeding season, while in the non-breeding season both sexes are equally represented in this hummock. In hummock V-4, the pattern is reversed, males are more common during the population peaks at the beginning and end of the study period, while females are encountered more often during the low phase of the population. As a rule, males do disperse more often and further than females (Greenwood 1980). Female have to compete for resources to rear their offspring, and should therefore be philopatric and stay in the maternal territory. Males do compete for mates, and, to avoid incest, should therefore disperse and find a new territory (Greenwood 1980). As suitable habitat for *Rhabdomys* is limited in the Namib, and suitable breeding territories are in short supply, dispersal in higher population density might not be an option for subadults (Solomon & Getz 1997), and animals of both sexes stay behind in the maternal territory.

Survival from first capture

Longevity of animals in the population after first capture differs between sexes and hummocks. With exception of hummock V-1, females are shorter lived than males, and stay in the population for 2.2 months on average. Females have the shortest lifespan in hummock V-7 and V-8, and the longest in hummocks V-1, V-2, and V-3.

Males have an average life span in the population of 2.9 months, and live longest in hummock V-3, shortest in hummocks V-1, V-4 and V-8. The longest-lived individual was in the population for 15 months, and about 18 months old at the time of its death. Longevity in the Namib corresponds very well with data for a *Rhabdomys* population on the Cape Flats. Mean survival from first capture was calculated at 1.9 – 2.5 months (David & Jarvis 1985), 2.3% of the population lived for more than a year, the oldest individual was trapped for 16 months (David 1980). Mortality rates of *Arvicanthis niloticus* are similar, only 14% of the population reach 6 months of age, 8% nine months, and 5% of the population lives for longer than 1 year (Delany & Monro 1986). According to David & Jarvis (1985) are these high mortality rates responsible for the sharp fluctuations in population size.

iii.) Reproduction and Life History

Animals can adapt in difference ways to their environment to maximise reproductive success. Age at sexual maturity can vary between populations; those living in a more stable environment delay sexual maturity, while those living in unpredictable environments mature at an earlier age. The timing of the breeding period also plays an important role, animals in some populations breed strictly seasonal and react to environmental cues, others are opportunistic and breed as long as a specific resource can be exploited, and still other populations breed throughout the year. Females are able to regulate litter size within limits either at implantation or by resorption of embryos later during gestation.

In the Namib, male *Rhabdomys* mature earlier than the females. Above a body condition index of $7.0g*cm^{-2}$, all males in all hummocks are sexually mature, while only a percentage of the females are reproductively active, ranging between 20% and 66%. Males reach sexual maturity at a mean body mass of 41g, females with a mean body mass of 47g. As an animal must meet the energetic expenses for all other bodily functions before they can allocate energy to reproduction (Bronson 1985), delaying sexual maturity until a desirable body condition is reached enables females to store valuable energy resources for pregnancy and lactation.

Compared to four-striped fieldmouse populations living in the more mesic areas of the Cape Flats (David & Jarvis 1985) and the Highveld (Brooks 1974), animals inhabiting the Namib Desert reach sexual maturity at a higher body mass and later age. In *Arvicanthis niloticus*, body mass increases and sexual maturity is delayed in those populations that live in more stable environments, while populations inhabiting habitats that are more variable are lighter and mature at an earlier age (Neal 1980). This indicates that the environment *Rhabdomys* occupies in the Namib, the nara hummocks, are to be considered a stable habitat for the species.

The timing of reproductive activity can be controlled in two ways – indirectly and directly. External environmental factors, e.g. photoperiod (Bronson 1989) or secondary plant compounds (Berger et al. 1981), that predict the duration of the increased resource supply, control reproducitive activity indirectly. Food availability and quality, factors governing caloric or protein intake and determining the energy available for reproduction, control reproductive activity directly (Bronson & Manning 1991), and shape the reproductive performance of small mammals (Veloso &

Bozinovic 2000). The energy to iniate or maintain reproduction in small mammals cannot be gained from carbohydrate rich foods, but must be provided by foods rich in protein (Taylor & Green 1976).

