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

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Zusammenfassung

Tiere in ariden Gebieten müssen sich an eine Anzahl von Umweltfaktoren anpassen, darunter intensive Sonneneinstrahlung, Temperaturextreme, niedrige Luftfeuchte, (trockene) Winde und zeitliche sowie räumliche Unvorhersagbarkeit von Wasser- und Nahrungsverfügbarkeit. Anpassungen an aride Gegebenheiten können von morphologischer und physiologischer Natur sein, oder als Verhaltensänderungen auftreten (Costa 1995). Die Afrikanische Striemengrasmaus (*Rhabdomys pumilio*, Sparman 1784), die im südlichen Afrika weitverbreitet ist, und in einer Vielzahl verschiedener Habitate vorkommt, wurde über zwei Jahre hinweg in der Namib auf ihre Anpassungen an das aride Klima untersucht. Zur Erfassung der Daten wurden drei verschiedene Methodiken ausgewählt:

1) Fang und Wiederfang (Capture-Mark-Recapture)
2) Beobachtung von Fokalindividuen
3) Sezierung der Geschlechtsorgane von totgefangenen Weibchen.

Daten über Nahrungszusammensetzung, Populationstruktur, Sozialstruktur, räumliche Verteilung und Aktivitätsmuster der Art wurden erhoben.

Die Vegetationsdecke in der Namib ist gering, und tagaktive Tiere finden vorwiegend in der Narapflanze (*Acanthosicyos horridus*), die grosse Sandanhäufungen ("Hummocks") bildet, ausreichend Deckung. *Rhabdomys* sind daher gezwungen, sich in diesen Pflanzen zu aggregieren, was Einfluss auf die Populationsstruktur, Sozialstruktur und räumliche Verteilung der Art hat. Populationsdichten sind hoch, und Populationszahlen schwanken. Die Tiere leben in Familiengruppen, und Paarbildung und väterliche Fürsorge werden beobachtet. Die Homeranges beider Geschlechter überlappen, es gibt keine ausschliesslichen Homeranges. Die Narapflanze ist im untersuchten Gebiet die hauptsächliche Futterquelle für die Art, und Rhabdomys ist ausschliesslich herbivor. Die Fortpflanzung ist opportunistisch, und von Futterverfügbarkeit beeinflusst; Weibchen zeigen einen postpartum Östrus unter guten Umweltbedingungen. Die Wurfgrössen sind im Vergleich zu feuchteren Gebieten reduziert, und Würfe, die gemeinsam mit einem Männchen aufgezogen wurden, sind grösser. Die Art ist tagaktiv, die Hauptaktivitätsperioden liegen am Morgen und späten Nachmittag. Die opportunistische Natur von *R. pumilio* und die Wahl des Habitats ermöglicht es der Art, in einem feuchten Mikroklimat in einem Trockengebiet zu überleben.

Abstract

Animals living in arid conditions need to adapt to a number of environmental factors, namely intense solar radiation, extreme temperatures, low humidity, (dry) winds, and temporal and spatial unpredictability of both water and nutrient availability, which shape life in deserts. Adaptations to survival under these arid conditions can be of morphological, physiological and behavioural nature (Costa 1995). In a 2-year study of *Rhabdomys pumilio* (Sparmann 1784), the fourstriped fieldmouse, it was examined how this species, which is widespread throughout Southern Africa and lives in wide variety of habitats, adapts to the arid conditions in the Namib Desert. Three different methodological approaches were used to collect information for this study:

1) Capture-Mark-Recapture,
2) direct observation of focal individuals and
3) dissection of the reproductive tract of female casualties.

Data on diet, population structure, social structure, spatial structure and activity pattern of the species were obtained.

Vegetation cover, which is important for the diurnal species, is mainly available under nara (*Acanthosicyos horridus*) plants, which form large hummocks. *Rhabdomys* are therefore forced to aggregate in these plants, which in turn influences population structure, social structure and spatial structure. Population densities are high, and fluctuate over the seasons. Animals live in extended family groups; pairbonding and paternal care are observed. The homeranges of males and females overlap, no mutually exclusive homerange are found. The nara plant provided most of the food available to the species, *Rhabdomys* is found to be mainly herbivorous. Breeding was opportunistic, and tied to food availability; females exhibit a postpartum oestrus under good conditions. Litter sizes are reduced compared to more mesic areas, and litters raised with a male present were larger. The species retains its diurnal activity pattern, with the main activity period in the morning and evening hours. The true opportunistic nature of *R. pumilio* and the choice of habitat enables the species to survive in a mesic micro-environment in the arid macro-environment of the Namib Desert.

Table of Contents

List of Figures

List of Tables

List of Maps

I. Introduction

> "…most plants and animals survive in the desert because they do not live in the desert."
>
> (Louw & Seely 1982)

> "A terrestrial animal can pick and choose among the different environmental conditions that occur from place to place and time to time in its habitat. By its behaviour, it can assemble its own microenvironment. This behaviourally generated physical microenvironment is the one with which the organisms physiological capacities can cope."
>
> (Bartholomew 1987)

Deserts can be described as 'water-controlled ecosystems with infrequent, discrete and largely unpredictable water inputs' (Noy-Meir 1973). Thus, irregularity and unpredictability of precipitation are the main factors creating arid conditions (Costa 1995), contributing to immature soil and sparse vegetation (Evenari et al. 1971). Many arid and semi-arid regions are furthermore characterised by high temperatures, and intense solar radiation that is not reduced by clouds, atmospheric humidity, or vegetation (Costa 1995). Consequently, animals inhabiting arid environments need to adapt to the following factors that influence life in deserts: intense solar radiation, extreme temperatures, low humidity, wind, and temporal and spatial unpredictability of both water and nutrient availability. Adaptations to survival under these arid condition are of morphological, physiological and behavioural nature (Costa 1995), and the numbers of ways in which animals can adapt to these environmental factors influencing life in deserts are discussed below.

Solar radiation: in deserts, atmospheric humidity, cloud cover or vegetation do not mitigate the intensity of solar radiation. Desert animals are therefore exposed to high levels of radiation (Louw & Seely 1982) to which they can adapt in several ways. A thick dense pelage, for example, reduces the penetration of solar radiation (Louw & Seely 1982; Costa 1995), while a light, short and glossy coat reflects more energy than a dull dark coat (Louw & Seely 1982). In *Rhabdomys pumilio*, the skull is heavily pigmented (Coetzee 1970), and the skin is comparatively thick with a slaty-black colouration (De Graaff 1981), both offering protection against intense solar radiation. Furthermore, individuals from the arid west have a lighter coat colour than animals from more mesic areas, and a very pale belly (De Graaff 1981), which assists in reflecting energy from the ground surface. Small mammals can further escape intense solar radiation by exploiting substratum resources, e.g. by adopting a fossorial

life style (e.g. *Chrysochloridae*, *Bathyergidae*), making use of underground burrows or nests (e.g. *Cricetidae*, *Muridae*), or using sheltered microhabitats in rock crevices (e.g. *Procaviidae*, DEGEN (1997)). *R. pumilio* is known to construct both burrows (Shortridge 1934; Roberts 1951; Smithers 1971; De Graaff 1981) and spherical grass nests (Coetzee 1970; Chaote 1971; Taylor & Green 1976; Day & Taylor 1998), which provide shelter from solar radiation. In the Kalahari, four-striped fieldmice also use fallen branches as shelter (Nel & Rautenbach 1975).

Temperature and temperature extremes: High to very high temperatures are common in many arid and semi-arid areas, and as solar radiation is not reduced, the soil surface can reach temperatures up to 70ºC (Costa 1995). Due to the lack of atmospheric humidity and plant cover, the heat accumulated throughout the day is re-radiated rapidly during the night and ambient temperatures can drop considerably (Louw & Seely 1982), leading to substantial diurnal and annual thermal fluctuations. With increasing soil depth, those diurnal fluctuations and temperature extremes are diminishing (Costa 1995), and temperature in small mammal burrows stays nearly constant throughout the day (Du Plessis et al. 1992). Small mammals (due to their high body surface : body mass ratio) have low thermal inertia (Degen 1997), implicating a high rate of heat exchange between the animal and its surroundings. This limits time small mammals can spend exposed to high ambient temperatures while maintaining homoeothermy within physiological limits.

The smallest known diurnal desert mammals are *Acomys russatus* and *R. pumilio*. Their adult body weight of approx. 50g may be the lower limit that allows mammals to remain active during the day for any reasonable length of time (Degen 1997). There is also variance in head-body length along the distribution range of *R. pumilio*. Reportedly, individuals found in Namibia, especially those of the Namib, were of larger size than those living in other areas of Southern Africa (Shortridge 1934). This observation is supported by Coetzee (1970) and Yom-Tov (1993), who both state that, contrary to Bergman's rule, body size in *R. pumilio* is positively correlated with ambient temperature. With a larger body size, the body surface : body mass ratio decreases, and with this, the rate of heat exchange between the animal and the environment is reduced.

Most small desert mammals are nocturnal, like *Gerbillurus paeba*, *G. tytonis* and *Desmodillus auricularis* of the Namib Desert, spending the daylight hours in burrows, and thereby avoiding the desert heat during the day (Costa 1995; Nowak 1999).

However, several small mammal species living in desert areas are diurnally active and have adapted to cope with daytime conditions (Degen 1997). Temporal behaviour patterns play a vital role in the thermal balance of small mammals. Many diurnal small mammal species in arid areas are actually crepuscular, and modulate their activity rhythm over the seasons. Examples are the Indian gerbil, *Meriones hurrianae*, which shows crepuscular activity in summer and diurnal activity over the winter months (Ghosh 1975), or the fat sand rat, *Psammomys obesus*, which also shows seasonal shifts in its activity, and exhibits sunbasking behaviour in winter to store heat for locomotion and activity (Ilan & Yom-Tov 1990). Similar observations have been made in *R. pumilio*. Although the species is regarded as being principally diurnal (Roberts 1951; Nel & Rautenbach 1975; De Graaff 1981), it shows in fact a bimodal (crepuscular) activity pattern with peaks in the early morning and late afternoon (Coetzee 1970; Chaote 1971; Smithers 1971; Hubbard 1973). In cooler winter months, the activity shifts to a more continuous activity throughout the day (Christian 1977; Perrin 1981), but animals are also active in warm, moonlit nights, especially during summer (Shortridge 1934; Hughes et al. 1994). Alternatively, diurnally active small mammals can escape the harsh and hostile conditions by using more thermally comfortable, mesic micro-environments within a harsh, xeric macro-environment. Christian (1979b) observes four-striped fieldmice gathering in the shadow under bushes to escape high temperatures. Seeking refuge in burrows or grass nests during the day is also a way to escape the arid environment. Most rodent burrows reach a depth of 20-70 cm (Goyal & Ghosh 1993), which is also the depth where daily temperature fluctuations are low. In summer, burrow temperatures are close to the thermo-neutral zone (TNZ) of the animal, but in winter, especially during the night, burrow temperatures are considerably lower (Degen 1997). During those times, animals must resort to insulating the burrow with nesting material to improve thermal conditions.

Small mammals living in groups can furthermore make use of social resources, e.g. huddling, for thermoregulatory purposes. In general, temporal activity is influenced by body size, dietary habits, water requirements, and energy needs of the species considered. Other factors, like predation pressure, also seem to influence the choice of temporal activity (Degen 1997). Colour and physical characteristics of the pelage determine the rate of heat exchange with the environment (Louw & Seely 1982). As discussed in the context of solar radiation, the insulation properties of a dense thick

pelage can reduce the heat uptake during the day, and protect against heat loss during the night. The coat of *R. pumilio* is rather shaggy, and has poor insulation qualities, aiding in the dissipation of heat during the day (Haim & le R. Fourie 1979). A poorly insulating pelage increases heat loss during the night, and sunbasking activity can be expected on cool mornings or during the winter months.

Humidity: Atmospheric humidity in arid areas is generally rather low, as rainfall is scarce and erratic, and solar radiation, which is not mitigated by vegetation cover, leads to rapid evaporation (Costa 1995). During the day, with the increase in ambient temperature, relative humidity decreases, and thus air over arid areas has a low vapour pressure, furthering the desiccating effect (Louw & Seely 1982). Hence, animals living in desert areas need to minimise their water loss experienced throughout the day. With the drop in ambient temperature over night, relative humidity raises until dew point is reached. Both plants and animals can then use the moisture droplets available to them (Louw & Seely 1982). Again, refuges can provide a mesic micro-environment within the xeric macro-environment. Humidity in a rodent burrow is fairly constant, at about 55% relative humidity (Shkolnik 1971), and it is shown that above-ground nests of *Otomys unisulcatus* are as or even more effective in maintaining favourable temperature and humidity than *Parotomys brantsii* burrows in the same habitat (Du Plessis et al. 1992). Therefore, both grass nests and burrows could provide adequate shelter for *R. pumilio* in the Namib Desert.

Wind: wind speed determines the rate of convective heat exchange of animals with their environment, and the rate of evaporative water loss (Mitchell, *in litt*). In cool coastal deserts like the Namib, moderately strong winds are common. As these are usually cold winds with high moisture content, animals will exploit the cooling effects of the air by positioning their body in such a way as to maximise convective heat loss (Louw & Seely 1982).

Water availability: Water is the most important limiting factor in arid ecosystems. Rainfall is usually infrequent, highly unpredictable, and patchily distributed (Noy-Meir 1973). In addition, the lack of vegetation leads to a quick run-off and fast evaporation of rainwater. Nevertheless, there are certain features in the desert landscape that are able to retain considerable amounts of water, like eroded washes, dry riverbeds, sand at dune bases, and soil at the periphery of rocky outcrops (Louw & Seely 1982).

Three sources of water are available to desert animals: free water (e.g. as moisture droplets or water holes), water in their food, and metabolic water obtained through oxidation of fat. Moisture is lost via evaporation from skin and respiratory surfaces, urine, faeces and saliva, and this water loss is influenced by radiation, ambient temperature, body size and surface of the animal, wind speed and vapour pressure of the air. During lactation, females also loose water through the milk. In small mammals, due to their small body size, evaporative water loss to maintain a constant body temperature is higher than in large animals. Adaptive responses to water loss include efficient absorption of water in urine and faeces, feeding on plants with a high water content, escape to favourable micro-environments, or restricting foraging times to the early hours of the morning when humidity is highest (Louw & Seely 1982). The use of succulent plants growing in arid areas is important for most animals having difficulties finding water (Costa 1995). Many small mammals exploit a diet high in water and drink only when the opportunity occurs, and most small desert mammals obtain the water they require from their food, and do not need to drink in addition (MacMillen & Christopher 1975). Granivorous rodents, whose food contains the least water, have evolved efficient water-conserving mechanisms, like high urine concentration, dry faeces and low evaporative water loss (Schmidt-Nielson 1964; Schmidt-Nielson 1975; Christian 1979b; Remmert 1992; Lovegrove 1993; Nowak 1999). Herbivorous, insectivorous and carnivorous rodents can afford to be more liberal with their water losses, as they obtain proportionally more water from their food, but require additional water when raised only on seeds (MacMillen 1983; Nowak 1999). Non-granivorous rodents shift food intake seasonally to maximise water intake (e.g. *Ammospermophilus leucurus*, Karasov (1985)). Withers et al. (1980) observe higher water turnover rates (WTR) in Namib Desert rodents *Aethomys namaquensis*, *Petromyscus collinus* and *Petromus typicus* after the occurrence of advective fog, indicating that these species use fog as a source of water. As *R. pumilio* has only limited urine concentration abilities (Buffenstein et al. 1985), and is also unable to metabolise water from food (Christian 1979b), the species requires a diet with high water content to maintain its water balance (Christian 1979b). By choosing mainly succulent foods, green plants or insects, *Rhabdomys* might, even in arid areas, be independent of drinking water (Christian 1980b; De Graaff 1981; Willan & Meester 1987). In contrast to this, Shortridge (1934) observes that the distribution of

R. pumilio in Namibia largely coincides with the presence of surface water of some kind.

Nutrient availability: Due to the low primary production and patchy distribution of plants, energy, certain macronutrients, especially protein, as well as micronutrients can be in short supply (Louw & Seely 1982). Periodic nutritional stress is therefore an important factor in the overall unpredictability of the desert environment. As small mammals have a higher metabolic rate and therefore higher nutritional needs than large mammals, they are more affected by a limited nutrient availability. Adaptive responses are storage of energy as fat, migration, reduction of the metabolic rate through torpor or aestivation, sunbasking and the selection for small body size (Louw & Seely 1982).

Food resources in arid areas are scarce and scattered; therefore, opportunism or opportunistic trophism, e.g. as a reaction to the flushing of ephemeral plants or insects after rain, is common among desert animals (Costa 1995). Diurnal rodents in deserts are mainly herbivorous or polyphagous-omnivorous, choosing foods with high water balance, and none of them are granivorous (Degen 1997). In contrast, nocturnal small mammals are mainly granivorous. As seeds are hydroscopic, taking up moisture during the night, the amount of preformed water increases dramatically at night, enabling these species to meet their water demands. Small mammals are further limited by their gut capacity, which is linearly related to body mass, while energy requirement is related exponentially. They are therefore forced to select more digestible, energy-rich diets (Demmet & Van Soest 1985). Often, dietary preference depends directly on food availability, as is the case with *R. pumilio*. Because of their occurrence in a wide variety of habitats, four-striped fieldmice also have a rather varied diet. They are described as being granivorous (David & Jarvis 1985), granivorous-omnivorous (Day & Taylor 1998), folivorous (Kerley et al. 1990), and graminivorous (Rautenbach 1971). The diet of the species consists mainly of seeds, green plant material and arthropods, all in varying proportions, as well as roots and bark (Roberts 1951; Chaote 1971; Smithers 1971; Taylor & Green 1976; Curtis & Perrin 1979; Perrin 1980b; De Graaff 1981; Churchfield 1985; David & Jarvis 1985; Rowe-Rowe 1986; Kerley 1989; Day & Taylor 1998); and is dependent on food availability (Perrin 1980b). There are marked changes in feeding habits between winter and summer (Nel & Rautenbach 1975; Perrin 1980b), or between dry and wet seasons (Rowe-Rowe 1986). Among arthropods, four-striped fieldmice prefer

grasshoppers and termites (Curtis & Perrin 1979), and beetles (Rowe-Rowe 1986). De Graaff (1981) reports that *R. pumilio* also takes snails, worms, and eggs and nestlings of birds. Cannibalism can occur as well, Brooks (1974) reports finding large pieces of tissue with *Rhabdomys* hairs still attached among the contents of a stomach of a four-striped fieldmouse. Therefore, Perrin (1980b) regards the species as an opportunistic omnivore, which exploits transient but nutritious food sources.

Reproduction in desert animals is also opportunistic, and timed with environmental cues, like rainfall, food availability, photoperiod and temperature (Cloudsley-Thompson 1991). Small mammals inhabiting arid areas are usually opportunistic, as discussed above, and food availability and protein content are the limiting factors for reproduction. Various studies of tropical vertebrates indicate that protein can be regarded as a limiting factor for reproduction, with an increased availability of insects important for the initiation of breeding (Perrin 1980b). Small desert mammals are particularly vulnerable to unpredictable energy and nutrient supplies. Reproductive activity is therefore often linked to seasonal rainfall and subsequent emergence of green vegetation, or the availability of free water (Degen 1997). Small mammal species are found to be breeding during the rainy season, or shortly before precipitation falls, or, in some cases, breeding throughout the year with a peak during rainfall (Prakash 1971). *R. pumilio* reacts with a higher incidence of pregnancy and higher proportion of lactation when provided with additional water source (Christian 1979a). Those females with access to additional water also extend their breeding period. A water shortage can thus be regarded as one of main factors influencing reproductive seasonality and seasonally restricted breeding pattern. Such a rapid response to favourable conditions is a typical reaction of rodents inhabiting unpredictable arid environments (Christian 1979a; Christian 1979b). *Petromyscus collinus*, *Aethomys namaquensis,* and *Petromus typicus* show a similar reaction, as these species become only reproductively active in the fog season in the Namib Desert (Withers 1983). Their reproductive pattern is highly seasonal and of short duration, resulting in low reproductive potential but high annual survival of individuals. Withers (1983) is therefore of the opinion that "low reproductive potential and high annual survival are adaptations, or preadaptations, for the successful exploitation of desert niches by small mammals". Generally, *R. pumilio* is considered to be a seasonal breeder (Rautenbach 1971; Perrin 1980a; Rowe-Rowe 1986), usually with a summer peak, and breeding cessation in winter (Chaote 1971; David & Jarvis 1985; Rowe-

Rowe 1986; Wirminghaus & Perrin 1993; Day & Taylor 1998), but there are also indications that they breed throughout the year (Smithers 1971). Jackson & Bernard (1999) suggest that there is a latitudinal shift from continuous reproduction at tropical latitudes to seasonal reproduction at more temperate latitudes. But reproduction in *R. pumilio* seems to be affected by a number of factors (Delany 1972), and in many areas, breeding season coincides with the rainy season and reproductive activity decreases or ceases during hot, dry months (Taylor & Green 1976; Christian 1979a; Perrin 1980a). Rain only seems to be an indirect cause of reproduction, as rain during the warm summer months leads to an increase in both plants and insects (Perrin 1980a). Plant biomass is regarded as one of the dominant factors governing small mammals numbers (Bowland & Perrin 1993), but main breeding activity can also correspond with a high proportion of insects in the diet, e.g. during the moist summer months (Wirminghaus & Perrin 1993). In East Africa, a high population density of *R. pumilio* occurs when food is most abundant, or when the animals are feeding on clover, a food with a high crude protein content (Taylor & Green 1976). It is also shown experimentally that food supplementation with oats results in a population increase in the four-striped fieldmouse (Perrin & Johnson 1999). A certain level of body fat is essential for breeding in this species (Perrin 1980a), and a correlation between male and female reproductive status and fat deposits exists (Taylor & Green 1976).

The four-striped fieldmouse is described as an opportunistic omnivore that exploits transient nutritious food sources, of which various components then account for the seasonality of breeding (Perrin 1980b). R. White (pers. comm.) supports this view, considering *R. pumilio* as an opportunistic breeder, which relies on a combination of environmental cues to trigger the onset of reproductive activity, but photoperiod as a regulating factor for reproduction has been ruled out (Jackson & Bernard 1999). The secondary plant compound 6-MBOA, which induces reproduction in a number of rodent species from the northern hemisphere (Berger et al. 1981), has no effect on *Rhabdomys* (N. Mzilikazi pers. comm.). In accordance with their opportunistic nature, females are known to have a post-partum oestrus under good environmental conditions (Chaote 1971; Brooks 1974; David & Jarvis 1985).

While the nutritional state of the female is important for the survival of the offspring (Bronson 1985), territoriality of the parents ensures the availability and security of the limiting resource. Sociality is therefore a tool to ensure offspring

survival, and in those areas where food resources are irregular, competition is less important than the maximum exploitation of the resource. Species showing territorial habits in non-desert areas are less sedentary and aggressive in arid areas (e.g. lizards, Stamps (1977); Cloudsley-Thompson (1991)). According to Costa (1995), "polygamy [is] the basic nuptial system among animals inhabiting dry habitats, and monogamy is a response to high environmental pressure", therefore, pairbonding might be necessary to assure survival of the offspring.

The nature of *Rhabdomys* sociality and social structure seems to depend on the habitat occupied. Nel (1975) states that individuals living in savannah biomes are somewhat asocial (territorial), but that in the Kalahari their behaviour can be regarded as social, their communal nature being dictated by the availability of cover, or rather, the lack thereof. He regards the species as being solitary clustered, with individuals living in close proximity to each other and displaying a fair degree of social interaction. Chaote (1972) and De Graaff (1981) both regard the four-striped fieldmouse as a solitary rather than a communal animal. In field studies on the Cape Flats, male four-striped fieldmice form a structured, age-graded hierarchy and only the alpha male has an exclusive territory, while the territories of subordinate males overlap (Johnson 1980a). In contrast to this, Chaote (1972) observes that, in Zimbabwe, male four-striped fieldmice occupy well-separated areas in the field. In captivity, males form a dominance hierarchy (Chaote 1972; Marais 1974; Johnson 1980a), as do *Mus musculus* in confined spaces (Crowcroft 1955). Females studied in the field on the Cape Flats, Western Cape, are only territorial with exclusive home ranges when they are breeding, and never form a hierarchy (Johnson 1980a). In captivity, those females associated with the dominant males show characteristics of dominance, but otherwise do not form a social hierarchy. Groups of one male and 2-3 females settled together in captivity show minimal aggression and all the young are raised together with both sexes caring for the offspring. Weaned young of both sexes are allowed to stay in the nest with a newly born litter (Chaote 1972). Willan (1982) describes a two-phase dispersal in the wild, where newly weaned offspring stay in their mother's territory until the subsequent litter is weaned. The social structure of *R. pumilio* can thus be described as an extended family group, with the breeding females forming the nucleus. Present data indicate that the four-striped fieldmouse shows a certain degree of flexibility in both social behaviour and social structure. Detailed information on the social structure of *R. pumilio* in the Namib Desert is not available,

but it is expected that similar pattern to the Kalahari emerge. The vegetation cover in the Namib Desert is limited, which forces individuals to live in close proximity to each other and increases social interaction. The social structure of populations inhabiting the Namib is therefore expected to be of a communal and less aggressive nature.

The opportunistic nature of *Rhabdomys* and the great adaptability of the species to a variety of habitats indicate that the four-striped fieldmouse will show specific morphological, physiological, and behavioural adaptations to the arid climate of the Namib Desert.

The aims of this study are:

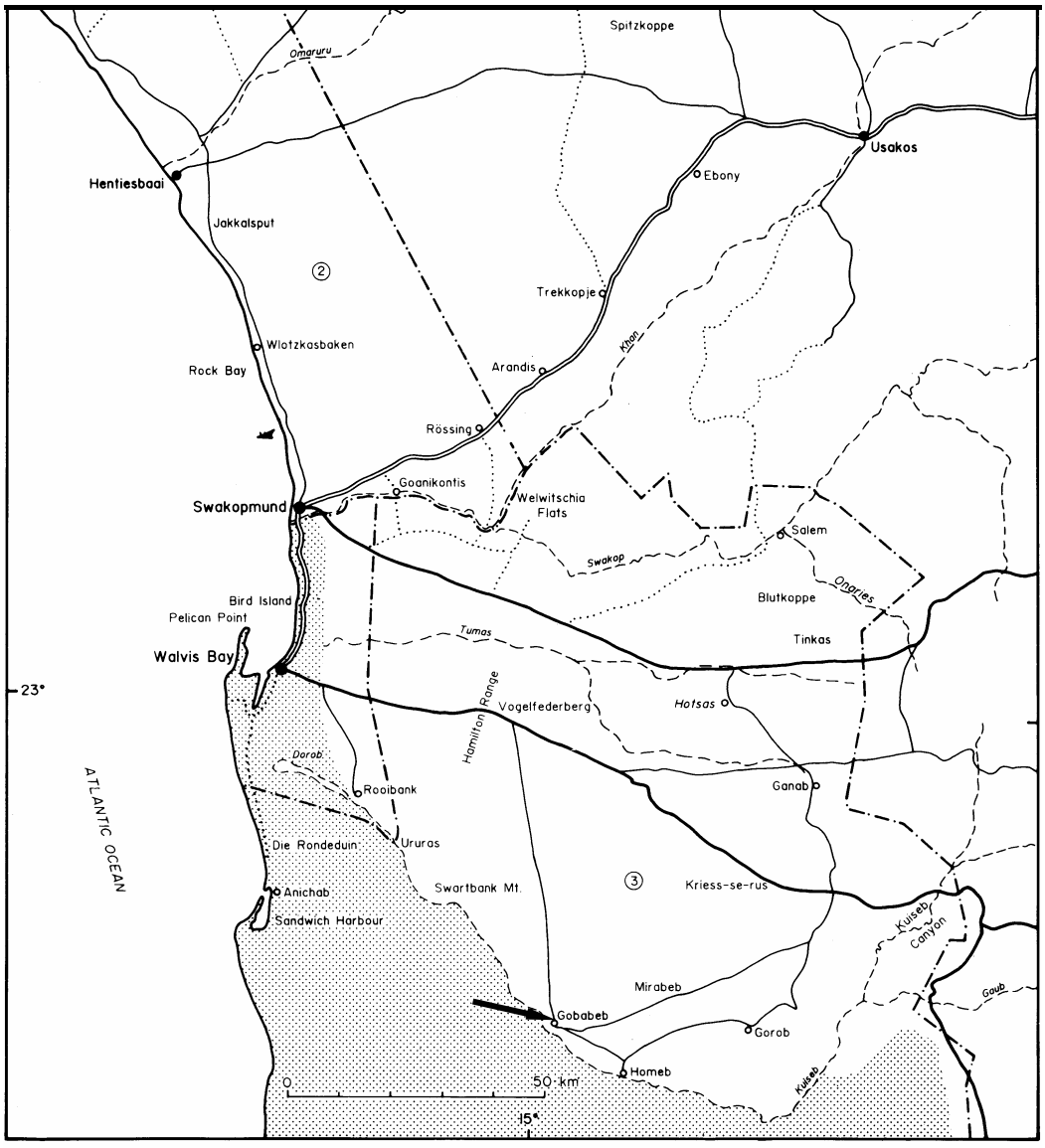
- to complement the existing data and knowledge on *R. pumilio* by studying population demography, spatial and social structure as well as reproduction in an extreme biotope, the Namib Desert and
- to establish how these factors contribute to the adaptation to and survival of *R. pumilio* in an arid climate.

Owing to its special vegetation structure, the Namib Desert allows direct observation of *Rhabdomys pumilio* in the field, this being usually impossible in the more mesic regions. Thus, the aims of this study can be addressed empirically and directly rather than by inference.

II. Study Site

i. Location

The study site, Visnara (Visitor's nara) is situated in the Namib Desert, Namibia, approx. 1km south of the Gobabeb Training and Research Centre (GTRC), formerly called DERU (Desert Ecological Research Unit of Namibia at Gobabeb), within the Namib-Naukluft National Park. Gobabeb (15º03'E, 23º33'S) is located on the banks of an ephemeral river, the Kuiseb River, approx. 60 km inland from the Atlantic Coast at 407 m above sea level (Map II-1). The linear oasis of the Kuiseb marks the border between the sand dunes ("sand sea") of the Southern Namib, and the gravel plains of the Central Namib.



Map II-1: Map of the Namib-Naukluft Park and location of the Gobabeb Training & Research Centre (GTRC, marked by arrow). Map from Seely (1987)

The Namib forms a narrow strip (~ 200 km wide) between the coast and the inland plateau ("Hochland"), with a more or less distinct escarpment. It extends for more than 2000 km, from the Olifants River (South Africa) in the south, to the Carumjamba River (Angola) in the north. The eastern boundary ("Pronamib") is about 1000 m above sea level, at the 100 mm rain isocline (Seely 1987). At the latitude of Gobabeb, the escarpment has a very gentle slope (1000 metres over a distance of 100 kilometres).

ii. Climate

The Namib Desert is a cool coastal desert, like the Atacama Desert in Chile and the Californian Desert in the USA (Louw & Seely 1982). A cool sea current, the Benguela current, and resulting advective fog influence its climate. Fog precipitation is highest at a distance 35 – 60 km inland from the coast at an altitude of 300 – 600 m above sea level. This zone along the coast where the most fog events occur is also the zone with the most substantial climate extremes, i.e. with high differences in humidity and temperature throughout the day (Seely 1987).

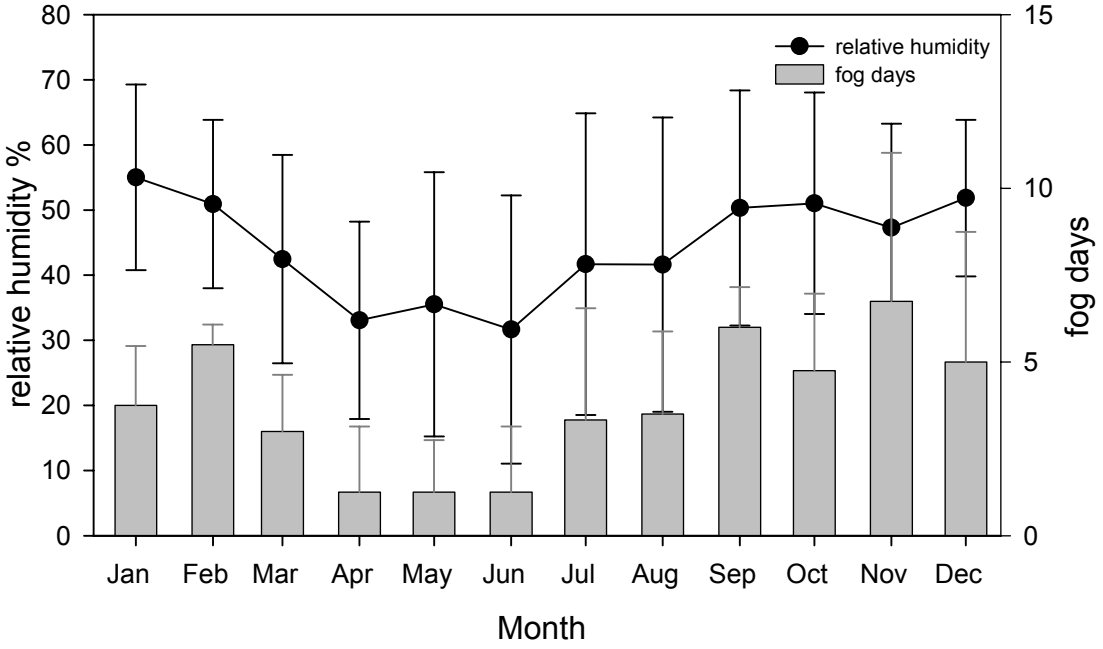


Figure II-1: Average number of fog days per month and average monthly relative humidity at Gobabeb between 01/02/1996 and 31/01/2000. Data collected at the first order weather station Gobabeb, data not available for the period between 20/06/1997 and 07/08/1997. Means ± SD

Over a period of four years (between 1996 and 2000), fog events were recorded every month, amounting to an average of 45.3 fog days per year (Figure II-1). This is 25% more than the 37.23 days per year reported earlier by Lancaster et al. (1984), based on data over a period of 15 years. The mean annual fog precipitation of this

period is 30.79 mm. Fog events are recorded more often in the second half of the year (August – December), but fog precipitation per day is highest during the winter months, in June and July (Lancaster et al. 1984). Fog events are rare in April, May and June, which is the hottest and driest season in the Namib Desert. During that time, the wind direction changes to northeast, and hot dry air flows down the escarpment, leading to the so-called "Eastwind" conditions. Corresponding with the occurrence of fog, relative humidity is highest during the second half of the year, and lowest during the "East Wind Season" from April to June (Figure II-1).

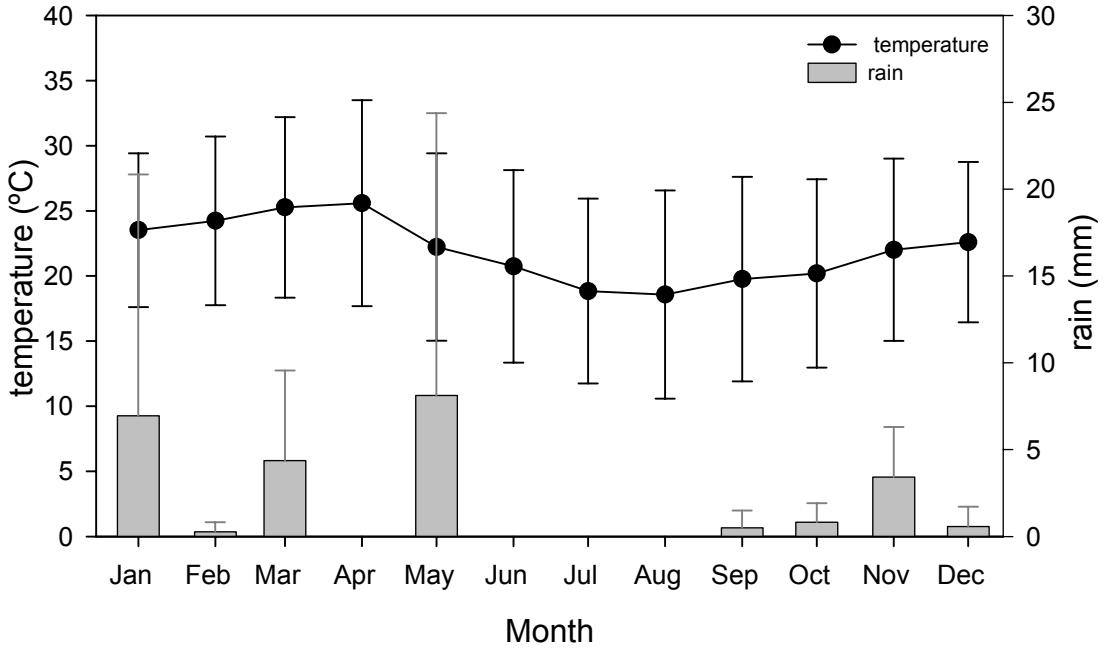


Figure II-2: Average monthly rainfall and mean monthly temperature at Gobabeb between 01/02/1996 and 31/01/2000. Data collected at the first order weather station Gobabeb, data not available for the period between 20/06/1997 and 07/08/1997. Means ± SD.

As in most desert areas, rainfall in the Namib Desert is episodic and highly localised (Besler 1972, *in litt*.), and amount of precipitation is highly variable between years. As the Central Namib is situated at the southwestern edge of the summer rainfall zone, most rain falls between January and April (Schulze, *in litt*.). Rain may occur at any month, however, and mostly as short and heavy showers, but also as light rain of longer duration (Lancaster et al. (1984); C. Krug pers. obs.). Between February 1996 and January 2000, rain precipitation is only recorded in nine of 48 months observed, and within those months, on 22 days in total (Figure II-2). Total rainfall between February 1996 and January 2000 amounts to 100.2 mm, with an average of 25 mm per year, ranging from 2.6 mm (in 1998) to 78.2 mm (in 1997) per year. The average rainfall per month in this period ranges from 0mm to 8.1mm. In comparison,

mean annual rainfall at Gobabeb over a period of 18 years is 27.20 mm, with a range from 0-50 mm (Lancaster et al. 1984). On the whole, the Namib Desert is a hyper-arid region, receiving most of its moisture from fog events, and many of the plant and animal species living in the Namib Desert show unique adaptations to this phenomenon (Louw & Seely 1982; Costa 1995; Degen 1997).

Due to the location at the coast of Namibia, and the proximity to the cold Benguela current, temperatures in the Namib are not as extreme as in inland deserts at approximately the same latitude (e.g. Kalahari). In summer, mean daily temperatures rarely rise above 25°C at Gobabeb (Figure II-2), with the mean daily maximal temperatures seldom reaching more than 35°C (Lancaster et al. 1984). The highest maximum daily temperature ever recorded at Gobabeb is 42.6°C, in March 1998 (C. Krug, pers. obs.). In winter, the mean daily temperature is approx. 17°C, ranging between 10°C and 25°C. Minimum temperatures rarely fall below freezing point (Lancaster et al. 1984). Mean daily soil temperatures recorded at various depths (5 cm, 10 cm, 20 cm, 30 cm, 60 cm and 120 cm) also show seasonal variation. Unlike the pattern shown by ambient temperature, highest temperatures in the soil at various depths occur during the summer months (November - January), when solar radiation is most intensive.

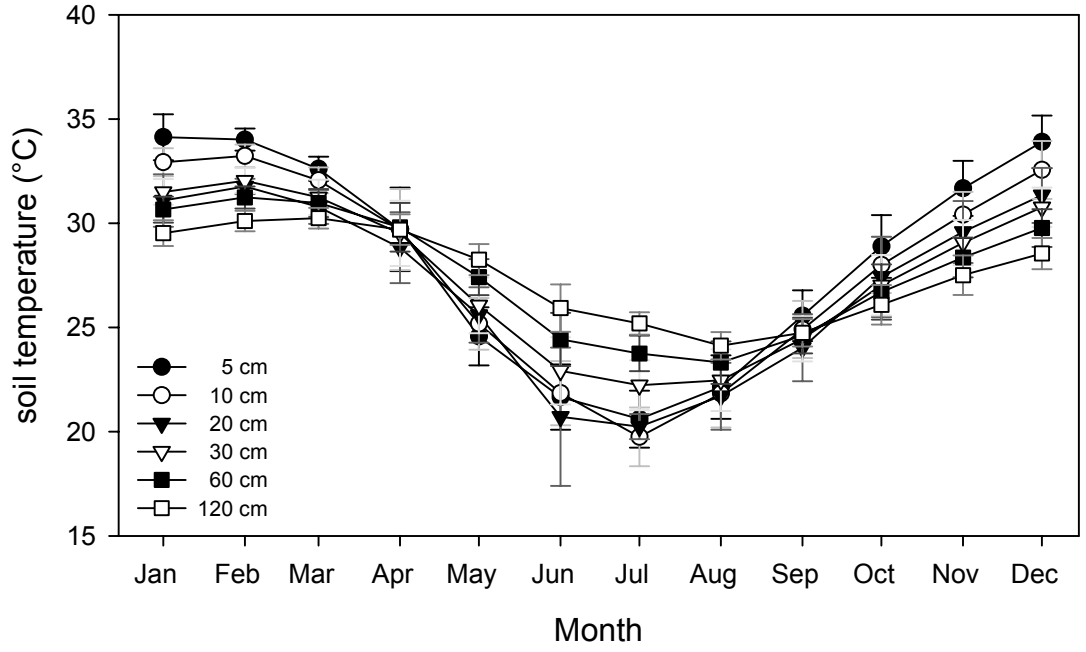


Figure II-3: Average monthly soil temperatures at 5 cm, 10 cm, 20 cm, 30 cm, 60 cm and 120 cm soil depth recorded at Gobabeb between 01/02/1996 and 31/01/2000. Data collected at the first order weather station Gobabeb, data not available for the period between 20/06/1997 and 07/08/1997. Means ± SD.