Female small mammals increase their food intake to meet the higher energy demands during reproduction (Kenagy 1987). During the lactational period, females of species living in arid areas do not only have increased energy demand which they can meet by adjusting their food intake (Rogowitz & McClure 1995), but they also have an increased need for water, as moisture is lost with the milk. Timing of female reproduction in the population studied is therefore be shaped by two main factors: 1) availability of high-quality food to meet the increased energy demands of reproduction and 2) availability of moisture to compensate for the water loss during lactation. As the food quality and food availability differs between the nara plants, timing of the reproductive period differs between hummocks. Females breed seasonally in hummocks V-1, V-2 and V-3, when nara flower buds and nara flowers are available, and number of fog days and relative humidity are highest. Reproduction ceases during the hot, dry months, when nara shoots are the biggest component in the diet. The males inhabiting these hummocks do not breed seasonally, they are reproductively active throughout the year. Reproduction is less costly for males than for females, and they do not need high-quality food sources to provide energy for reproduction.

In hummock V-4, females breed throughout the year, and juveniles are caught throughout the study period. Reproductive activity of females is tied to the availability of moisture rich food (nara shoots), the presence of juveniles in the population is correlated with the availability of nara melons and nara shoots. During the time period when females in hummocks V-1, V-2 and V-3 rely mainly on nara shoots, females in hummock V-4 increase their intake of nara melons, and are able to remain reproductively active. Reproductive output drops, though, when the proportion of acacia seed pods in the diet increases, and raises again when females have access to acacia flowers. Males in this hummock are also reproductively active throughout the year, as the males in the other hummocks.

Animal numbers were very low in hummock V-7, and reproductively active females were mainly found in the second half of the study period. The occurrence of juveniles in June indicates that reproductively active females were present throughout the year, and breeding was not seasonal. The occurrence of perforate females is tied to the availability of high quality food (nara flower buds, nara flowers) and moisture-rich food (nara shoots), pregnant females are found in months with high humidity. As in the other hummocks, the males were reproductively active throughout the year.

Hummocks V-8 and V-9 are only trapped from July 1999 onwards. Pregnant females are found in the winter months, indicating that breeding in these hummocks is not seasonally restricted, as in hummocks V-1, V-2 and V-3, where females in breeding condition are only found from October onwards. Female reproductive activity in V-8 is tied to the availability of protein-rich food (nara flowers), while it can not be determined which factors are tied to the breeding activity of females in hummock V-9. Males in hummock V-8 were also reproductively active throughout the study period, indicating year-round breeding.

Breeding of *Rhabdomys* in the Namib Desert is therefore not strictly seasonal, but opportunistic. Reproduction in opportunistic species is continuous (Jackson & Bernard 1999), as in hummocks V-4 and V-7, but is inhibited when there is an energy deficit, as in hummocks V-1, V-2 and V-3. Reproductive activity in the Namib is controlled directly via the availability of protein-rich food. In the Highveld (Brooks 1974) and the Cape Flats (David 1980), where females experience a four-month anoestrus, reproductive activity is controlled indirectly by ambient temperature. In the Natal midlands, breeding of *Rhabdomys* is linked to the rain season, when animals have access to a high quality food source in the form of insects (Wirminghaus & Perrin 1993). Breeding males and females are present in this population throughout the year, although in low numbers in June/July, and juveniles are recruited into the population throughout the year. This recruitment coincides with body fat content of females (Wirminghaus & Perrin 1993). In the tropics, breeding of *Rhabdomys* is associated with rains (Delany 1972), (Taylor & Green 1976), but this in turn is again associated with a high quality food supply (David & Jarvis 1985). Reproductiv status of male and female *Rhabdomys* is related to fat deposits (Taylor & Green 1976), and body fat content, which can vary in relation to season, rainfall, diet, sex and reproductive tactics, serves as an indicator for body condition (Perrin 1980b). Experimental food supplementation in *Rhabdomys* leads to an increase in population densitiy and reproductive output, as well as the extention of the breeding season (Perrin & Johnson 1999). The same has been shown for *Mastomys natalensis* (Monadjem & Perrin 1998), and a number of vole species, where supplemental food leads to an increase in population density, reproductive activity and recruitment

(Cochran & Solomon 2000). In a population in the Pronamib, a similar effect is obtained with the supplementation of additional water (Christian 1979a), indicating that in arid areas, access to water is as important for reproductive success as access to high-quality food.