Soil temperatures in the upper strata of the soil (5 cm, 10 cm and 20 cm) are lowest during June and July, while temperatures in the lower strata (60 cm and 120 cm) are lowest in July, August and September (Figure II-3). Mean daily soil temperature just below the surface ranges from 20ºC in the winter months to 36ºC in summer. At a soil depth of 120 cm, mean daily soil temperature ranges between 27ºC in winter and 31ºC in the summer months. At 5 cm depth, sand temperature can vary as much as 20ºC daily in summer and 10ºC in winter but at 30 cm and below, there is little seasonal or diurnal fluctuation (Figure II-4). Burrowing or fossorial animals can therefore escape the temperature extremes at the soil surface rather easily (Louw & Seely 1982; Du Plessis et al. 1992; Costa 1995).

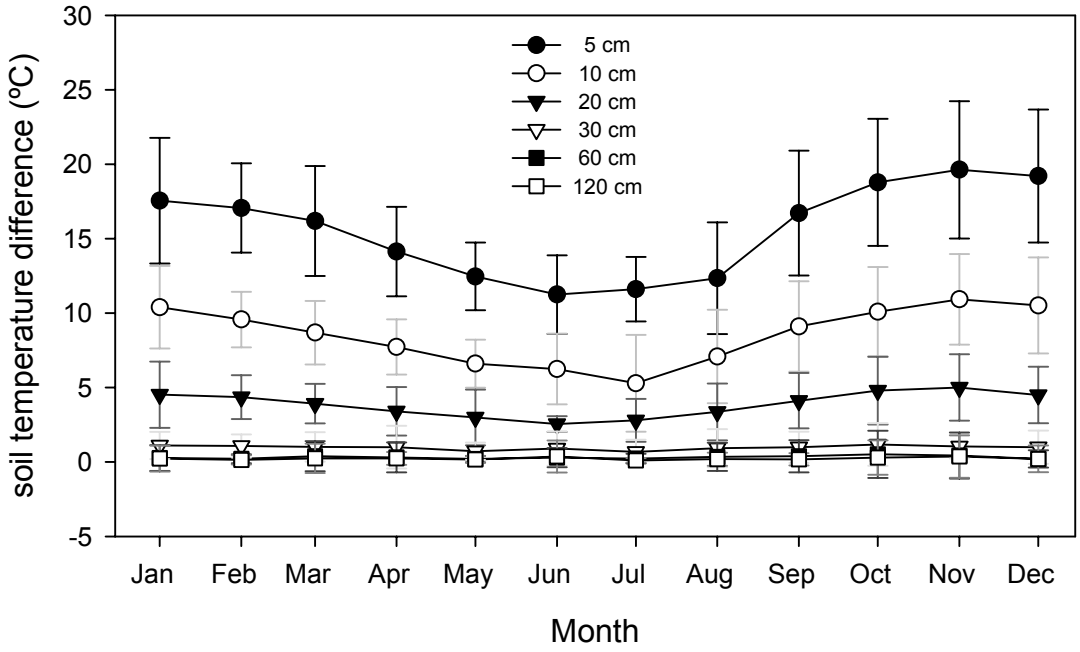


Figure II-4: Average diurnal fluctuations of soil temperatures per month at 5 cm, 10 cm, 20 cm, 30 cm, 60 cm and 120 cm soil depth recorded at Gobabeb between 01/02/1996 and 31/01/2000. Data collected at the first order weather station, data not available for the period between 20/06/1997 and 07/08/1997. Means ± SD.

iii. Vegetation

The vegetation at the study site is typical for the dune valleys of the Southern Namib, but is also influenced by its proximity to the dry riverbed and the vegetation therein. The characteristic plant at the study site is *Acanthosicyos horridus*, the nara, a member of the *Cucurbitaceae,* and an endemic of the Namib sand dunes. The species grows in the dune valleys were there is access to underground water (Sandelowsky 1990). The nara is well adapted to the arid climate of the Namib Desert. Its leaves are

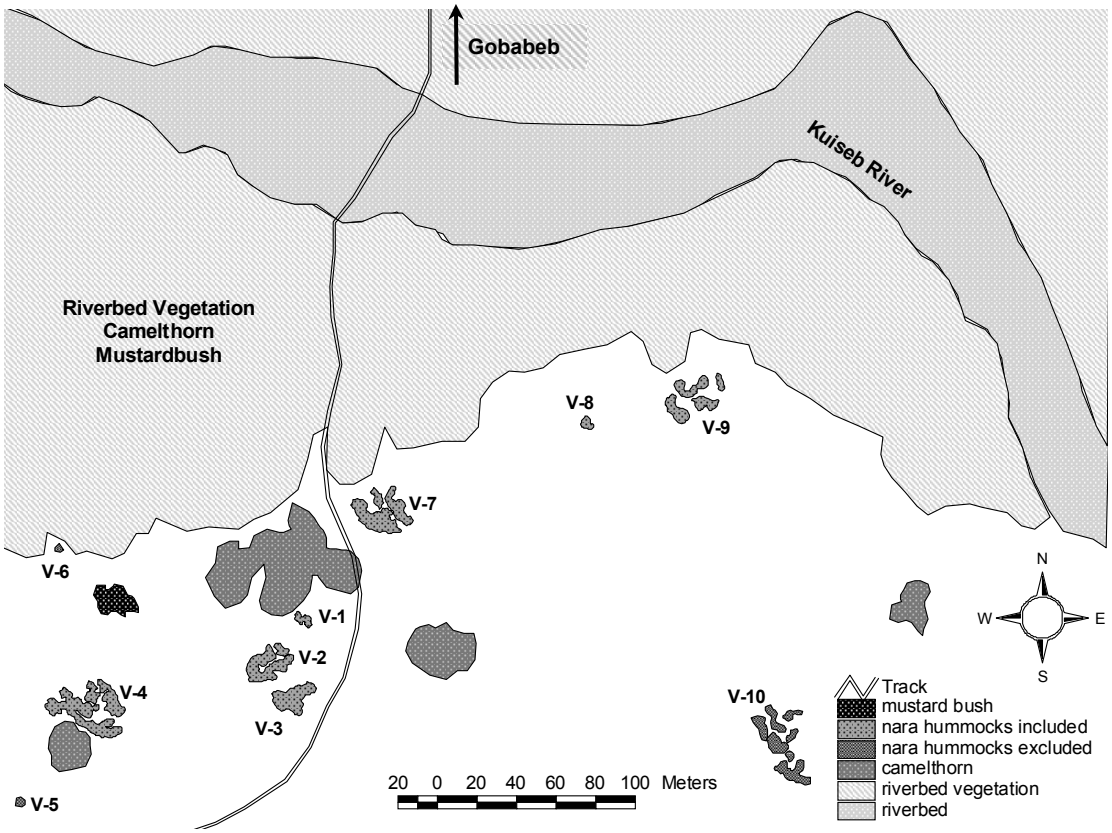
reduced to small stiff scales (Sandelowsky 1990), and the tendrils are reduced to thorns or spikes (Meeuse 1962). Photosynthesis takes place in the branches and thorns (Sandelowsky 1990). The species grows two types of roots: long, woody taproots that reach the ground water table (Meeuse 1962; Kutschera et al. 1997), and subsurface roots that take up the moisture from both fog and rain precipitation (Kutschera et al. 1997). The nara also 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 in desert environments (Klopatek & Stock 1994).

The plant is dioecious, both sexes bearing fleshy, pale green flowers. Flowering usually starts in August and September, and ending in late autumn, around May. Male plants produce a large number of flowers that appear about 4 weeks earlier than the female flowers (Herre 1975). Female plants produce few flowers with an inferior ovary that are pollinated by two species of solitary bees (C. Meier, pers. com.). The large, spiny fruits set from December onwards and mature between February and April (Sarafis 1999). The indigenous Topnaar people have harvested this so-called "nara melon" for many centuries (Herre 1975; Arnold et al. 1985; Sandelowsky 1990; Moritz 1992; Dentlinger 1997), and utilize both the pulp and the seeds. It is also believed that the root has medicinal properties (Moritz 1992).

Nara plants form dense, tangled bushes and as sand is trapped underneath the branches, a hummock reaching considerable size is built up. These hummocks can reach sizes up to 4m in height and cover an area of up to 1000 m^2, forming micro-ecosystems within the dunes of the Namib Desert. The species is regarded as a keystone species (Klopatek & Stock 1994). Nara fruit, seeds, growing tips (shoots) and flowers are highly nutritious, and provide food for a number of species, ranging from beetles to gemsbok and ostrich. In addition, the dense spiky branches offer shelter for many smaller animals, among them *R. pumilio*. Other small species encountered in the Nara hummocks are short-tailed gerbils (*Desmodillus auricularis*) as well as black-tailed tree rats (*Thallomys nigricauda)*, which use nara plants located close to camelthorn trees. Another small dweller of the Namib, the pygmy hairy-footed gerbil, *Gerbillurus paeba*, was inhabiting the open sandy areas between the nara clumps, but was never found in the nara hummocks.

Other plants found at the study site are clumps of the grasses *Eragrostis spinosa* and *Stipagrostis sabulicola*, which grow in the sandy areas between the nara hummocks, and, as the study site was located in close proximity to the Kuiseb river,

Acacia erioloba (Camelthorn) and *Salvadora persica* (mustard bush or tooth brush tree). Map II-2 gives an overview over the study site. Ground cover underneath the camelthorn trees is rather low, and as domestic livestock use the seedpods of the acacias regularly, disturbances underneath and around the trees are rather high. The vegetation in the riverbed consists mainly of *Acacia erioloba*, *Falherba albicans* (Anaboom), *Salvadora persica* and few annual and perennial shrubs and grasses. Ground cover in the riverbed is rather low, and food sources are limited. Floods can change the course of the river considerably (C. Krug, pers. obs.).



Map II-2: Overview over the study site with the location of nara hummocks, mustard bushes and camelthorn trees. Map created in ArcView GIS version 3.0a. Nara hummocks included: nara hummocks included in the study, nara hummocks excluded: nara hummocks that were not included in the study.

III. Material and Methods

Three different approaches were used to collect information for this study:

- Capture-Mark-Recapture (C-M-R) study to gather data on population demography, reproduction and spatial structure
- Direct observation (OBS) of focal individuals to obtain information on the behaviour and social structure
- Dissection of the reproductive tract of female casualties to augment the data on reproduction

i. Collection of Field Data

Collection of field data took place between September 1997 and January 2000. Reconnaissance trapping at various sites near Gobabeb was conducted from September to December 1997 (Nara Valley, Khommabes and Visnara), and in June and July 1998 (Visnara). Trial observations were conducted from January to March 1998 in Visnara, which was then chosen as the final study site. Data for the C-M-R-study were collected from September 1998 – January 2000, Observations were conducted between October 1998 and January 2000.

Climate data

Weather data was obtained from the first order weather station at Gobabeb, which lies approx. 1km north of the study site, across the Kuiseb River. Readings were conducted three times a day, at 08:00, 14:00 and 20:00 GMT + 2:00. The following parameters were used for analysis in this study: dry bulb temperature (mean ambient temperature), minimum and maximum air temperature, relative humidity, precipitation, soil temperature at 5cm, 30cm, 60cm and 120cm depth.

Habitat and resource availability

At all sites surveyed, *Rhabdomys* was restricted to nara hummocks (C. Krug, pers. obs.). At the study site, only four (V-1, V2, V-3, V-4) of the ten nara plants situated at the site were occupied by mice at the beginning of the study (September 1998). Hummock V-7 was included in the Capture-Mark-Recapture (C-M-R) study in December 1998, after it was identified as being colonised. In July 1999, two more hummocks (V-8 and V-9) were integrated into the C-M-R study, after tracks indicated that these two plants had also been colonised by four-striped fieldmice. A third

hummock (V-6), which was also colonised in the middle of 1999, was not included in the study, as the branches were too dense for observation and trapping. Size and height of each hummock and distance between plants was measured using 50m measuring tapes. Data on plant cover were provided by Sarah Eppley and Elizabeth Wenk, University of California, Davis. A more accurate measure of nara hummock size as well as the distance between hummocks was later obtained by digitising the hummocks from aerial photographs in ArcView® 3.0a.

Hummock	plant sex	hummock size (m^2)	hummock height (m)	plant cover (%)	study type	trapped from
V-1	female	37	1.5	95	CMR, OBS	Oct-98
V-2	male	255	2.5	60	CMR, OBS	Oct-98
V-3	male	195	2.5	50	CMR, OBS	Oct-98
V-4	female	494	3.5	75	CMR, OBS	Nov-98
V-7	female	359	4.0	60	CMR	Dec-98
V-8	male	28	1.5	100	CMR	Jul-99
V-9	male	261	2.0	60	CMR	Jul-99

Table III-1: Description of nara hummocks included in the study. CMR: capture-mark-recapture study, OBS: observation study.

To assess the availability of green vegetative matter to *Rhabdomys* in each of the nara plants occupied, 10 random 0.25 m^2 squares were laid out in each hummock once per month. Within each square, the number of fresh shoots (growing tips), flower buds, open flowers, and, in female plants, the number of melons were counted.

Trapping

Traps were non-foldable Sherman–type small mammal box traps locally made from tin sheets and were provided by DRFN/DERU, MET–DSS, UNAM and Polytechnikon of Namibia. Traps provided by MET had to be returned in May 1999 and could only be replaced by July 1999. The number of traps available was not sufficient to cover all hummocks simultaneously (104 until May 1999, 50 from July 1999). The trapping session was therefore split: V-4 was trapped alone, V-3 and V-2 as well as V-1 and V-7 were trapped simultaneously. Later on, when V-8 and V-9 were included in the study, V-4 was trapped alone; V-1, V-2 and V-3; and V-7, V-8 and V-9 were trapped during the same sessions. Even though fewer traps were available from July 1999, the number of traps per hummock could be increased. Once trapping was concluded in one hummock or in a group of hummocks, the traps were moved and trapping continued in the next set of hummocks. Locations of the traps

were marked with a small signpost bearing the number of the trap. For the number of traps used and trap density in each hummock throughout the study, see Table III-2.

	until May 1999		from July 1999		
Hummock	No of Traps	Traps per 100m²	No of Traps	Traps per 100m²	Hummock size (sqm)
V-1	11	29.73	12	32.43	37
V-2	16	6.27	23	9.02	255
V-3	10	5.13	15	7.69	195
V-4	57	11.54	50	10.12	494
V-7	10	2.79	20	5.57	359
V-8	-	-	7	25.00	28
V-9	-	-	23	8.81	261
Total	**104**	**55.46**	**150**	**98.65**	**1629**

Table III-2: Number of traps set out and number of traps per 100 m^2 in each hummock occupied by *Rhabdomys*.

Due to the special habitat *Rhabdomys* inhabits in the Namib Desert, the traps were not set up in a grid or line transect, as it is customary in small mammal studies (Gurnell & Flowerdew 1990). Instead, the traps were placed along the contours of the nara plant on the hummock (Map III-1). As four-striped fieldmice generally avoid open areas in the Namib Desert (C. Krug, pers. obs., Hughes et al. (1994)), no traps were set out in the open sandy areas between the hummocks studied. Previous studies had shown that Rhabdomys enters traps rather readily (Brooks 1974; David 1980), therefore, trapping was conducted without a pre-baiting period.

As the trapping had two aims – providing data for the study on population demography and reproduction, and to mark all animals residing in the nara plant for observations – each hummock was trapped once every month for 1½ days to 3 days per hummock, until no new (unmarked) animals for this session were captured. As the reconnaissance trapping had revealed that no four-striped fieldmice were trapped before sunrise or after sunset, trapping was restricted to daylight hours. The length of each daily trapping session was dictated by activity of the animals observed, as well as ambient and ground temperatures, to avoid overheating of the metal traps. Trapping was conducted in the early morning for 2-4 hours, starting within half hour after sunrise, and 2-3 hours in the late afternoon, starting 2-3 hours before sunset and ending within half hour after sunset, or until all traps were checked after sunset. In total, trapping was conducted over 13 256 trap hours. The traps were checked at 45 – 60 minute intervals during each trapping session. In total, 278 individuals were

trapped between September 1998 and February 2000 in 830 trapping events. Of those, seven animals died during trapping, which equals 2.54% of all animals trapped, or 0.84% of the total number of trapping events.

Traps were set to a minimum weight of approx. 15 grams and no nesting material was provided. As a mixture of peanut butter and rolled oats mixed with various other ingredients used in previous studies (Dippenaar 1974; David 1980) was effective in attracting four-striped fieldmice, a similar bait mixture was used in this study. Crunchy peanut butter, rolled oats, sunflower seeds and some melted butter or margarine were mixed. The mixture was then rolled into small balls, which were placed into the traps.

After capture, the animals were weighed, measured, sexed, their reproductive status assessed, and checked for markings. For weighing, animals were shaken from the trap into a into a plastic string bag, which was attached to a Pesola spring scale (100 gram, with 1 gram increments). Body mass was determined to the nearest gram. After weighing, the length of body, tail and left hind foot were measured with a standard ruler. Body and tail length were measured in cm to the nearest 5mm, hind foot length in mm in 1mm increments. Finally, the reproductive status of the individuals was determined. In males, testes were classified as being abdominal (non-scrotal), descending or scrotal. In female a perforate or imperforate vagina, visible pregnancy, lactation and nipple size (small, medium or large) were used as indicators to assess reproductive maturity. Individuals heavier than 36 grams and bigger than 7.5 cm body length, or those smaller but in breeding condition (criteria: perforate vagina, signs of pregnancy or lactation in females and descending or scrotal testes in males) were regarded as adults. All other animals captured were regarded as juvenile. The marking was either refreshed, or a new unique marking was applied, and the animal was released next to the trapping station. If a previously caught animal was not identifiable, i.e. when the marking was very faded, a new number was assigned, and this was noted on the trapping sheet. Possible casualties were stored in a plastic bag and later frozen at -18ºC until dissection. The trap was re-baited, if necessary, and reset. At the end of each trapping session, the back doors of the traps were opened, and the traps were either left in place or transferred to the next hummock.

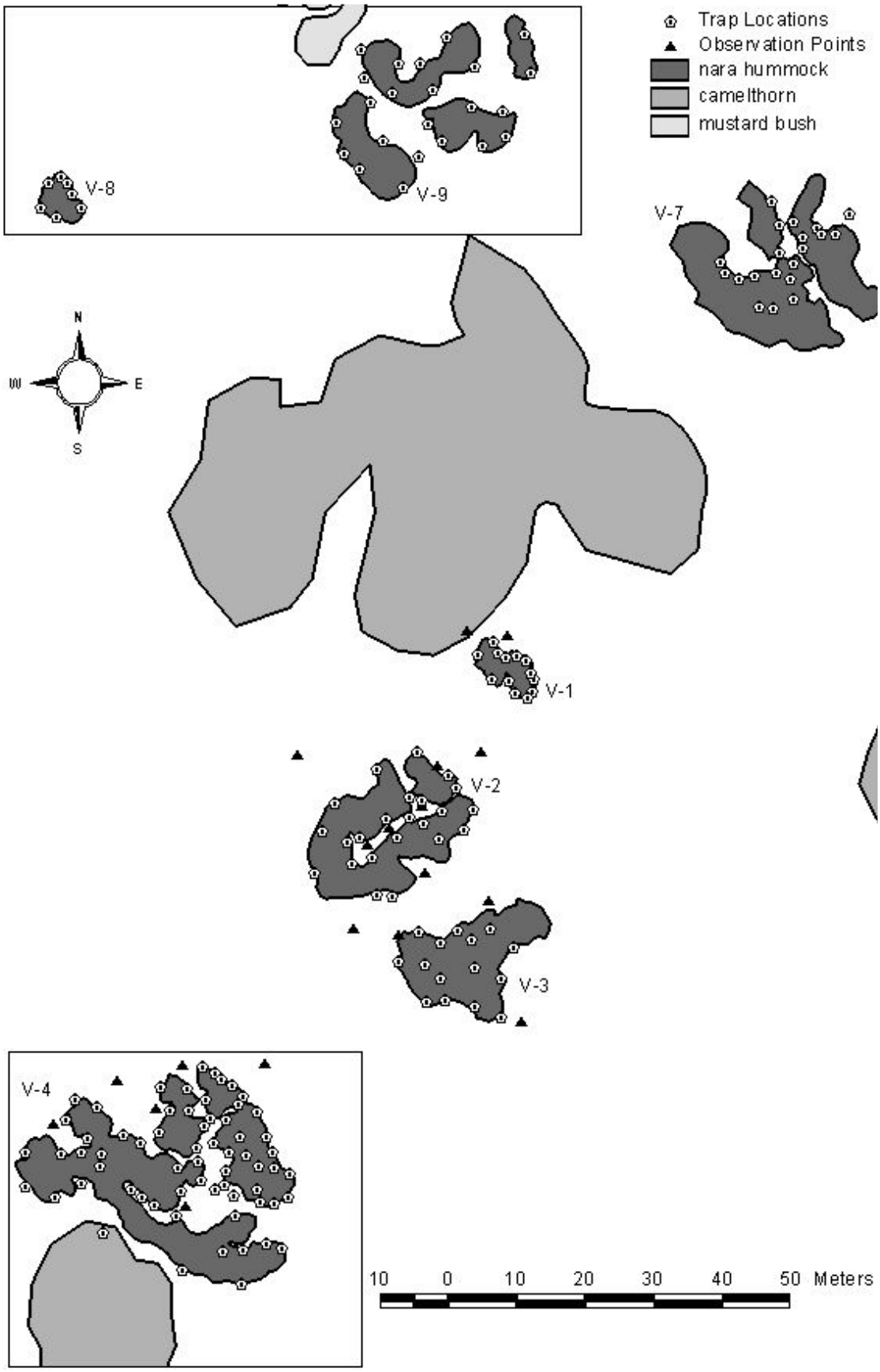
Individual markings had to be both suitable for capture–mark–recapture and observation purposes. The marking method therefore had to fulfil two main criteria: the mark had to be as permanent as possible for the C-M-R study, to enable an

identification of the recaptured animals over consecutive trapping sessions, as well as to provide an obvious marking on the animal for easy and quick recognition of individuals during observation. The best solution proved to be the use of permanent black hair dye (Inecto Rapid®), which is readily available in Southern Africa. Instead of using a marking code, Arabic numbers were applied with a paintbrush on both sides of the rump of the mice as an individual marking, so individuals could be identified no matter how they faced the observer.

Observation

Animals were observed by eye or with binoculars from set vantage points in and around the nara hummocks V-1, V-2, V-3 and V-4 (Map III-1). V-7 and V-9 were very "loose" plants with low population densities and were therefore not included in the observations; V-8 was too small and dense to allow successful observation of individuals. To increase the range of view, observations were conducted from a stepladder (8 steps) that served as an observation tower. The observation method of choice was scan sampling (Altmann 1973), but due to the structure of the vegetation and fixed vantage points, the animals were not observed for a set time period, but for as long as they were visible to the observer, between five and 45 minutes per individual. Focal animals could not be followed, as this would have disturbed the whole group. After the disappearance of the focal individual, the nearest animal in sight was chosen as the next focal individual. While the focal animals were observed, a scan observation at regular intervals was conducted to assess which other individuals were active near the focal animal. Observation of each group of animals was conducted once a month for 2-3 consecutive days. In total, 169 focal individuals were observed over 525.5 observation hours. Observation took place in the early morning and afternoon, for 2-4 hours each, depending on the ambient temperature, weather conditions and activity of the animals. Usually, observations started within half hour after sunrise, and ended when activity of animals ceased. Date and Time of observation, location of the animal, type and duration of behaviour as well as object or individual at which the behaviour was directed were at first recorded on tape, later on minidisk. Any type of behaviour was recorded, the categories and behaviour types used followed Eisenberg (1967).

After each observation, fresh *Rhabdomys* tracks between all hummocks included in the observation study were counted and their direction noted.



Map III-1: Location of all trapping stations and observation vantage points in the nara hummocks. Map created in ArcView GIS version 3.0a. For the relative position of the hummocks to each other, see Map II-2.

Dissection

Adult female casualties were dissected, the reproductive organs examined and the number of uterus scars and / or embryos in each uterus horn counted. After exanimation, the animals and the reproductive organs were stored in formalin. The animals and organs are currently housed at the University of Stellenbosch, but will be transferred into the care of Dr. Rehema White, Department of Zoology, University of Transkei, for further studies.

ii. Data Analysis

Diet and food preference

Data on diet and selection of food types was obtained from direct observation of the focal individuals. Food type consumed and time spent feeding on this food type were recorded. To obtain diet composition, the time spent feeding on a specific food type was summed up for an individual, and divided by the total time this individual spent feeding during the observation. These individual diet compositions were then averaged to obtain the proportion each food type contributed to the diet of adult females, adult males and juveniles.

The individual diet compositions were used to determine preferences for food types available from the nara plants (nara flower buds, nara flowers, nara melons and nara shoots). This was done using the rank preference method developed by Johnson (1980b). The advantages of this method, as given by Johnson (1980b), were that the components were placed in order according to preference, and the method was relatively insensitive to inclusion / exclusion of items. The results obtained were therefore less subjective than other rank-preference methods. Furthermore, measures used to determine preferences needed not be estimated exactly or without bias, and needed not be percentages, as ranks of usage and availability were employed. Another advantage was that tests of significance were possible (by calculating F-statistics, or, in this case, H-statistics, as non-parametric tests were used), allowing for statistical comparisons among components. The null hypothesis is that all components are equally preferred.

The rank preference indices are calculated as follows:

X_{ij}: measure of usage of component i by individual j, with i = 1, 2, ..., I (I = number of components) and j = 1, 2, ...,J (J = number of individuals)

Y_{ij}: measure of abundance of component i to individual j

r_{ij}: is defined as the rank of X_{ij} within j (animal / individual)

s_{ij}: is defined as the rank of Y_{ij} within j

$t_{ij} = r_{ij} - s_{ij}$: measure of preference for component i by individual j

The lower the value of the difference t_{ij}, the more preferred the item. To obtain a measure of preference for nara food types, the difference t_{ij} was then averaged over adult females, adult males and juveniles inhabiting each of the hummocks observed.

Population estimates

Population size was estimated with direct enumeration or Minimum Number Alive Method (MNA, Krebs (1966)) and the method of Jolly-Seber for estimating population size (Begon 1979). To be able to use capture-mark-recapture methods to estimate population size of an open population, i.e. a population where there is possibly death, recruitment, emigration and immigration, the following underlying assumptions need to be true (Seber 1973; Begon 1979):

- all marks are permanent, i.e. marked animals do not loose their marks, and the marks are noted correctly at recapture.
- being caught, handled and marked one or more times has no effect on an individual's subsequent probability of being captured
- being caught, handled and marked one or more times has no effect on the probability of an individual dying or emigrating, and every animal caught in the sample has the same probability of being returned to the population, i.e. the chance of accidental deaths due to handling is the same for all individuals
- every individual in the population has an equal probability to be caught during a sample, given that it is alive and present in the population when the sample is taken. This equal probability of being caught might be violated for three reasons (Eberhardt, *in litt.*):
  - the behaviour of individuals changes in the vicinity of the traps
  - individuals already caught learn either to come to traps, or to avoid them, resulting in "trap-happy" or "trap-shy" individuals
  - territoriality of individuals which limits access to certain traps positioned within homeranges or territories of individuals.
- every marked individual in the population has the same probability of surviving from one sampling period to the next, and of being in the population

at the time of the sample, given it is alive and in the population immediately after the release

- all individuals in the population – marked or not – die or emigrate with the same probability
- the sampling periods are short in relation of the total time the population is studied

MNA is the number of individuals captured in one trapping period, plus the Parameter z_i of Jolly's, which is the number of individuals captured in at least one prior and one subsequent trapping period. Population size is therefore estimated as

$$\hat{N}_i = n_i + z_i ,$$

with

N_i: Estimated population size at sample i

n_i: number of individuals captured in sample i

z_i: number of individuals marked before sample i, not caught in sample i but captured or sighted in subsequent sample.

The population estimate of Jolly-Seber, as well as survival rate and number of additions to the population was calculated following the parameters and equations of (Begon 1979):

m_i: the number of marked individuals caught in sample i

n_i: the number of animals caught in sample i

r_i: the number of marked individuals released in sample i

y_i: number of individuals marked in sample i and caught subsequently

z_i: the number of individuals marked before sample i, not caught in sample i, but in subsequent sample

B_i: the number of additions to the population between sample i and sample i+1

M_i: estimated population of marked individuals in sample i

N_i: the population size at sample i

ϕ_i: the proportion if the sample i population surviving until sample i+1; or the chances of an individual in the sample i population surviving until sample i+1.

The parameters n_i, m_i, r_i, y_i and z_i are obtained directly from the data, and with these, the total number of marked individuals M_i can be estimated:

$$\hat{M}_i = m_i + \frac{z_i * r_i}{y_i}$$

The population size N_i is then estimated as follows:

$$\hat{N}_i = \frac{\hat{M}_i * (n_i + 1)}{(m_i + 1)}$$

The estimate of survival rate ϕ_i from day i until day i+1 is calculated as follows:

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + r_i}$$

New additions to the population B_i between days i and i+1 are given by:

$$\hat{B}_i = \hat{N}_{i+i} - \phi_i * \hat{N}_i$$

To obtain these population estimates, data of the C-M-R and observation studies were combined, i.e. resightings of marked individuals in any given month were regarded as recaptures; an individual could therefore either be recaptured or resighted in a sampling period.

Both recapture and resighting data were used to estimate average length of survival from first capture. The first capture date for an individual was subtracted from the date of last capture or last sighting, whichever was later, to obtain length of survival from first capture for this individual.

Sexual Maturity

Body condition index (BCI, see below) was used to compare sexual maturity in males and females. BCI combines body mass and body size of an individual: the heavier and larger the individual, the higher the BCI. In individuals of similar body length, the heavier individual will have the higher BCI and is considered to be of better condition.

$$BCI = \frac{body \cdot mass \cdot (g)}{body \cdot length \cdot (cm)} * 10$$

Indicators of sexual maturity in males were descending or scrotal testes ("scrotal males"), and a perforate vagina in females ("perforate females"). To compare BCI at sexual maturity between males and females, all those individuals were selected who showed signs of sexual maturity for the first time in their capture history. Males were considered sexually mature when they were first captured with descending or scrotal testes, females were considered sexually mature when they were found to be perforate or pregnant for the first time. As pregnancy itself changes the body mass of a female, only non-pregnant perforate females were included in the analysis.

Reproductive seasonality

To estimate the influence of climatic variables and resource availability on the occurrence of reproductively active individuals, the number of perforate females, pregnant and/or lactating females and the number of males with scrotal testes captured in each month was correlated with climate and resource variable at time, one month and two months previously using the Spearman rank correlation.

Litter sizes

Litter sizes were estimated in three different ways. Firstly, the number of embryos or the number of uterus scars in each uterus horn of the dissected females was counted, and the age of the uterus scars were assessed. The uterus scars were then assigned to one of the following age classes: recent, medium and old, and could thus be attributed to consecutive litters. In cases were very large embryos were found, no uterus scars were visible, and a litter number could not be assigned. Secondly, litter sizes were assessed by either counting the number of juveniles in close vicinity to a female, or by assigning the juveniles of similar size and weight trapped in a home range of a previously pregnant individual to this female. Finally, if juveniles of the same size were trapped simultaneously in the same trap, they were regarded as littermates. Innes & Millar (1987) suggest that data obtained from uterus scars are unreliable, as scars fade rather quickly, and it is difficult to distinguish between scars of different ages. They therefore recommend that the mean number of litters be estimated from CMR data. When trappability is high, and traps are set at frequent intervals, pregnancies and subsequent lactation will not be overlooked.

Social behaviour

Social structure and parental care were evaluated using events of social behaviour. Within social behaviour types, the following types were distinguished: contact or socio-positive behaviour (Sniffing (naso-nasal, naso-anal), Grooming and Body Contact), agonistic behaviour (Threat, Chase, Fight) and submissive behaviour (Retreat, Escape).

Spatial Analysis and GIS

To establish homerange size, the Animal Movement Analysis ArcView extension “Movement”, developed by P.N. Hooge and B. Eichenlaub of the Alaska Biological Science Centre, Anchorage, was used to calculate the 95%, 75%, 50% probability of the Kernel Homerange size. Kernel Homerange size gives an estimate of the

utilization density of the area used by the focus individual. Data of adult individuals from both the C-M-R and observation study were integrated in the homerange computation, but only data of those individuals that had been trapped and observed at a minimum of three different locations, as well as over a period of more than 60 days were included. To establish the area of the homerange in favourable vegetation, the 95% probability was intersected with the shape of the *Acanthosicyos horridus* hummocks, using the XTools extension for ArcView GIS, developed by Mike DeLaune, Oregon Department of Forestry. This "favourable homerange" was then used for further calculations and analysis.

Statistical Analysis

As the data were not normally distributed, non-parametric, two-tailed statistic tests were used. Spearman rank correlation was used to establish relationships between climate and resource availability, and between climate, resource availability and reproduction. Mann-Whitney U-test and Kruskal-Wallis ANOVA were applied for comparisons between individuals, groups (hummocks) or months. For comparisons within individuals, Wilcoxon Matched Pairs test and Friedman ANOVA were used. The Chi-square test was used to determine differences between MNA and Jolly-Seber estimates, and deviation of the sex ratio from 1:1. A p-value of $p<0.1$ indicates marginal significance.

IV. Results

i. Demographic Structure

i.) Ecological Correlates

Weather and Climate

The weather pattern observed throughout the study period followed the long-term pattern, but the period was drier and hotter than the long-term average. No fog was observed between April and June, the hot and dry season (Figure IV-1), and the number of fog days experienced during July and August was lower than the average for those months. Mean monthly relative humidity was closely associated with the number of fog events per month (Spearman rank correlation r_s=0.68, N=15, p<0.01), with relative humidity highest in those months where fog occurred, and lowest in the hot and dry season (March – June 1999). The number of days with fog events was significantly higher in October, November and December 1998 than in the same months in the following year (χ^2_3=26.17, p<0.001).

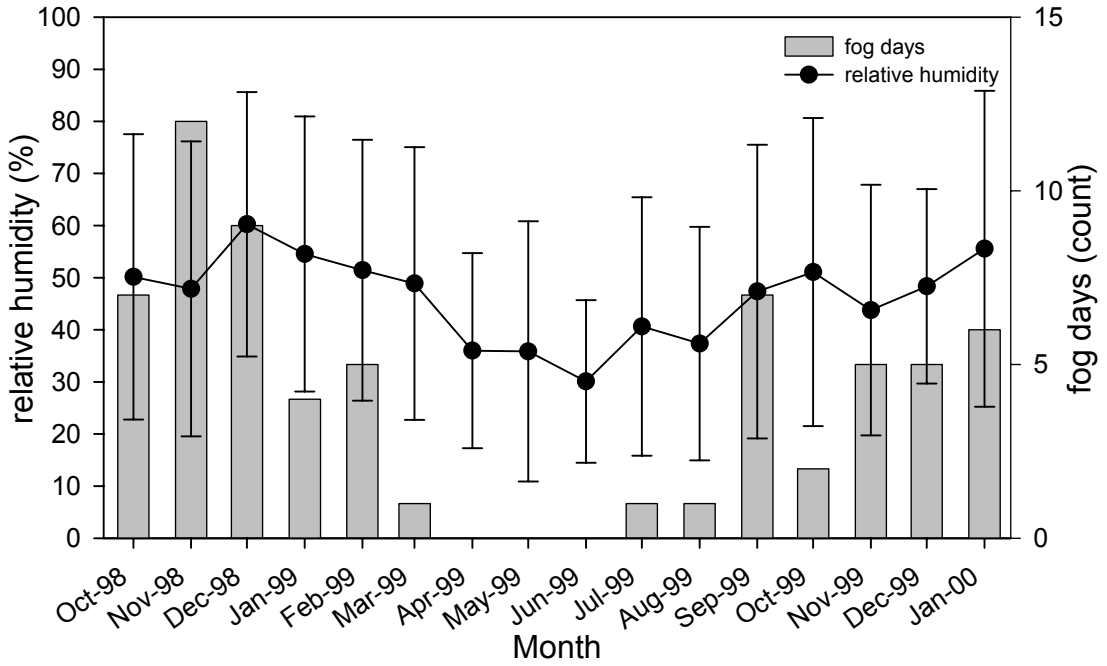


Figure IV-1: Cumulative days with fog events per month and average relative humidity (mean ± SD) over the study period at Gobabeb. Data collected at the first order weather station Gobabeb.

Rain events were very scarce, and precipitation was very low during the study period. In 1998, a total of 2.6 mm of rain fell, and in 1999, 7.4mm, which is a quarter of the average yearly rainfall in this area, and a tenth of the amount that was received

in the year preceding the main study (78.2mm, 1997). Virtually all of the rain fell towards the end of the study period, at the start of the warm-hot moist season, although one rain event was also observed in March 1999 (Figure IV-2).

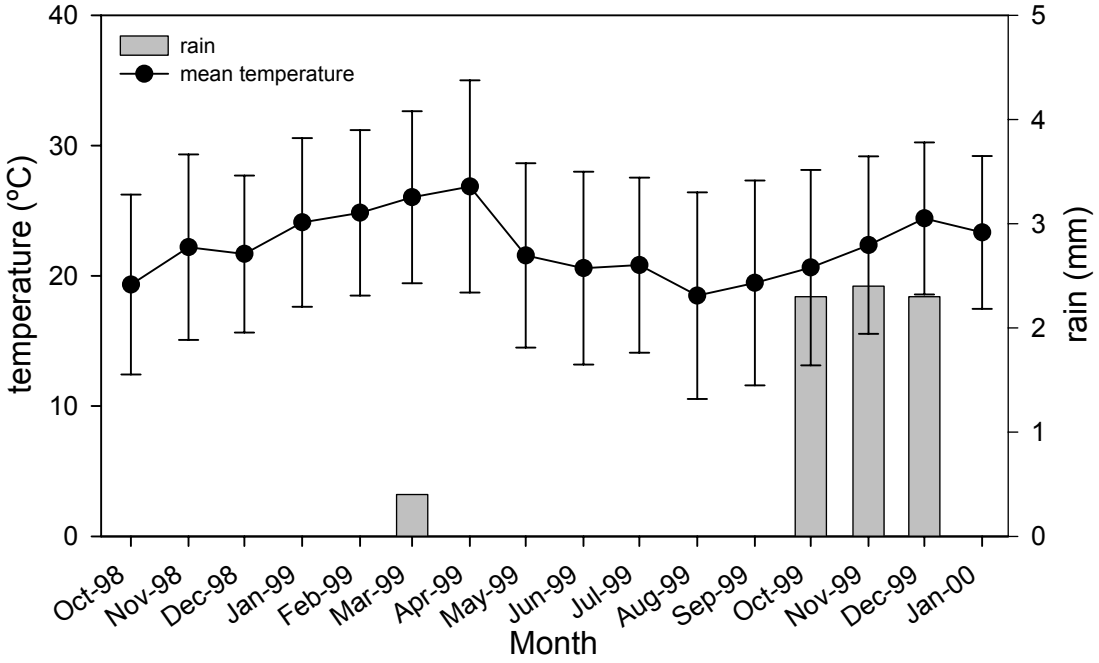


Figure IV-2: Total amount of rain per month and average monthly temperature (mean ± SD) recorded at Gobabeb over the study period. Data collected at the first order weather station Gobabeb.

During the study period, mean monthly temperatures ranged between 18ºC and 27º Celsius. Ambient temperature was highest in April 1999. In this month, the highest temperature ever recorded at Gobabeb, an absolute maximum of 42.6ºC, was reached (Figure IV-2). Ambient temperature was lowest in August 1999, but the lowest temperature for the study period, an absolute minimum of 3.4ºC, was recorded in July 1999. Unlike the mean monthly temperatures, which were highest in autumn, mean soil temperatures peaked during the summer months, when solar radiation was presumably highest (Figure IV-3). At 5 cm soil depth, lowest mean monthly temperatures were recorded in June 1999, while at 30 cm, 60 cm and 120 cm soil depth, mean monthly soil temperatures were lowest in August 1999. Seasonal temperature fluctuations were highest just below the surface, at 5 cm soil depth, with a difference of more than 15ºC between June 1999 and December 1999.

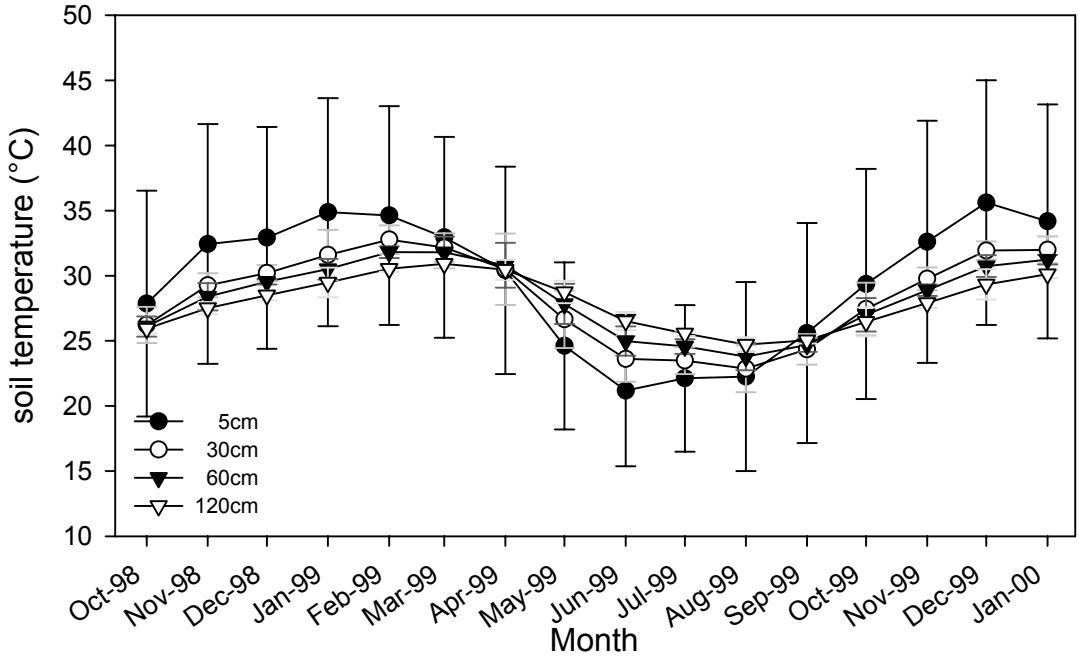


Figure IV-3: Average monthly soil temperature at 5 cm, 30 cm, 60 cm and 120 cm soil depth over the study period. Data collected at first order weather station Gobabeb. Means ± SD.