Females can adjust their reproductive effort in a number of ways (Jacquot & Vessey 1998). They can shorten or lengthen the interval between litters, e.g. with a postpartum oestrus, reduce the litter size at implantation or during gestation by resorbing embryos and vary the amount of investment in their offspring during lactation or postnatal care. Litter sizes in the Namib are drastically reduced compared to the litter size of *Rhabdomys* in the Highveld (5.9 offspring per litter, Brooks (1982), Fish River Valley, Eastern Cape (4.9, Perrin (1980a)) and the Cape Flats (4.9, David (1980)). The number of litters per female produced in the Namib is as high as the number of litters females produce per season in the Cape Flats population (David and Jarvis 1985). As the litter sizes of *Rhabdomys* in the Namib are emerging litter sizes which are determined by trapping and observation, and the litter sizes given by Brooks (1974) , David (1980) and Perrin (1980a) are results of dissection of killtrapped females, litter sizes in the more mesic areas might be overestimated. Litter sizes obtained from dissection are significantly higher than litter sizes obtained from trapping and observation (C. Krug, unpublished data), indicating death of juveniles during or shortly after birth, and before weaning. Emerging litter sizes of females are larger in those females where a male is present, and these females generally have short litter intervals due to a postpartum oestrus. In *Peromyscus californicus*, a monogamous species, litter sizes born to females without a male present are as large as those born to females with a male present, but the number of young emerging is significantly smaller in the females without a male present (Gubernick & Teferi 2000). Female *P. californicus* raising their litter alone are only able to support two pups, and have longer birth intervals than females that raise their litter with a male. Those females are able to support larger litters and have shorter birth intervals (Cantoni & Brown 1997). A similar observation has been made in *Phodopus campbelli*, pup survival was reduced when the male was absent, and females who were forced to raise their litter without a male reduced the size of the litter and were thus able to wean at least one offspring (Wynne-Edwards 1987). In the European rabbit, *Oryctolagus cuniculus*, females living groups with more than one other female had lower lifetime reproductive success than those living with a male only. In this case, the costs of group living outweighed the potential benefits (Cowan 1987).

Male *P. californicus* contribute mainly to offspring care by foraging for food and huddling to keep the litter warm. *Peromyscus leucopus* males associate with their young after weaning, possibly to lead them on foraging trips while the female prepares for next litter (Schug et al. 1992). Male *Rhabdomys* can care in similar ways as *P. californicus* and *P. leucopus* males for their young to enhance their survival. As male care in rodents seems to be tied to monogamy (Elwood 1983; Cantoni 1993; Gubernick & Teferi 2000), *P. californicus* are monogamous, *P. leucopus* monogamous-polygynous (Schug et al. 1992), changes in the social structure of *Rhabdomys* can be expected in the Namib Desert. Some of the groups observed were breeding cooperatively, e.g. in hummock V-2, as cooperative breeding occurs when mature offspring remain at nest beyond weaning and assist in the care of young (Cochran & Solomon 2000).

Animals adapt their life history strategies in different ways to an arid climate. An opportunistic strategy might be the most favourable in an unpredictable climate, as it allows the species to respond rapidly to any change in food availability (Jackson & Bernard 1999). *Parotomys brantsii* breeds opportunistically in response to the semi-arid and arid areas they inhabit, and modify their breeding period in relation to rainfall, and the resulting emergence of fresh green vegetation. Their reproductive potential is maximised by larger litter sizes and and more rapid development compared to other *Otomyinae* (Coetzee & Jackson 1999). In *Arvicanthis niloticus*, breeding rates, litter size and potential reproduction rates increase, as the environment they inhabit becomes more variable, and body size and age of maturity decrease (Neal 1980). In more stable habitats, body weight is higher and maturity delayed. Females are reproductively active throughout the year, and produce smaller litters. *Saccostomys campestris* adapt to unpredictable habitats by being able to breed throughout the year, and reduce their litter size through resorption of foetuses when conditions are less favourable (Westlin & Ferreira 2000). *Cynictis penicillata*, the yellow mongoose, also exhibits opportunistic breeding. Females breeding under favourable conditions showed indications of a post-partum oestrus, which might be dependent on climatic factors influencing food type and food availability. Small litter size and rapid succession of litters maximise juvenile survival in environments with fluctuation food supply and protection against predators (Rasa et al. 1992).