Diurnal fluctuation of soil temperature was only evident just below the soil surface, at 5 cm depth. At this depth, variation in soil temperature can be as high as 25ºC during the hot months, and in the cool season, difference between minimum and maximum temperature recorded is 10ºC (Figure IV-4). At 30 cm soil depth and below, temperatures varied very little throughout the day, and variation in temperature did no change over the study period.

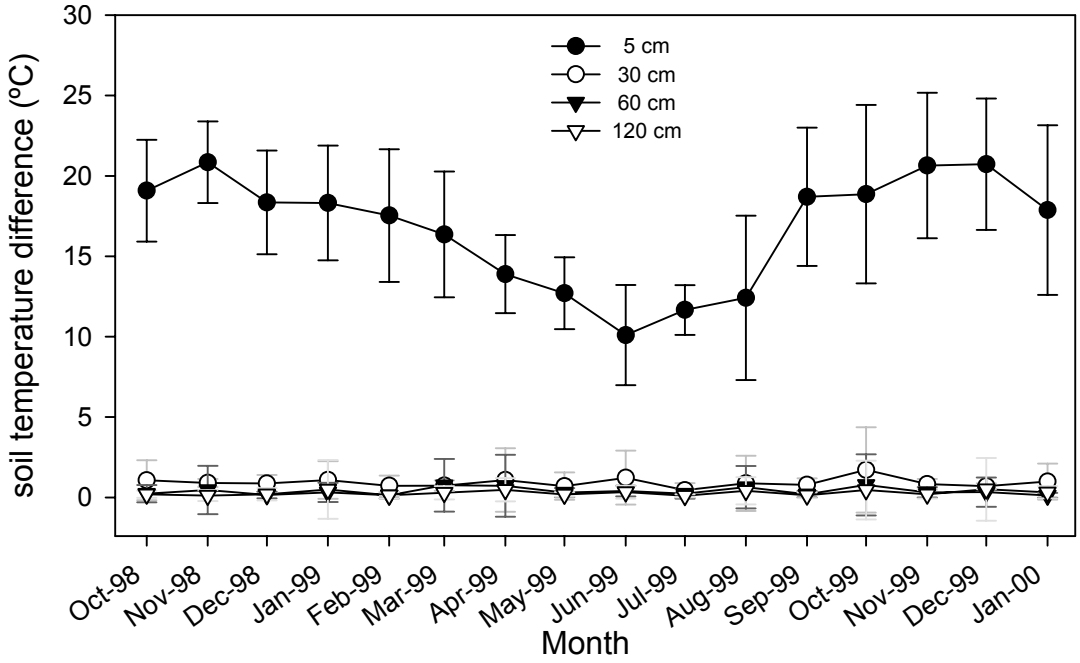


Figure IV-4: Average daily fluctuation of soil temperature per month at 5 cm, 30 cm, 60 cm and 120 cm. Means ± SD.

Food and Water availability

Food was available to four-striped field mice from a number of plant and animal sources. Green vegetative matter was obtainable from nara plants (*Acanthosicyos horridus*, flower buds, flowers and shoots); and camelthorn (*Acacia erioloba*, flowers and leaves). Fruits and seeds were available from camelthorn and female nara plants, as well as from the grasses *Eragrostis spinosa* and *Stipagrostis sabulicola*. Insects occurring at the study site included a number of tenebrionid beetles (e.g. *Onymacris plana*, *Stenocara phalangium*, *Stips stali*, *Zophosis sp.*), as well as species from other beetle families (*Scarabaeidae*, *Meloidae*, *Carabidae*), ants (mainly *Camponotus detritus*, *Hymenoptera*: *Formicidae*), silverfishes or fishmoths (*Thysanura*), crickets (*Orthoptera*) and ant lions (*Neuroptera*), (J. Henschel & R.M. Krug, DERU unpublished data). Free water was very scarce and its availability unpredictable at the study site. Moisture droplets did form on plants only during very wet fog events or precipitation, and animals therefore had to rely on other sources to meet their water demands. During the study, individuals were never observed drinking free water.

Seasonal changes in the occurrence of plant food were only documented with the phenological changes in nara plants, namely the varying availability of buds, open flowers, melons and shoots. Acacia (camelthorn) seedpods were available throughout the year, while flowering was not associated with a particular season and did depend on the individual tree (C. Krug, pers. obs.). No data were collected on the seasonality of insect species.

The seasonal occurrence of buds, open flowers, shoots and melons did differ between the individual plants, but general patterns emerge. In the female plants V- 1, (Figure IV-5), V-4 (Figure IV-6) and V-7 (Figure IV-7), buds were found throughout the moist seasons, and none were growing on the plants during the hot dry season. The flower buds on plant V-7 did emerge a month earlier, in June 1999, than on plants V-1 and V-4. On the male plants V-2 (Figure IV-8) and V-3 (Figure IV-9), buds were found throughout the year, and the number of buds was about five times as high as the number of buds on the female plants. The number of emerging buds on V-2 and V-3 decreased significantly during the hot dry months (Kruskal-Wallis test, V-2: $H_{14,150}=28.64$, $p<0.05$; V-3: $H_{14,150}=38.25$, $p<0.001$). On V-8 (Figure IV-10) and V-9 (Figure IV-11), also male plants, buds were found from the inclusion in the study from July 1999, but no information could be given on whether buds were growing on the plants throughout the hot dry season. The number of buds emerging on V-8 and

V-9 decreased significantly towards the end of the study period (Kruskal-Wallis test, V-8: $H_{6,70}$=15.57, $p<0.05$, V-9: $H_{6,70}$=43.01, $p<0.001$), as in the other male plants, V-2 and V-3. The emergence of buds was negatively associated with ambient temperature, rain events and relative humidity in female plants (Table IV-1, p.36), and had a negative relationship with ambient temperature in male plants (Table IV-2, p.37).

In all plants considered, open flowers showed a similar seasonality as the flower buds. Open flowers occurred only during the moist seasons, and on none of the plants, female or male, were open flowers found during the hot dry season. Flowers opened about a month after the buds emerged, showing a significant positive relation in female plant V-1 (Spearman rank correlation, r_s=0.54, N=13, $p<0.05$), and male plant V-2 (Spearman rank correlation r_s=0.75, N=14, $p<0.001$). The number of open flowers per square metre was of a similar magnitude in all plants, indicating that large numbers of buds on the male plants did not mature. Buds on the male plants did break off very easily, often at a mere touch, and the soil around the plant was littered with flower buds (C. Krug, pers. obs.). In female plants, open flowers showed a negative correlation with ambient temperature (Table IV-1), while, in male plants, the number of open flowers was positively related to relative humidity and the number of fog days in the preceding months (Table IV-2).

The occurrence of fruits (melons) on the female plants was different for each plant examined, and no correlation could be found between the number and opening of flowers in any previous month, and the number of ripe melons. On plant V-1, nara fruits were only found in the second half of the study period, and melons ripened about 3 months after the flowers opened. Ripe melons were available on V-4 throughout the study period with exception of the coldest months, July and August 1999, while, on V-7, ripe melons were found throughout the study period. The occurrence of ripe melons was positively associated with rain events (Table IV-1).

Fresh shoots were emerging on both female and male plants in all seasons throughout the study period, and, in all plants, the number of shoots varied significantly over the study period. In hummock V-1, the number of emerging shoots was greatest during the hot dry months (Kruskal-Wallis test, $H_{13,140}$=21.08, $p<0.1$), and decreased with the emergence of buds in the cool moist months (Spearman rank correlation, r_s=0.57, N=15, $p<0.05$). In plant V-4, the emergence of shoots also showed seasonal variation (Kruskal-Wallis test, $H_{13,140}$=36.26, $p<0.001$), but the picture was slightly different, as the number of emerging shoots decreased earlier than

in V-1. No correlation between the emergence of buds and shoots in this plant could be found. The number of emerging shoots in hummock V-7 also varied seasonally (Kruskal-Wallis test, $H_{11,120}$=27.32, p<0.01). The number of fresh shoots was highest during the hot, dry months and decreased with the onset of cool weather, and as the number of buds increased. No correlation could be found, though, between the emergence of shoots and buds in this plant. In the female plants, the emergence of fresh shoots showed a positive association with ambient temperature and relative humidity in the preceding months (Table IV-1).

Plant part	Environmental factor	Time	r_s-value	Significance
buds	mean temperature	at time	-0.693	**
	maximum temperature	at time	-0.689	**
	minimum temperature	at time	-0.623	**
	rain	at time	-0.533	*
	mean temperature	-1 month	-0.715	**
	maximum temperature	-1 month	-0.568	*
	rain	-1 month	-0.533	*
	minimum temperature	-2 months	-0.574	*
	relative humidity	-3 months	-0.572	*
flowers	mean temperature	at time	-0.595	*
	maximum temperature	at time	-0.591	*
	minimum temperature	at time	-0.644	*
	mean temperature	-1 month	-0.692	**
	minimum temperature	-1 month	-0.604	*
melons	rain	at time	0.659	**
	rain	-1 month	0.659	**
shoots	minimum temperature	-1 month	0.626	**
	relative humidity	-1 month	0.560	*
	mean temperature	-2 months	0.543	*
	relative humidity	-3 months	0.547	*

Table IV-1: Environmental factors influencing the phenology of female nara plants (V-1, V-4, V-7). Mean temperature: mean monthly temperature, maximum temperature: mean monthly maximum temperature, minimum temperature: mean monthly minimum temperature, relative humidity: mean monthly relative humidity, rain: total rain per month. ** p<0.01, * p<0.5.

In the male plants V-2 and V-3, the occurrence of buds also followed a seasonal pattern (Kruskal-Wallis test, V-2: $H_{14,150}$=37.24, p<0.001; V-3: $H_{14,150}$=36.25, p<0.001). While the number of fresh shoots in V-2 did increase over the hot dry months, the number of shoots in V-3 decreased. In both plants did the number of shoots increase towards the end of the study period, as in V-8 and V-9. This seasonal change was not significant in plant V-8 (Kruskal-Wallis test, $H_{6,70}$=9.84, NS), but was

significant in V-9 (Kruskal-Wallis test, $H_{6,\ 70}$=21.52, p<0.001). The emergence of fresh shoots in male plants was only positively related to ambient temperature, as well as relative humidity three months previously (Table IV-2).

Plant part	Environmental factor	Time	r_s-value	Significance
buds	minimum temperature	at time	-0.557	*
	mean temperature	-1 month	-0.564	*
	maximum temperature	-1 month	-0.550	*
	mean temperature	-2 months	-0.568	*
	rain	-3 months	-0.549	*
flowers	relative humidity	-1 month	0.557	*
	relative humidity	-3 months	0.589	*
	fog days	-3 months	0.542	*
shoots	maximum temperature	at time	0.514	*
	minimum temperature	at time	0.557	*
	mean temperature	-1 month	0.569	*
	minimum temperature	-2 months	0.564	*
	relative humidity	-3 months	0.601	*

Table IV-2: Environmental factors influencing the phenology of male nara plants (V-2, V-3, V-8, V-9). Mean temperature: mean monthly temperature, maximum temperature: mean monthly maximum temperature, minimum temperature: mean monthly minimum temperature, relative humidity: mean monthly relative humidity, rain: total rain per month, fog days: total number of days with fog events per month. ** p<0.01, * p<0.5.

Summing up the above results, animals inhabiting V-1 had access to fresh shoots throughout the year, to buds and open flowers in the moist seasons, and to ripe melons in the moist season in the second half of the study period. In addition to this, they also had access to acacia seedpods, as nara plant V-1 was growing next to a camelthorn tree. In both V-2 and V-3, buds and fresh shoots were available to the mice throughout the year, and open flowers could be found during the moist season. As both the nara plants were some distance (5 – 20 m) away from the nearest camelthorn tree, access to seedpods was limited. Mice living in nara plant V-4 had access to fresh shoots throughout all seasons, to buds and open flowers in the moist seasons, and to ripe melons in all months except for the coldest months. In addition to this, acacia seedpods were also available, as this nara was growing next to a camelthorn tree. In nara V-7, animals could rely on fresh shoots and ripe melons throughout the year, buds and open flowers were mainly available during the cooler moister months of the study period. A number of camelthorn trees were standing next to this nara plant, giving the mice access to seedpods. In both V-8 and V-9, buds, open flowers and shoots were available to the animals throughout the time they inhabited the plants in the study period. Mice in V-8 had no access to any other food plants, and mice living in V-9 could make use of mustard bushes growing in the vicinity.

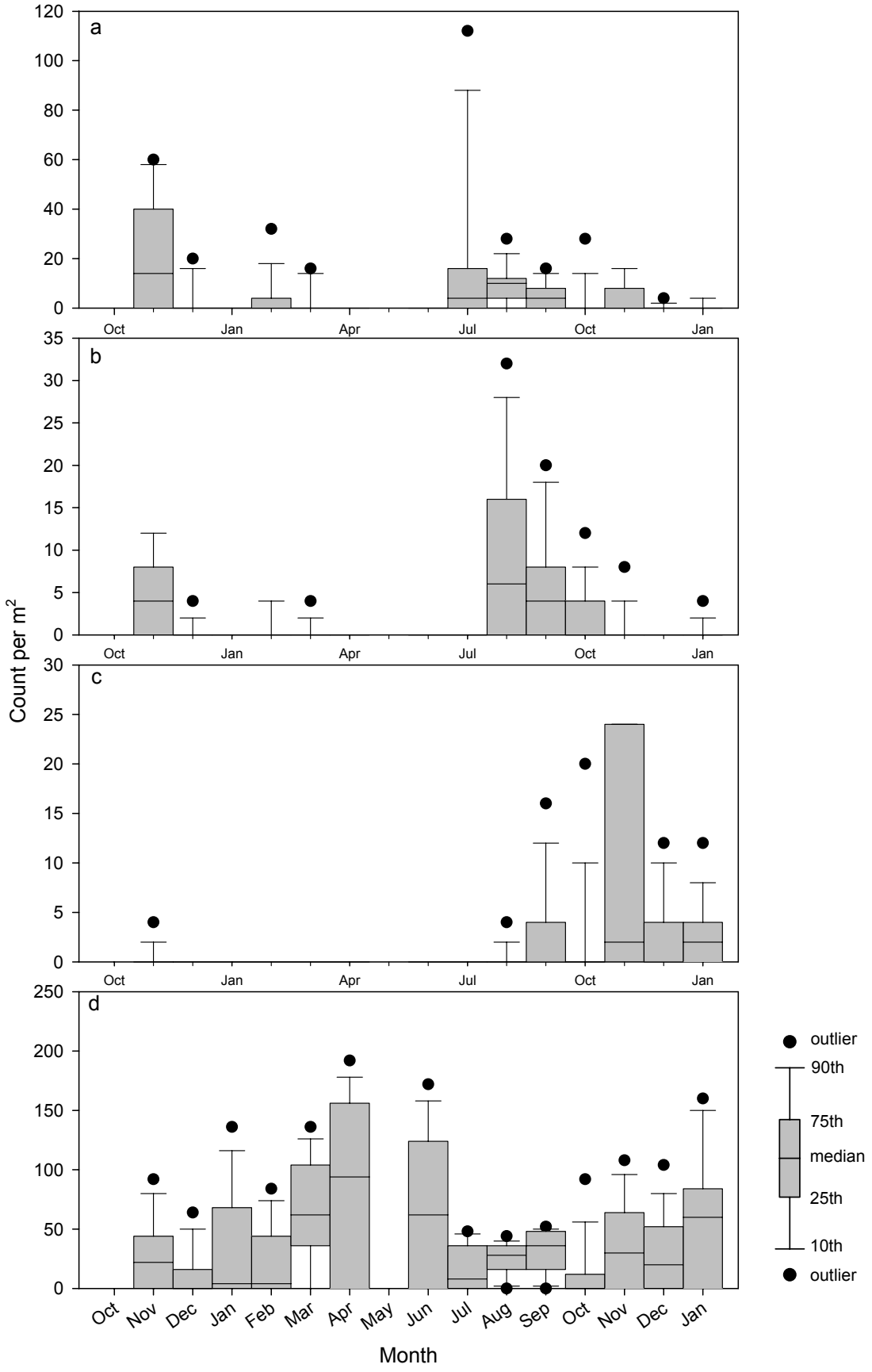


Figure IV-5: Count of (a) buds, (b) flowers, (c) melons and (d) shoots in nara plant V-1 (female). Median, 10th, 25th, 75th and 90th percentiles with outliers. No data available for May 1999.

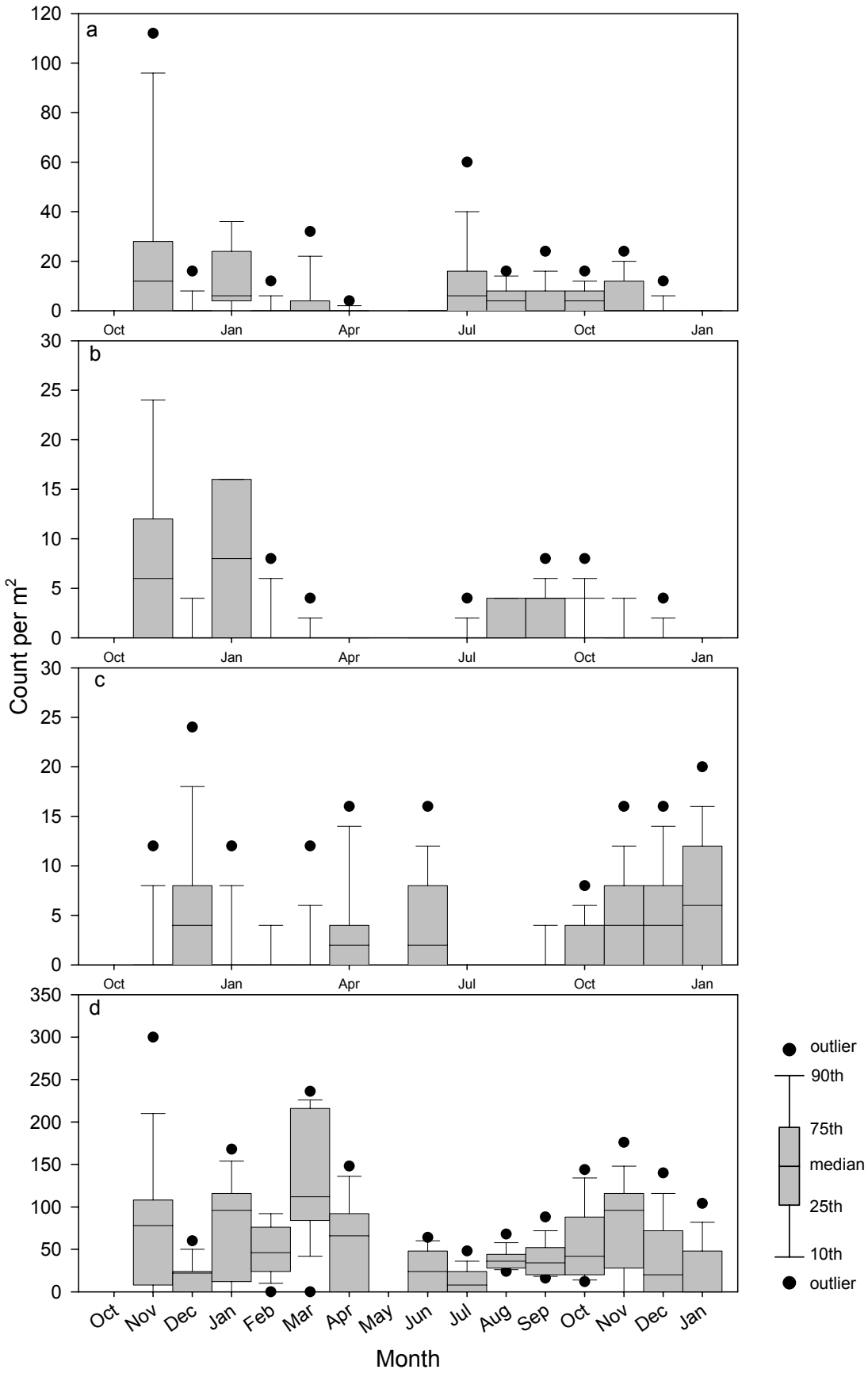


Figure IV-6: Count of (a) buds, (b) flowers, (c) melons and (d) shoots in nara plant V-4 (female). Median, 10th, 25th, 75th and 90th percentiles with outliers. Sampling from November 1998, no data available for May 1999.