Rhabdomys pumilio living in the Namib follow a strategy that is very similar to that of the yellow mongoose. Food availability is the trigger for reproductive activity, litter size is reduced, and litters are produced in rapid succession under favourable conditions. Male parental care and indications of cooperative breeding also increase the survival of offspring under variable environmental conditions. Delayed sexual maturity, which is not typical for fluctuating environments, enables the females of the species to store energy and enhance body condition for the breeding period. Opportunistic breeding, unenforced by a predictor, as displayed by *Rhabdomys* in the Namib, may be the most prevelant reproductive strategy amongst today's mammals (Bronson 1985).

ii. Social Structure

The social structure of a species is depended on the species' general habitat requirements and can be influenced by mate availability, availability and quality of food sources, predation rates as well as suitable nesting places (Crook & Goss-Custard 1972). Availability of cover, as well as access to food and water shape the social structure of animals inhabiting arid areas. Species of the same family or subfamily occurring in more open, subdesertic habitats tend to have larger groupings and a more complex social structure than when occurring in denser vegetated areas (*Otymyinae*, *Rhabdomys,* Nel (1975)). He reports that in the Kalahari, *Rhabdomys* shifts from a more solitary and territorial animal in the savannas to a more social system due to the clumped availability of suitable shelter in the form of bush clumps and thickets. The distribution of suitable vegetation cover for *Rhabdomys*, the nara hummocks, is clumped. As four-striped fieldmice are dependend on cover, animals will aggregate in the nara hummocks, and as this leads, combination with the resource availability in the nara hummocks, to localised populations with high densities high fluctuations, the social structure of the four-striped fieldmouse will also be influenced. In this study, *Rhabdomys* exhibits pair bonding and monogamy, as most groups consist of a breeding pair and their offspring of various ages. In some of the groups, one reproductively active male lives with two sexually mature females. The social structure of Rhabdomys in the Namib is therefore very similar to the social structure of *Peromyscus californicus* and *P. leucopus*. *Peromyscus californicus* is exclusively monogamous in the wild, and persistent pair bonds are formed (Cantoni & Brown 1997). *Peromyscus leucopus* are described as monogamous – polygynous, the species forms pair bonds, or the males share their homerange with a number of females (Schug et al. 1992). Parental care has been described for both species (*P. californicus*: Cantoni & Brown 1997, *P. leucopus*: Schug et al. 1992), and biparental care is thought to be most common in monogamous rodents (Elwood 1983; Cantoni 1993). Paternal behaviour either occurs when there are few other mating opportunities, i.e. the chance for the males to find potential mates is very low, or very few potential mates are available (Emlen & Oring 1977), or when paternal care contributes to male reproductive success (Wittenberger & Tilson 1980).