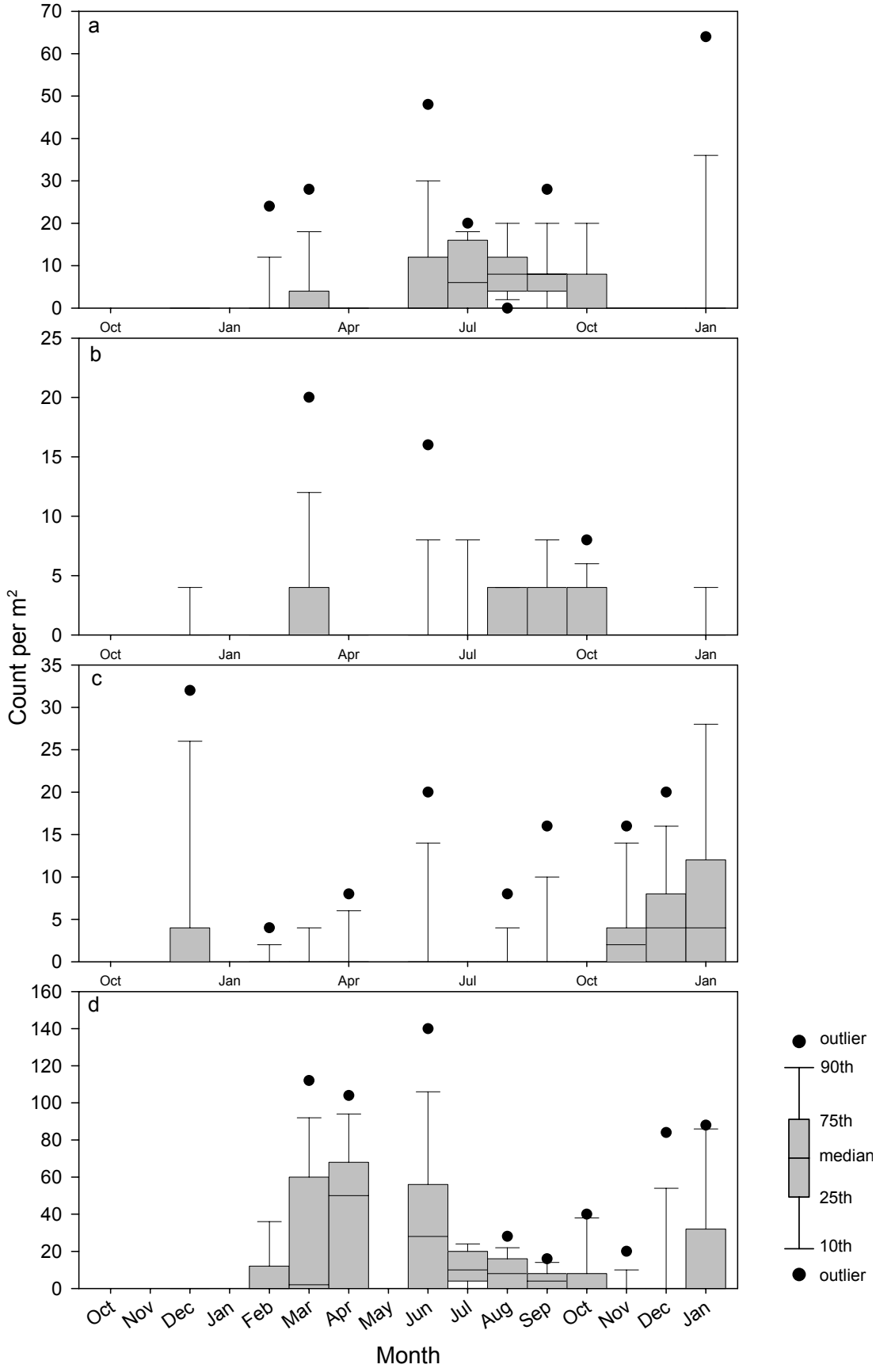


Figure IV-7: Count of (a) buds, (b) flowers, (c) melons and (d) shoots in nara plant V-7 (female). Median, 10th, 25th, 75th and 90th percentiles with outliers. Sampling from December 1998, no data available for January and May 1999.

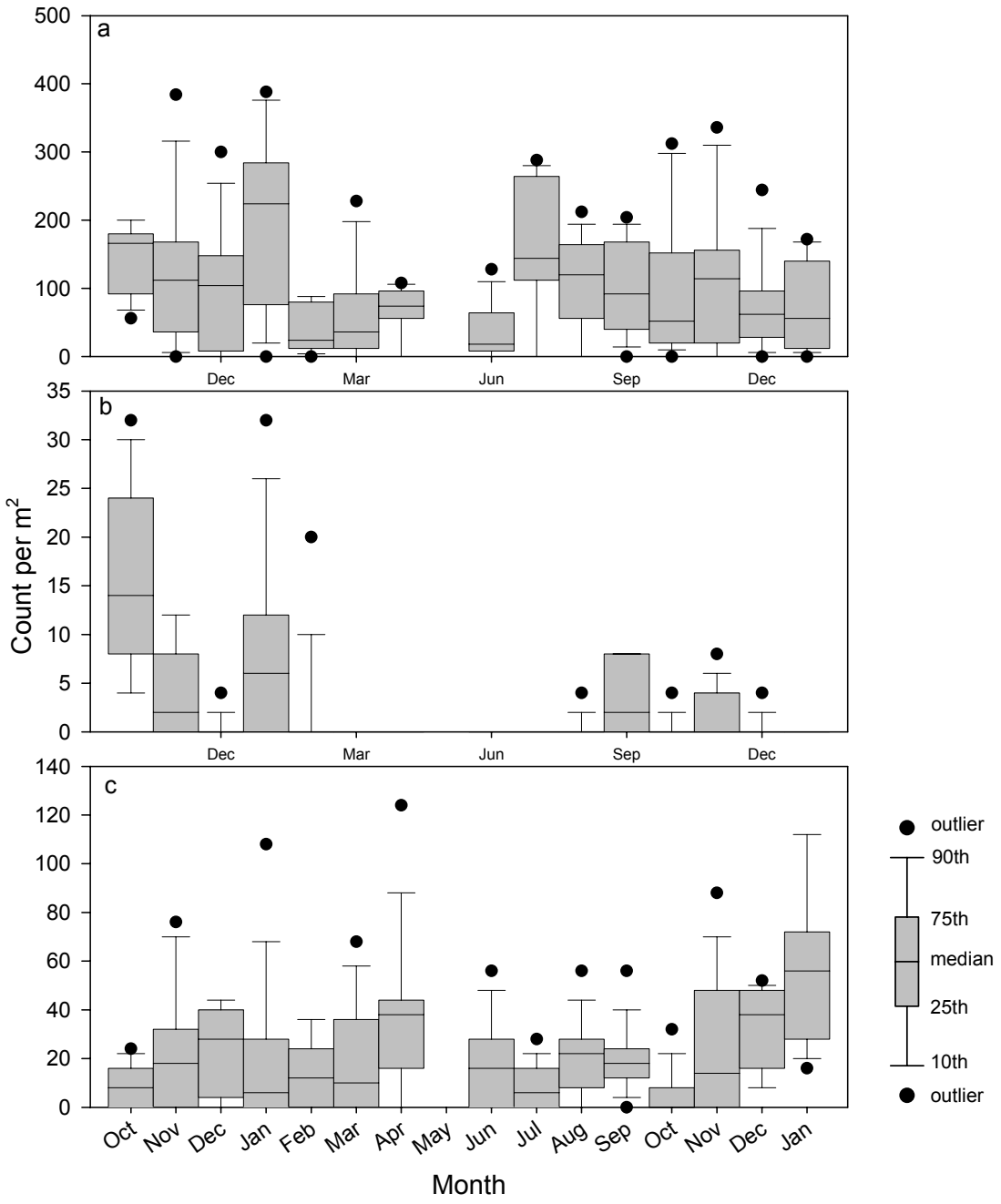


Figure IV-8: Count of (a) buds, (b) flowers and (c) shoots in nara plant V-2 (male). Median, 10th, 25th, 75th and 90th percentiles with outliers. No data available for May 1999.

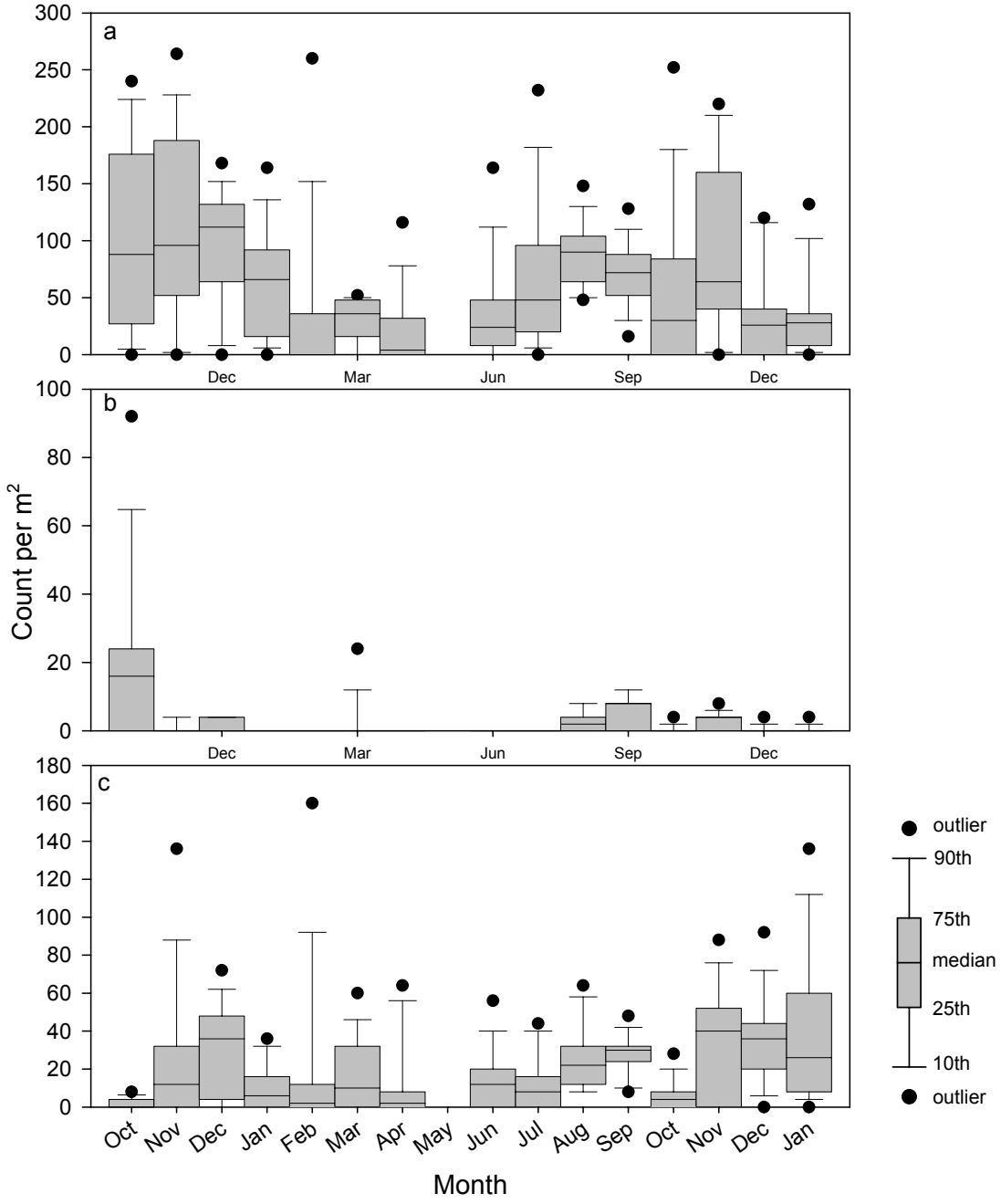


Figure IV-9: Count of (a) buds, (b) flowers and (c) shoots in nara plant V-3 (male). Median, 10th, 25th, 75th and 90th percentiles with outliers. No data available for May 1999.

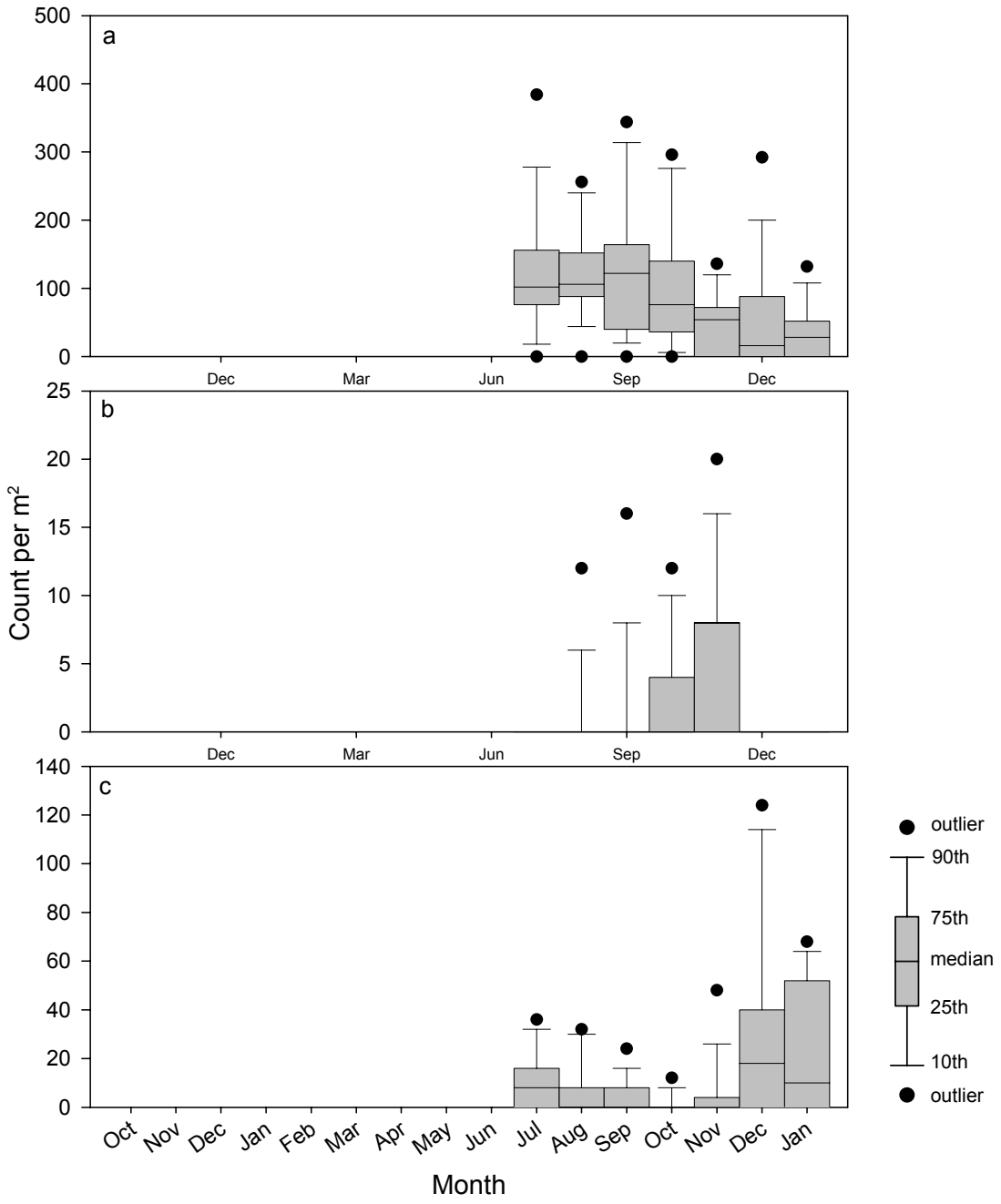


Figure IV-10: Count of (a) buds, (b) flowers and (c) shoots in nara plant V-8 (male). Median, 10th, 25th, 75th and 90th percentiles with outliers. Sampling from July 1999.

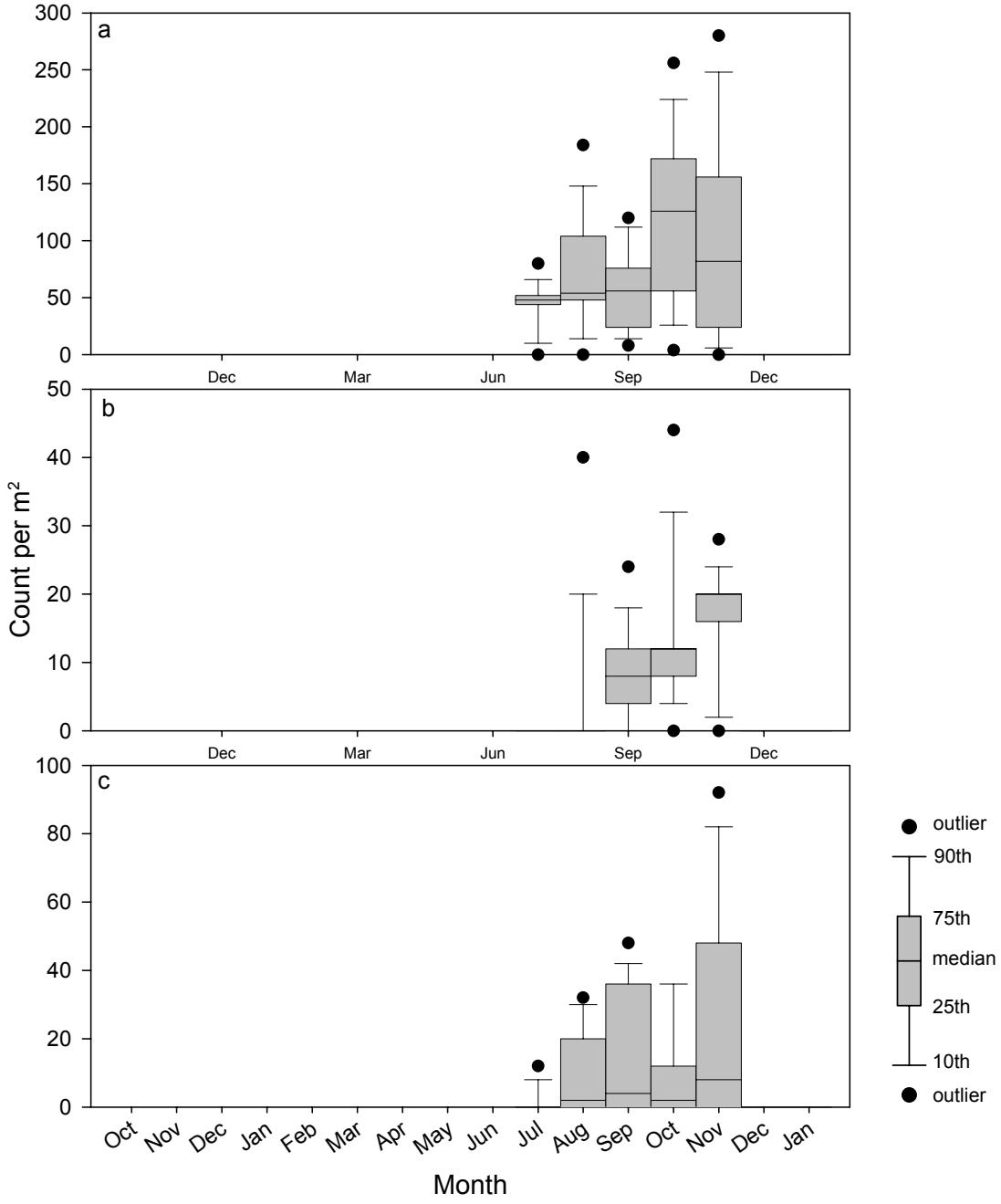


Figure IV-11: Count of (a) buds, (b) flowers and (c) shoots in nara plant V-9 (male). Median, 10th, 25th, 75th and 90th percentiles with outliers. Sampling from July 1999.

Diet

Individuals observed fed nearly exclusively on plant material. Besides flower buds, flowers, melons and fresh shoots of the nara plant, camelthorn (acacia) seedpods and flowers as well as dry plant material (detritus) formed part of the diet. Occasionally (n=7, 4♂, 3♀), mice were observed gnawing at donkey faeces. Closer inspection of these scats showed that they contained acacia seeds, which the mice might have utilised. Intake of insects was very rare and only observed in two cases, both juveniles. One juvenile was found feeding on a scarabaeid beetle; the other one was observed catching and feeding on a lepidopteran. In October 1998, an act of cannibalism was also observed – two juveniles were feeding on a third juvenile, which presumably died after being caught by a fiscal shrike.

In hummock V-1, diet of adult females was composed of (in descending order) acacia seedpods, dry plant material, nara shoots, nara flower buds, nara flowers and nara melons. Acacia seedpods contributed to more than 50% of the diet of adult females (Figure IV-12a); dry plant material and nara shoots made up another 30%. Nara flower buds, nara flowers and nara melons accounted for the rest. The proportions of the various food types were significantly different (Friedman ANOVA: $\chi^2_{6,16}=17.78$, $p<0.01$). Adult males were observed feeding on three food types, acacia seedpods, nara shoots and dry plant material. Acacia seedpods also made up more than 50% of the diet. The other 50% was evenly divided between nara shoots and dry plant matter (Figure IV-12b). Differences in the proportion of these three food types were significant (Friedman ANOVA: $\chi^2_{6,6}=19.78$, $p<0.01$), as in the females. Diet of juveniles was very similar to those of the females, and consisted of acacia seedpods, dry plant material, nara shoots, nara flowers and other food items. In contrast to the adults, acacia seedpods made up a lesser proportion of the diet in juveniles, contribution only 35% (Figure IV-12c). Dry plant material accounted for a quarter, nara shoots for another fifth. Nara flowers and other items, like nara stems, made up the rest. The differences in proportion of the food types were again significant (Friedman ANOVA: $\chi^2_{6,10}=14.93$, $p<0.05$). Despite the apparent different diet composition and variance in proportion of food types, this difference was not significant between the three classes (adult females, adult males and juveniles), (acacia seedpods: Kruskal-Wallis test: $H_{2,32}=1.27$, NS; detritus: Kruskal-Wallis test: $H_{2,32}=1.39$, NS; nara flower bud: Kruskal-Wallis test: $H_{2,32}=1.69$, NS; nara flower:

Kruskal-Wallis test: $H_{2,32}$=1.77, NS; nara melon: Kruskal-Wallis test: $H_{2,32}$=1.13, NS and nara shoot: Kruskal-Wallis test: $H_{2,32}$=0.46, NS)

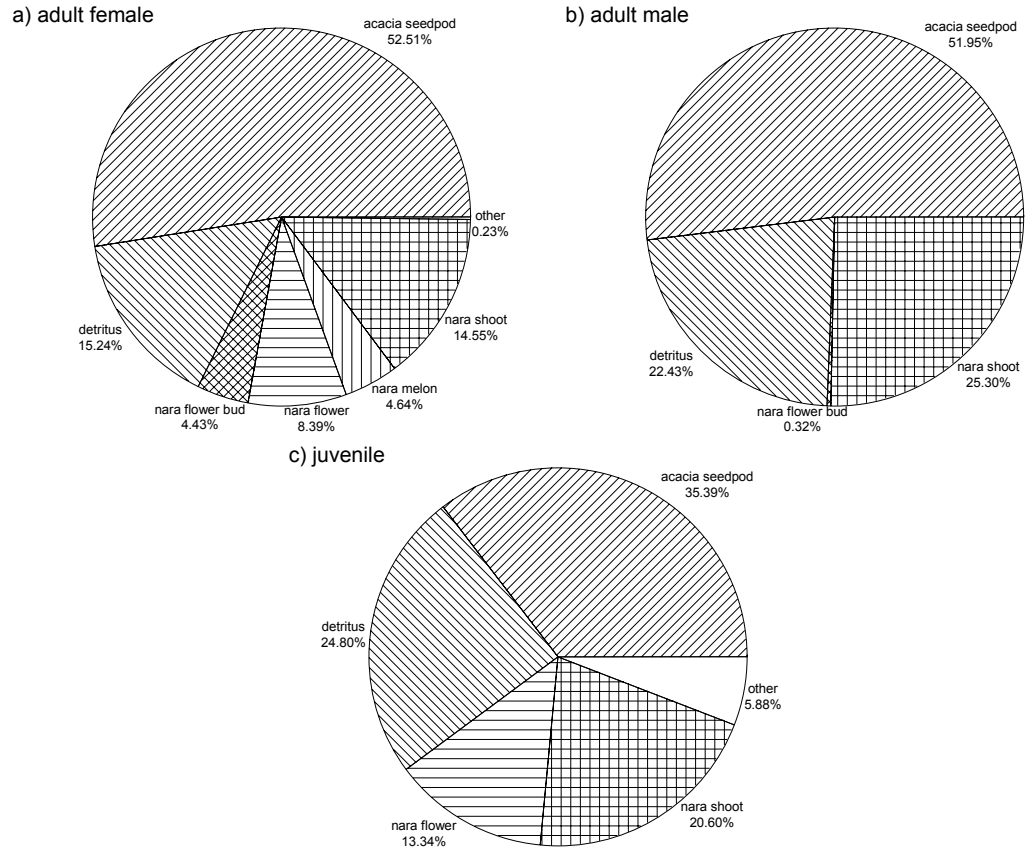


Figure IV-12: Proportion of total feeding time a) adult females (n=8), b) adult males (n=5) and c) juveniles (n=8) spent feeding on selected food items in hummock V-1. other: donkey scat and nara stem.

As the proportions of the food types in the diet were not significantly different between the classes, data were pooled to determine seasonal changes in diet composition. Acacia seedpods formed a major part of the diet for most of the observation period, animals were observed feeding on acacia seedpods in eight of twelve months of observation (Figure IV-13); no acacia seedpods were consumed in February, April, June and October 1999. The proportion of acacia seedpods in the diet did not differ significantly between the months in which they were eaten (Kruskal-Wallis test: $H_{11,32}$=11.88, NS). Detritus was consumed in seven out of twelve months observed, and differences in proportion of diet was not significant between these months (Kruskal-Wallis test: $H_{11,32}$=15.70, NS). Nara shoots were also eaten in seven months, they formed a major part in the diet in April and June 1999, and again in December 1999 and January 2000, but they were consumed to a lesser proportion in the other months. These differences in proportion of the diet between the months were

significant (Kruskal-Wallis test: $H_{11,32}$=20.98, $p<0.05$). Nara flower buds and nara flowers were only consumed in two of the twelve months observed, nara melons in one.

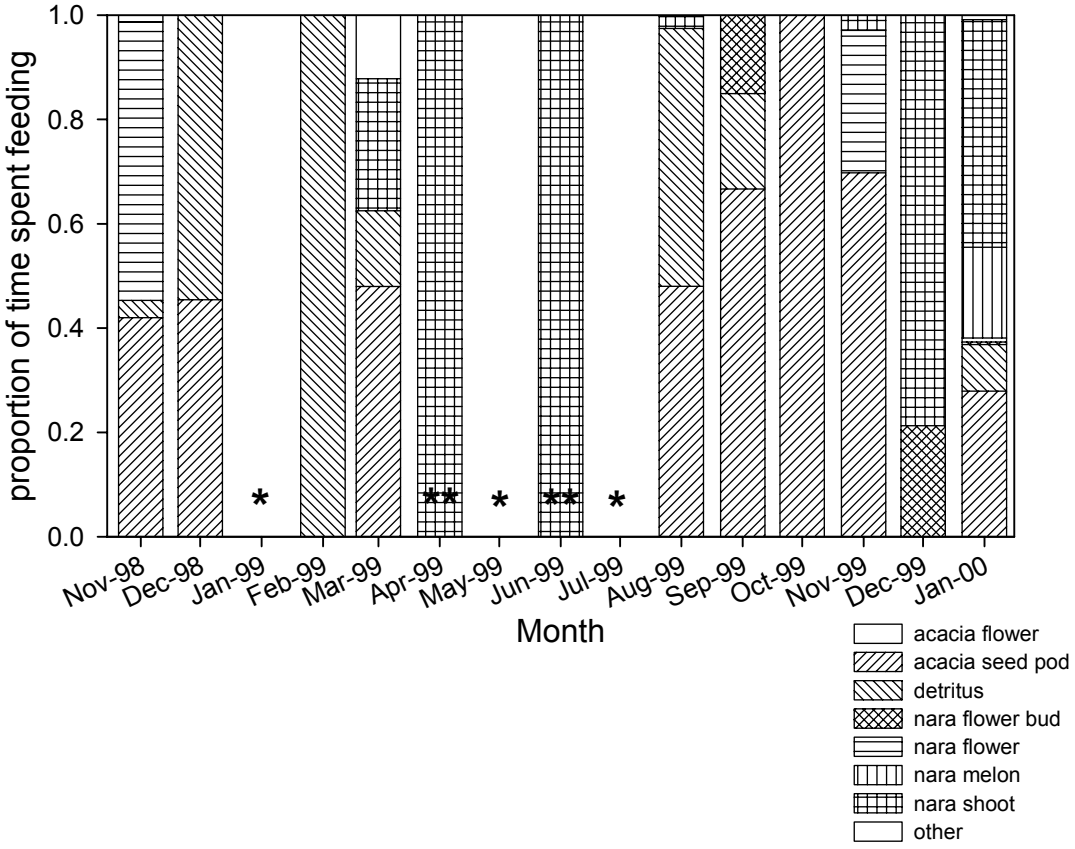


Figure IV-13: Seasonal changes in the proportion of total feeding time animals spent feeding on selected items in hummock V-1. Data for all individuals pooled, * no animal observed, ** single individual observed.

According to the rank preference Method of Johnson (1980b), adult females showed a preference for nara flowers, and a lesser preference for nara melons (Table IV-3). Nara shoots were the least preferred or the food types, but the differences in preference rank were not significant (Friedman ANOVA: $\chi^2_{3,8}$=4.48, NS). Adult males also showed a preference for nara flowers, albeit to a lesser extent than females (Table IV-3). Nara melons were the least preferred food type. Again, the differences in rank preference were not significant (Friedman ANOVA: $\chi^2_{3,3}$=0.15, NS). Unlike the adults, Juveniles showed the strongest preference for nara melons, followed by nara flowers (Table IV-3), while nara flower buds were the least preferred food type. The difference in rank preference between the food types was also not significant (Friedman ANOVA: $\chi^2_{3,5}$=10.02, NS).

As with the proportion of total feeding time for the various food types available, rank difference did not differ between the classes (nara flower bud: Kruskal-Wallis test: $H_{2,17}$=2.39, NS; nara flower: Kruskal-Wallis test: $H_{2,17}$=0.91, NS; nara melon: Kruskal-Wallis test: $H_{2,17}$=2.07, NS; nara shoot: Kruskal-Wallis test: $H_{2,17}$=1.46, NS).

	female	male	juvenile
bud	0.31	0.00	0.83
flower	**-0.94**	**-0.17**	-0.67
melon	-0.13	0.17	**-0.83**
shoot	0.75	0.00	0.67

Table IV-3: Food preference: Average rank difference in food item usage in females (n=8), males (n=5) and juveniles (n=8) in hummock V-1. Bold print indicates most preferred food type.

Month	Buds	Flowers	Melons	Shoots
Nov-98	1.0	**-2.0**	-1.0	2.0
Dec 98 #				
Jan-99*				
Feb-99 #				
Mar-99	1.0	0.0	**-1.0**	0.0
Apr-99 **	0.0	0.0	0.0	0.0
May-99 *				
Jun-99 **	0.0	0.0	0.0	0.0
Jul-99 *				
Aug-99	1.0	0.0	**-1.0**	0.0
Sep-99	**-2.0**	1.0	-1.0	2.0
Oct-99 #				
Nov-99	0.3	**-2.5**	1.3	1.0
Dec-99	**-1.0**	-0.5	1.5	0.0
Jan-00	0.7	**-0.5**	-0.2	0.0

Table IV-4: Seasonal diet preferences in hummock V-1: Average rank difference in the preference of nara flower buds, flowers, melons and shoots. Data for all individuals pooled, # no nara products consumed, * no individual observed, ** single individual observed. Bold print indicates most preferred food type.

Preferences for each of the four food types showed seasonal variation. Nara flower buds were the most preferred food type in September and December 1999, but the differences in rank preference were not significant between the months (Kruskal-Wallis test: $H_{8,17}$=10.66, NS). Nara flower buds were the most preferred food type in November 1999 and January 2000, and differences in rank preference were marginally significant for this food item (Kruskal-Wallis test: $H_{8,17}$=14.83, $p<0.1$). Nara melons were the most preferred food item in March and August 1999, and the least preferred food item in November and December 1999, but these differences in

rank preference were not significant (Kruskal-Wallis test: $H_{8,17}$=9.86, NS). Nara shoots were the least preferred food type in November 1998 and 1999, and in September 1999, and was never a preferred food type. Despite this, the differences in rank preference are marginally significant between the months (Kruskal-Wallis test: $H_{8,17}$=13.73, $p<0.1$)

In hummock V-2, nara flower buds contributed most to the diet of all classes. In adult females, nara flower buds, dry plant material, nara shoots and nara flowers as well as acacia seedpods and other items were part of the diet. Nara flower buds accounted for 63% of the total time feeding (Figure IV-14a), while dry plant material, nara shoots and nara flowers made up another 35%. Acacia seedpods contributed only very little to the diet, less than 5% in females, and differences in proportion of total time spent feeding was different between all food types (Friedman ANOVA: $\chi^2_{5,55}$=109.65, $p<0.001$). Adult males showed a very similar feeding pattern, they consumed nara flower buds, dry plant material, nara flowers, nara shoots, acacia seedpods and other items (Figure IV-14b). Nara flower buds accounted for 65% of their diet, consumption of dry plant material, nara flowers and nara shoots combined made up another 30%. As in adult females, differences in proportion of diet were significant between the food types (Friedman ANOVA: $\chi^2_{5,23}$=54.43, $p<0.001$). Juveniles were only observed feeding on nara flower buds, dry plant material and nara flowers, and very little on nara shoots and acacia seedpods. They also spent most of their total time feeding on nara flower buds, but to a lesser degree than adults (Figure IV-14c). Nara flower buds contributed 56% of the diet, dry plant material accounted for 25%, and nara flowers 14%. Nara shoots played a minor role – they contributed to only 0.3% of the diet. Again, the proportions of food types in the diet were significantly different (Friedman ANOVA: $\chi^2_{5,23}$=49.40, $p<0.001$).

Nevertheless, with exception of the nara shoots, proportion of food types in the diet were not significantly different between the classes (acacia seedpod: Kruskal-Wallis test: $H_{2,92}$=0.05, NS; detritus: Kruskal-Wallis test: $H_{2,92}$=1.44, NS; nara flower bud: Kruskal-Wallis test: $H_{2,92}$=0.70, NS; nara flower: Kruskal-Wallis test: $H_{2,92}$=3.55, NS). Juveniles consumed significantly less nara shoots than adult females and males (Kruskal-Wallis test: $H_{2,92}$=6.03, $p<0.05$).

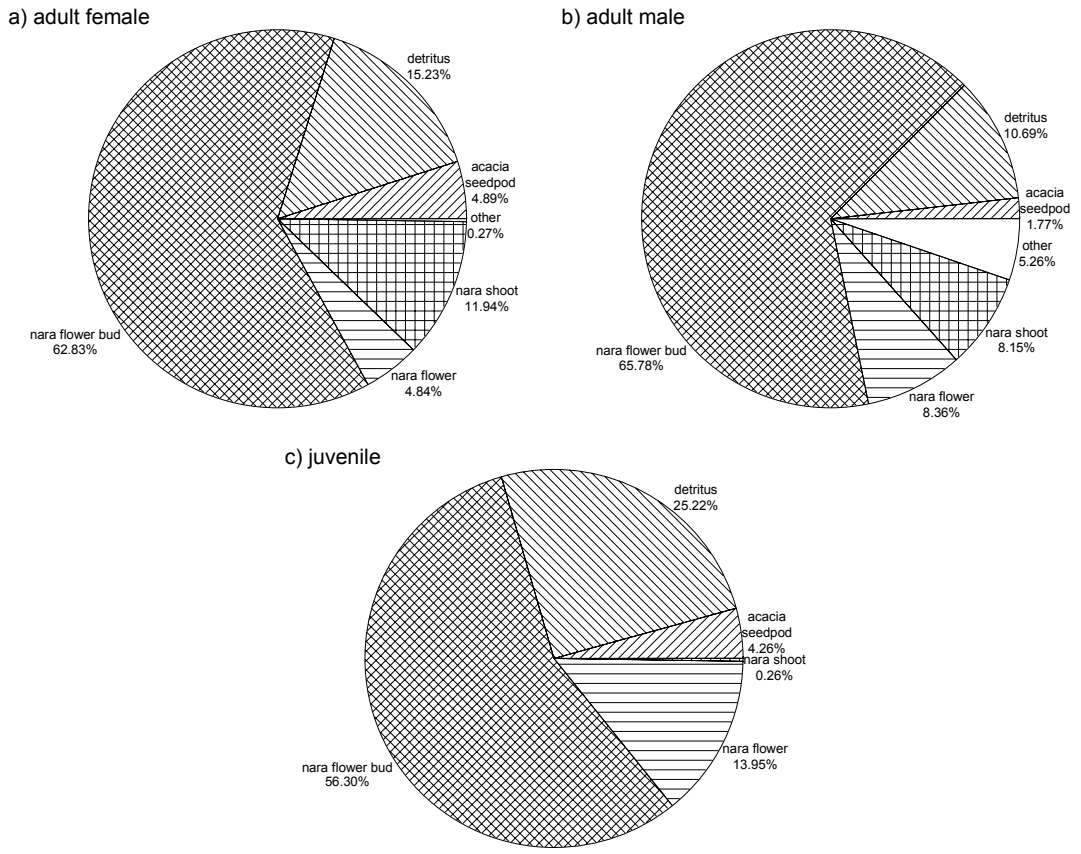


Figure IV-14: Proportion of total feeding time a) adult females (n=15), b) adult males (n=9) and c) juveniles (n=17) spent feeding on selected food items in hummock V-2. other: donkey scat and nara stem

As for hummock V-1, and despite the significant difference in use of nara shoots between the classes, data were pooled to determine seasonal changes in diet composition. With the exception of October 1998, nara flower buds were consumed throughout the year, but to a lesser proportion between April and June 1999, the driest months (Figure IV-15). The reduction in consumption of this food type was significant (nara flower bud: Kruskal-Wallis test: $H_{14,92}=35.54$, $p<0.01$). Dry plant material was consumed throughout the study period, with exception of June and August 1999, and the proportion in the diet changed significantly between the months (Kruskal-Wallis test: $H_{14,92}=25.52$, $p<0.05$). Nara flowers were only consumed in spring and early summer (October 1998 – January 1999 and November and December 1999). Proportions of nara flowers in the diet was significantly higher in October 1998 than in the other months (Kruskal-Wallis test: $H_{14,92}=39.07$, $p<0.01$). Nara shoots were mainly consumed in the hot and dry months, when very little other food types are available. Proportion of nara shoots in the diet was significantly higher in these months than in the other months they were consumed (Kruskal-Wallis test:

$H_{14,92}$=51.27, p<0.001). Acacia seedpods were only consumed in April and May 1999, when very little other food was available, and towards the end of the study period, from September 1999. Proportion of acacia seedpods in the diet did vary significantly between months (Kruskal-Wallis test: $H_{14,92}$=27.82, p<0.05).

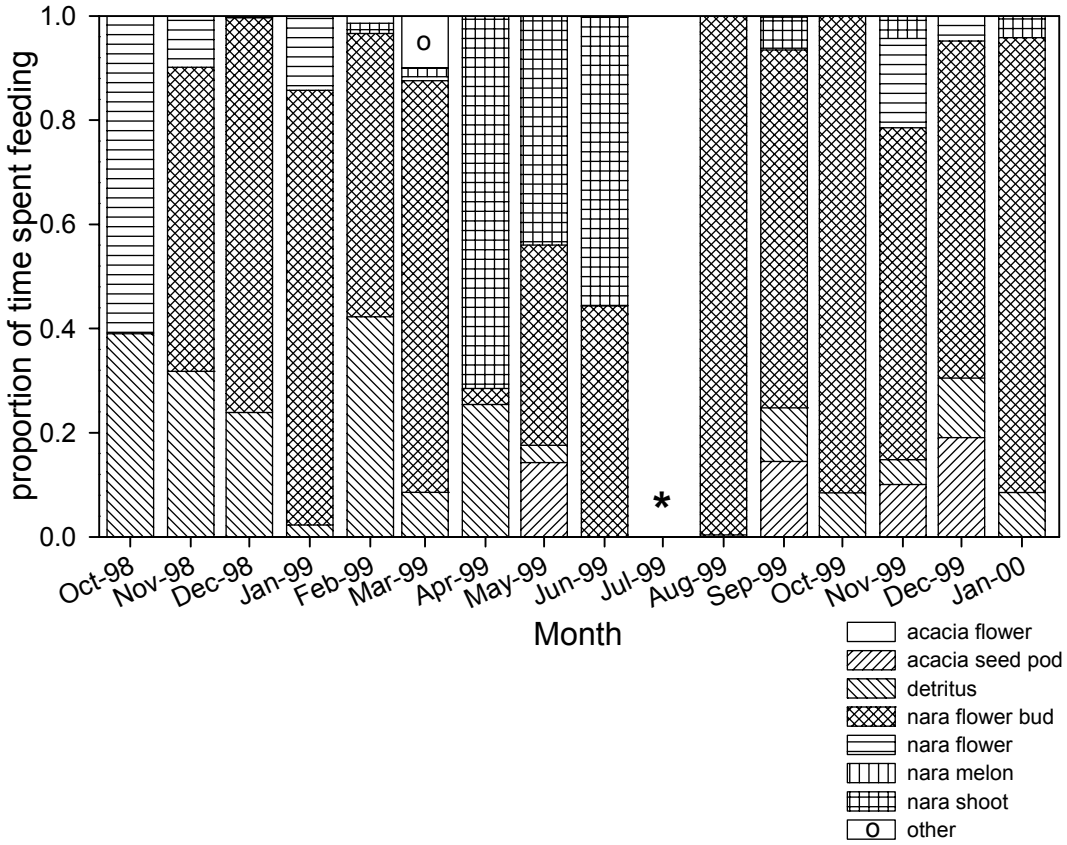


Figure IV-15: Seasonal changes in the use of selected food items in hummock V-2. Proportion of time spent feeding in a 10 min observation period. * no individuals observed

All three classes of animals (adult females, adult males and juveniles) showed a similar preference pattern (Table IV-5). Adult females preferred the most to feed on nara flowers, and showed less preference for nara flower buds and nara shoots. In contrast to hummock V-1, the differences in rank preference were significant (Friedman ANOVA: $\chi^2_{2,42}$=45.94, p<0.001). Adult males also preferred nara flowers over nara flower buds and nara shoots, and the differences in rank preference were also significant (Friedman ANOVA: $\chi^2_{2,16}$=24.57, p<0.001). Nara flowers also were the most preferred food type of juveniles, the preference being even stronger than in the adults, and nara flower buds and nara shoots were preferred less. As in the adults, differences in rank preference of food types were significant (Friedman ANOVA: $\chi^2_{2,19}$=29.93, p<0.001).