Wolff (1994) states that "the general nesting and dispersal pattern for small mammals is for mothers to nest solitary, and the pups usually disperse following weaning and before the birth of the subsequent litter. If space or resources are limited, juveniles do not disperse and form extended family groups with subsequent litters and juvenile females that do not disperse may nest communally with their mothers or sisters". Therefore, as *Rhabdomys* are restricted to nara hummocks, is the availability of suitable homeranges for limited, and the offspring will stay in the maternal territory for extended periods. Willan (1982) documents delayed dispersal of offspring in *Rhabdomys*, where weaned juveniles stay in the maternal territory until after the subsequent litter is weaned. Chaote (1972) also observes that in captivity, weaned young are allowed to stay in nest with newly born young. In these cases, the juveniles usually disperse before they reach sexual maturity, while in the Namib, both male and female offspring stay in the maternal terrority even after sexual maturity is reached. This increase in the number of individuals relative to suitable territory may be an important factor leading to the formation of extended breeding groups in rodents, as suitable breeding territories are limited and dispersal in higher density might not be an option for subadults (Solomon & Getz 1997). As the mature offspring of *Rhabdomys* who stay in the maternal territory, and are regularly seen interacting with and being close to their younger siblings, the species can be regarded as a cooperative breeder in the Namib. According to Cochran & Solomon (2000) cooperative breeding occurs when mature offspring remain at the nest beyond weaning and assist in the care of young. The newly born litter profits from the extended family group and cooperative breeding, as increased territorial defence, nest guarding, pup retrieval, huddling and practice parenting increases their chances of survival (Powell & Fried 1992). In *Peromyscus*, extended families do not increase juvenile survival. Communal nesting and extended families are responses to limited space, delayed dispersal and local grouping among related females; and can be considered alternative reproductive tactics to the solitary breeding that is normal for this species (Wolff 1994). Unfortunately, no information is available on juvenile survival rates in the Namib, as the juveniles lost their marking after their first moult, and could only be followed for a maximum of 2 to 3 months. As the overall mortality rates of Rhabdomys are comparable to those of the Cape Flats, it can be assumed that the survival rates of juveniles are also not increased, and that extended family groups are mainly a response to limited space. The formation of groups in *Rhabdomys* might be similar to the prairie vole (*Microtus ochrogaster*), which is not flexible in response to changes in food quality, but a density dependent response (Cochran & Solomon 2000). Other examples for rodent species with flexible social structure are the prairie voles (*Microtus ochrogaster*), they are either found in groups of a breeding pair, their offspring and and a number additional adults of either sex, which can be sexually mature offspring of the breeding pair, or they live in male-female pairs with their offspring (Getz et al. 1993). *Peromyscus leucopus* also adapts its social structure to te environmental conditions. Males are territorial and polygynous when females are forced to aggregate and are closely spaced, and display a mobile search strategy (i.e. have large homeranges) when potential mates can occupy mutually exclusive homeranges and are widely spaced (Schug et al. 1992).

iii. Spatial Structure

The need for a territory arises from the requirement to secure sufficient resources for survival and reproduction. Another important factor governing territoriality in arid areas is the need for adequate cover, especially for diurnal animals, who need to find shelter from predators. In the Kalahari, the social structure and communal nature of *Rhabdomys* is influenced by the sparse vegetation cover, and individuals are forced to live in close proximity to each other (Nel 1975). For the population studied, resource availability and adequate cover are closely linked, and the clumped and restricted distribution of the nara hummocks in the desert shape territoriality and social structure.

Females need not only secure resources for their own survival, but also the survival of their offspring into adulthood. Female murids are therefore generally territorial and occupy mutually exclusive homeranges in the breeding season. During the non-breeding season, females aggregate or share homeranges (*Rhabdomys pumilio*: Brooks (1974), David (1980), Johnson (1980a), *Microtus townsendii*: Lambin (1997); *Apodemus sylvaticus*: Randall (1993); *Peromyscus leucopus*: Wolff & Cicirello (1990); *Mus domesticus:* Chambers (2000)). Female *Rhabdomys* in the Namib do deviate from this spatial pattern, as they are forced to aggregate throughout the year, mainly due to the lack of cover and clumped distribution of resources. Their homeranges overlap with those of other females or they share their homeranges with other adult females. Females do not reduce their homerange size during the breeding season, and there is no marked increase in territoriality. Restricting the homerange size means restricting access to food resources, which compromises reproductive success and survival of the offspring. Some females, like female 67 of hummock V-3, actually increase their homerange size during the breeding season to gain access to adequate resources for themselves and their offspring.

Males only need to secure resources for their own survival, but must ensure that they have access to potential mates. Males murids therefore occupy mutually exclusive homerange that are larger than those of the females, and overlap a number of female territories (*Rhabdomys pumilio*: Chaote (1972), Brooks (1974), Johnson (1980a); *Peromyscus leucopus*: Wolff & Cicirello (1990); *Mus domesticus*: Chambers et al. (2000)). Non-breeding young males, or those without a territory, are "floaters" in the population and are often characterised by larger homeranges

(Johnson 1980a; Chambers et al. 2000). The spatial pattern of male four-striped fieldmice is not only be shaped by the access to resources and adequate cover, but also by the spatial distribution of the females in the population. As in the females, due to the clumped distribution of food resources and vegetation cover, the males cannot establish mutually exclusive homeranges, and their homeranges must overlap. As the females are forced to share homeranges, or have overlapping homeranges, the territories of the males need not be larger than the territories of the females to gain access to more than one potential mate. Therefore, homeranges of male four-striped fieldmice in the Namib Desert are of the same size as female homeranges, in some cases even smaller. Male homeranges generally overlap with the homerange of one or two females, some males even share a territory with a female. A few of the adult males, e.g. male 98, which moved between hummocks V-3, V-2 and V-1, have large homeranges, and can therefore be considered as floaters in the population.

Homeranges and habitat use are not restricted to the ground only. To gain access to the food resources, animals need to climb between the nara branches, and some individuals even climb high into acacia trees to feed on acacia flowers and fresh acacia seed pods. This three-dimensional use of the habitat is also reported from the Cape Flats, where animals climb into acacia trees to gain access to seedpods, (David 1980; Johnson 1980a), and from the Kalahari, where four-striped females climb onto bushes and branches (Nel 1975).

iv. Activity

As reported in previous field studies in other areas of southern Africa (Highveld: Brooks (1974), Cape Flats: David (1980) and Johnson (1980a), ProNamib: Christian (1977)), *Rhabdomys* also exhibits a bimodal diurnal activity pattern in this study. In contrast to the observations of Shortridge (1934) and Hughes et al. (1994) in Namibia, though, no nocturnal activity of this species could be recorded in this study. Retaining its diurnal activity rhythm in the arid conditions of the Namib places certain ecological constraints, i.e. high evaporative water loss and increased heat uptake, on the species, which nocturnal small mammals that inhabit the Namib generally avoid. To reduce these ecological constraints, which are increased by physiological constraints, *Rhabdomys* displays special adaptations. By being active only in the cooler morning and afternoon hours, and adjusting their activity times to surface and soil temperatures, four-striped fieldmice avoid the hottest and driest hours of the day and thus limit heat uptake and evaporative water loss. Continuation of activity in the shelter under large bushes during the day, as suggested by Coetzee (*in litt.*), could not be documented, as the nara hummocks were very dense, and activity of *Rhabdomys* was only recorded when the animals were visible in the open.

The seasonal shift in activity, which was influenced by sunrise and sunset times, likely through ground and soil temperatures, also aided in reducing evaporative water loss and heat uptake. In the warmer months, which also had longer daylight hours, activity of the four-striped fieldmouse shifted to the earlier, cooler hours of the day, while during the cooler, shorter days of the winter months, individuals were active closer to midday. This study thus confirms the similar shift in activity reported by Christian (1977) and Perrin (1981). The overall time animals were active, though, did not change over the seasons.

Hot and dry conditions are not the only problems for four-striped fieldmice living in the Namib. Ambient temperatures can drop considerably overnight, as the heat accumulated throughout the day is re-radiated and not retained by vegetation cover. The increased sunbasking activity on colder mornings, which was also regularly observed by Johnson (1980a) in the Western Cape, illustrates the necessity to combat the heat loss experienced during cool nights. The fact that Rhabdomys seeks shelter during adverse weather conditions like rain or heavy fog indicates that the mice are avoiding a too low drop in body temperature.

In addition to the thermoregulatory behaviours discussed above, the shorter body length and higher body mass found in this study lead to a decrease in the surface area : body mass ratio in *Rhabdomys* inhabiting the Namib. Therefore, thermal conductance of the animals is decreased, and in combination with the pale coat and off-white underside, heat uptake from the environment is reduced. Lower overall thermal conductance also reduces the heat loss experienced during cold nights. Haim & Fairall (1986) found that on the basis of VO_2, overall thermal conductance of *Rhabdomys* is lower than expected for an animal this size, which is an advantage for the species in the colonisation of arid areas. In addition to the lower overall thermal conductance, Haim et al. (1998) found that *Rhabdomys*, like the diurnal *Acomys russatus* that occurs in the arid areas of the Middle East, displayed the body temperature rhythm of a nocturnal small mammal, with the lowest body temperatures occurring throughout the day. Therefore, both species can tolerate a higher heat intake before a critical body temperature is reached. *Rhabdomys*, though, is a truly diurnal species, and nocturnal activity is very rare (e.g. Shortridge (1934)), while *Acomys russatus* is displaced by the larger species *Acomys cahirinus*, and reverts to a nocturnal activity rhythm when the other species is not present (Shkolnik 1971; Abramsky et al. 1985). It would therefore be interesting to compare whether the closely related species *Lemniscomys* and *Arvicanthis* also retained the body temperature rhythm of nocturnal rodents, or whether this phenomenon is unique in the evolutionary history of the four-striped fieldmouse.

Retaining a diurnal activity rhythm can further be advantageous for *Rhabdomys*: this reduces or avoids competition with other small mammal species, like the short-tailed gerbil, the pygmy hairy-footed gerbil and the black-tailed tree rat which also use the nara plant as a resource in the Namib (Hughes et al. 1994, C. Krug pers.obs.).

v. Special Adaptations of Rhabdomys pumilio to the Namib

i.) Morphological

thick dark skin: protects against solar and UV-radiation, but is also advantageous by increasing heat uptake on cool mornings.

thin fur and shaggy coat: increases heat dissipation during hot days, but also aids in rapid heat intake on cold winter mornings.

pale coat and pale/white underside: aids in reflection of energy and heat radiation from the ground

smaller body size and higher body mass: reduces surface:body mass ratio, which in turn decreases thermal conductance in the species. A reduction in thermal conductance means that less heat is taken up from the environment during hot days, and less heat is lost during cool nights.

bigger hindfeet: ease locomotion on sand

ii.) Physiological

Thermoregulation: Overall thermal conductance of *Rhabdomys pumilio* is lower than expected for an animal of this size (Haim & Fairall 1986), which aids in heat dissipation during hot days. The species of also has a daily body temperature rhythm similar to that of a nocturnal small mammal (Haim et al. 1998), increasing the amount of heat that can be taken up during the day before overheating. The Thermo-Neutral-Zone of individuals from the Namib is elevated compared to individuals from more mesic areas (Haim & Fairall 1986).

Reproduction: litter sizes are smaller than those from individuals inhabiting more mesic areas. Seasonal breeding is replaced by opportunistic breeding, with the males being reproductively active throughout the year. The female react to food availability. Females experience a post-partum oestrus under good conditions, and litters are then produced in rapid succession.

iii.) Behavioural

Temporal activity pattern: Rhabdomys displays a bi-modal diurnal activity pattern with activity periods during the cooler morning and afternoon hours. The timing of the activity period shifts between the seasons. During the hotter months, individuals are active earlier in the morning, and emerge later in the afternoon, in winter, the activity period shift more towards midday.

Thermoregulatory behaviour: Animals sunbask on cooler days to take up heat that is lost during cold nights, and individuals avoid activity on cold, foggy, mornings.

Social structure: The species is monogamous-polygynous, and pair-bonds are formed between males and females. Sexually mature offspring stay in maternal territory, leading to cooperative breeding in the species.

Care for offspring: Both sexes are involved in the care for offspring, as well as weaned young from previous litters. Paternal care contributes greatly to the survival of the offspring.

Territoriality: both males and females do not have mutually exclusive homeranges, instead, both sexes either have overlapping homeranges or share the homerange with animals of both sexes.