The differences in rank preference for the three nara plant food types were not significantly different between classes (nara flower bud: Kruskal-Wallis test: $H_{2,77}$=0.74, NS; nara flower: Kruskal-Wallis test: $H_{2,77}$=3.17, NS; nara shoot: Kruskal-Wallis test: $H_{2,77}$=1.42, NS).

	female	male	juvenile
bud	0.24	0.19	0.33
flower	**-0.51**	**-0.53**	**-0.78**
shoot	0.27	0.34	0.45

Table IV-5: Food preference: Average rank difference in food item usage in females (n=15), males (n=9) and juveniles (n=17) in hummock V-2. Bold print indicates most preferred food type.

With the change of diet composition over the seasons, preference for the nara food types also changed significantly. Nara flower buds were the most preferred food type throughout the study period, with exception of April and June 1999, the dry and hot months. In these months, nara shoots were the most preferred item, and nara flower buds the least preferred food type. The preference for all food types changed significantly over the seasons. (nara flower: Kruskal-Wallis test: $H_{13,77}$=27.59, $p<0.05$; nara shoot: Kruskal-Wallis test: $H_{13,77}$=42.01, $p<0.001$; nara flower bud: Kruskal-Wallis test: $H_{13,77}$=55.52, $p<0.001$)

Month	Buds	Flowers	Shoots
Oct-98	1.5	**-1.0**	-0.5
Nov-98	0.2	**-0.7**	0.5
Dec-98	0.0	**-0.6**	0.6
Jan-99	0.2	**-0.7**	0.5
Feb-99	0.0	**-0.4**	0.4
Mar-99	0.0	**-0.6**	0.6
Apr-99	1.2	-0.2	**-1.0**
May-99 *			
Jun-99	1.0	0.0	**-1.0**
Jul-99 *			
Aug-99	0.0	**-0.5**	0.5
Sep-99	0.0	**-0.5**	0.5
Oct-99	0.0	**-0.5**	0.5
Nov-99	0.3	**-0.8**	0.5
Dec-99	0.1	**-0.8**	0.6
Jan-00	0.0	**-0.3**	0.3

Table IV-6: Seasonal diet preferences in hummock V-2. Average rank difference in the preference of nara flower buds, flowers, and shoots. Data for all individuals pooled, # no nara products consumed, * no individual observed, ** single individual observed. Bold print indicates most preferred food type.

As in nara hummock V-2, nara flower buds were the most important component in the diet of animals inhabiting hummock V-3. In both adult females and adult males, diet consisted of nara flowers buds, nara shoots, dry plant material as well as other items and acacia seedpods. Nara flower buds accounted for 61% of the total time spent feeding adult females (Figure IV-16a). Nara shoots were the second most eaten item, and made up nearly a quarter of the diet. Dry plant material, other food types, like nara stems and donkey scats, and acacia seedpods were minor parts of the diet. Nara flowers played very little role – only 0.29% of the total time feeding was spent on this food type. Differences in the proportion of the diet was significantly different between food types (Friedman ANOVA: $\chi^2_{5,25}=73.96$, $p<0.001$). Nara flower buds were also the most consumed item in adult males, but contributed less to the diet than in females, only about 45% (Figure IV-16b).

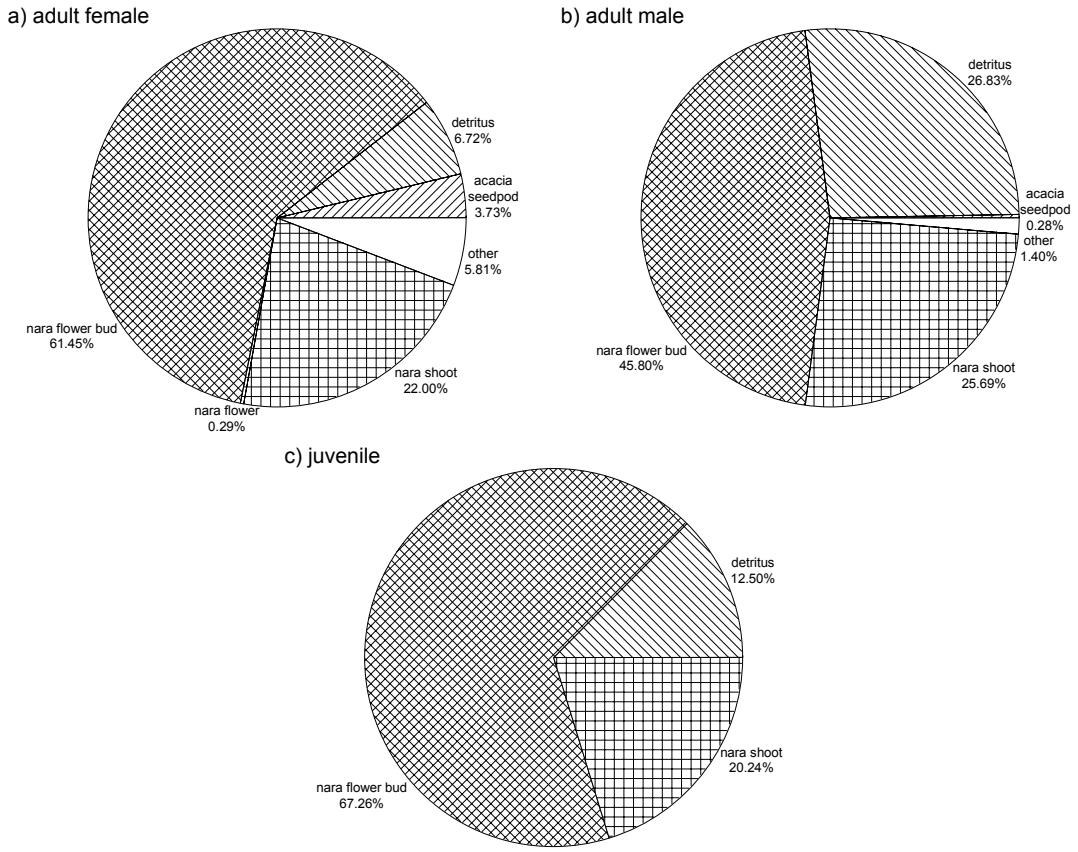


Figure IV-16: Proportion of total feeding time a) adult females (n=12), b) adult males (n=7) and c) juveniles (n=9) spent feeding on selected food items in hummock V-3. other: donkey scat and nara stem

Dry plant material was consumed more often than in females, and accounted for 26% of the diet, nara shoots contributed 25%. Other food items and acacia seedpods played only a very small role. The proportions of the various food types in the diet did

differ significantly (Friedman ANOVA: $\chi^2_{5,8}$=23.41, p<0.001). The diet of Juveniles was very similar to those of the adults, and was composed of nara flower buds, nara shoots and dry plant material. The diet consisted to 67% of nara flower buds (Figure IV-16c), 20% nara shoots and 12% dry plant material. Again, proportions of food types in the diet were significantly different from each other (Friedman ANOVA: $\chi^2_{5,9}$=37.65, p<0.001). As in hummock V-1, proportion of each food types in the diet did not differ significantly between adult females, adult males and juveniles (acacia seedpod: Kruskal-Wallis test: $H_{2,54}$=0.91, NS; detritus: Kruskal-Wallis test: $H_{2,54}$=2.94, NS; nara flower bud: Kruskal-Wallis test: $H_{2,54}$=2.44, NS; nara flower: Kruskal-Wallis test: $H_{2,54}$=0.80, NS; nara shoot: Kruskal-Wallis test: $H_{2,54}$=0.54, NS).

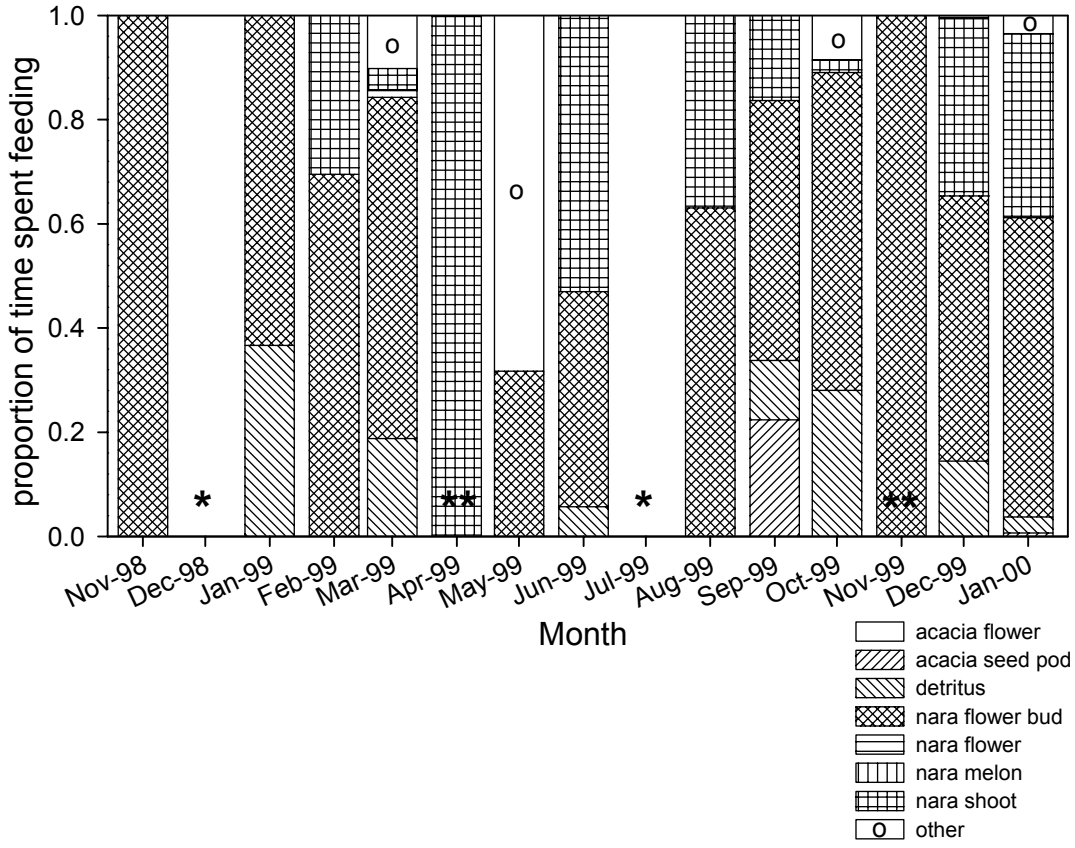


Figure IV-17: Seasonal changes in the use of selected food items in hummock V-3. Proportion of time spent feeding in a 10 min observation period. * no individuals observed, ** one single individual observed.

Therefore, data for all classes were combined to establish changes seasonal changes in diet composition. As in hummock V-2, nara flower buds were consumed throughout the study period, and were used to a lesser degree in the hot and dry months, May and June 1999 (Figure IV-17). The proportion of nara flower buds in the diet did not vary significantly between months (nara flower bud: Kruskal-Wallis test:

$H_{12,54}$=10.03, NS). Nara shoots were consumed throughout most of the study period, and the use increased during the autumn and winter months. These changes in proportion were significant between months (nara shoot: Kruskal-Wallis test: $H_{12,54}$=25.59, $p<0.05$). The consumption of dry plant material was only observed in about half of the months of the study, and the proportion in the diet did not change significantly between months (detritus: Kruskal-Wallis test: $H_{12,54}$=15.57, NS). Both nara flowers and acacia seedpods were only consumed in one or two months of the observation period.

Adult females, adult males and juveniles showed a similar preference pattern as the animals inhabiting hummock V-2. Animals of all classes preferred nara flowers the most, followed by nara shoots. Nara flower buds were the least preferred food item. These differences in preference between the three food types were significant in all classes (females: Friedman ANOVA: $\chi^2_{2,28}$=12.82, $p<0.01$; males: Friedman ANOVA: $\chi^2_{2,10}$=4.0, NS; Juveniles: Friedman ANOVA: $\chi^2_{2,11}$=7.4, $p<0.05$). Differences of preference within food types between classes were not significant for all food types (nara flower bud: Kruskal-Wallis test: $H_{2,49}$=1.77, NS; nara flower: Kruskal-Wallis test: $H_{2,49}$=3.45, NS; nara shoot: Kruskal-Wallis test: $H_{2,49}$=1.09, NS).

	female	male	juvenile
bud	0.21	0.45	0.36
flower	**-0.25**	**-0.25**	**-0.41**
shoot	0.04	-0.20	0.05

Table IV-7: Food preference: Average rank difference in food item usage in females (n=12), males (n=7) and juveniles (n=9) in hummock V-3. Bold print indicates most preferred food type.

Seasonal differences in preference of animals inhabiting hummock V-3 were very similar to those living in hummock V-2. Nara flowers were the most preferred food type for most of the study period (Table IV-8), nara shoots were the most preferred food item during the autumn and winter months, and again in December 1999 and January 2000. Nara flower buds were the least preferred item. Preferences for nara flower buds did not change significantly between months (Kruskal-Wallis test: $H_{11,49}$=13.52, NS); but the changes in preference were significant between months for nara flowers (Kruskal-Wallis test: $H_{11,49}$=20.04, $p<0.05$), and marginally significant for nara shoots (Kruskal-Wallis test: $H_{11,49}$=19.64, $p<0.1$)

Month	Buds	Flowers	Shoots
Nov-98	0.0	**-0.5**	0.5
Dec-98			
Jan-99	0.0	**-0.5**	0.5
Feb-99	0.4	**-0.4**	0.0
Mar-99	0.0	**-0.4**	0.4
Apr-99	1.5	-0.5	**-1.0**
May-99 *			
Jun-99	0.6	-0.2	**-0.4**
Jul-99 *			
Aug-99	0.3	0.0	**-0.3**
Sep-99	0.2	**-0.2**	0.0
Oct-99	0.0	**-0.3**	0.3
Nov-99	0.0	**-0.5**	0.5
Dec-99	0.6	-0.3	**-0.4**
Jan-00	0.4	-0.1	**-0.3**

Table IV-8: Seasonal diet preferences in hummock V-3. Average rank difference in the preference of nara flower buds, flowers, and shoots. Data for all individuals pooled, # no nara products consumed, * no individual observed, ** single individual observed. Bold print indicates most preferred food type.

Diet composition in hummock V-4 was comparable to hummock V-1. Adult females fed on nara shoots, acacia seedpods, nara melons, acacia flowers as well as dry plant material, nara flowers and other items. Nara shoots contributed 33% to the diet of adult females (Figure IV-18a), acacia seedpods accounted for 28%. Nara melons were consumed in 16% of the total feeding time, and acacia flowers in 9%. Dry plant material, nara flower buds, nara flowers and other items formed only a very minor part of the diet. Differences in proportion of diet were significant between food types (Friedman ANOVA: $\chi^2_{7,24}$=35.96, p<0.001). The diet of adult males consisted of nara shoots, nara melons, acacia flowers and seedpods, as well as dry plant material, nara flower buds and flowers. Nara shoots were also the most consumed item, and contributed 45% to the diet (Figure IV-18b). Nara melons accounted for a quarter of the total time spent feeding. Acacia flowers and acacia seedpods were used to a lesser extent than in females, while dry plant material, nara flower buds and nara flowers made up a higher proportion of the diet. The differences in proportion of total time spent feeding were significant between the food types (Friedman ANOVA: $\chi^2_{7,31}$=42.43, p<0.001). In Juveniles, nara melons and nara shoots were the also most consumed food types, other items eaten were acacia flowers and seedpods, dry plant

material and nara flower buds and flowers. Juvenile diet consisted to 40% of nara melons and 32% of nara shoots (Figure IV-18c). Acacia flowers, acacia seedpods, dry plant material, nara flower buds and nara flowers made up the rest of the diet, and each of these food types contributed five to six percent. The differences in proportion of diet were significant between food types (Friedman ANOVA: $\chi^2_{7,14}$=33.56, p<0.001). Only the proportion acacia seedpods contributed to the diet was significantly different between classes (Kruskal-Wallis test: $H_{2,89}$=9.30, p<0.01), all the other food types did not differ in their proportion in the diet (acacia flower: Kruskal-Wallis test: $H_{2,89}$=0.34, NS; detritus: Kruskal-Wallis test: $H_{2,89}$=1.93, NS; nara flower bud: Kruskal-Wallis test: $H_{2,89}$=3.82, NS; nara flower: Kruskal-Wallis test: $H_{2,89}$=1.21, NS; nara melon: Kruskal-Wallis test: $H_{2,89}$=3.18, NS; nara shoot: Kruskal-Wallis test: $H_{2,89}$=0.92, NS)

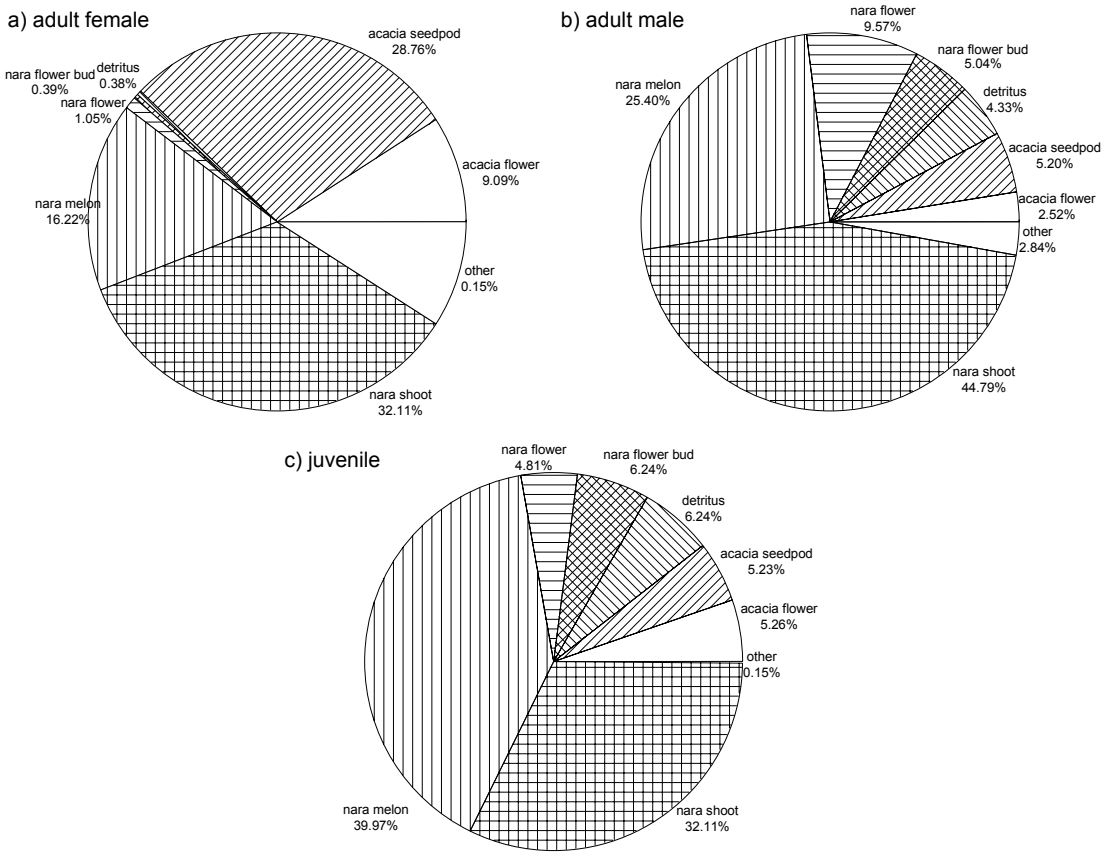


Figure IV-18: Proportion of total feeding time a) adult females (n=15), b) adult males (n=18) and c) juveniles (n=37) spent feeding on selected food items in hummock V-4. other: donkey scat and nara stem

To determine seasonal changes in diet composition, the data for adult females, adult males and juveniles were pooled. Nara shoots were consumed throughout the year, and the differences in proportion in the diet were significant between months

(Kruskal-Wallis test: $H_{11.89}$=27.48, p<0.01), (Figure IV-19). Nara melons were eaten in a high proportion during the dry and hot months (April – June 1999), and the proportion did differ significantly during these months (nara melon: Kruskal-Wallis test: $H_{11.89}$=39.41, p<0.001). Animals were feeding on acacia flowers in June 1999 and September and October 1999. The proportion of acacia flowers in the diet was significantly higher in October than in the other months (Kruskal-Wallis test: $H_{11.89}$=43.30, p<0.001). Acacia seedpods formed a major part of the diet in the winter and spring months, and proportion of this food type changed significantly between months (Kruskal-Wallis test: $H_{11.89}$=30.86, p<0.01). Nara flower buds and nara flowers were eaten during spring, while dry plant material was part of the diet during the autumn and winter months. Proportions of these food types in the diet also did differ significantly between months (nara flower bud: Kruskal-Wallis test: $H_{11.89}$=45.40, p<0.001; nara flower: Kruskal-Wallis test: $H_{11.89}$=37.35, p<0.001; detritus: Kruskal-Wallis test: $H_{11.89}$=11.09, NS)

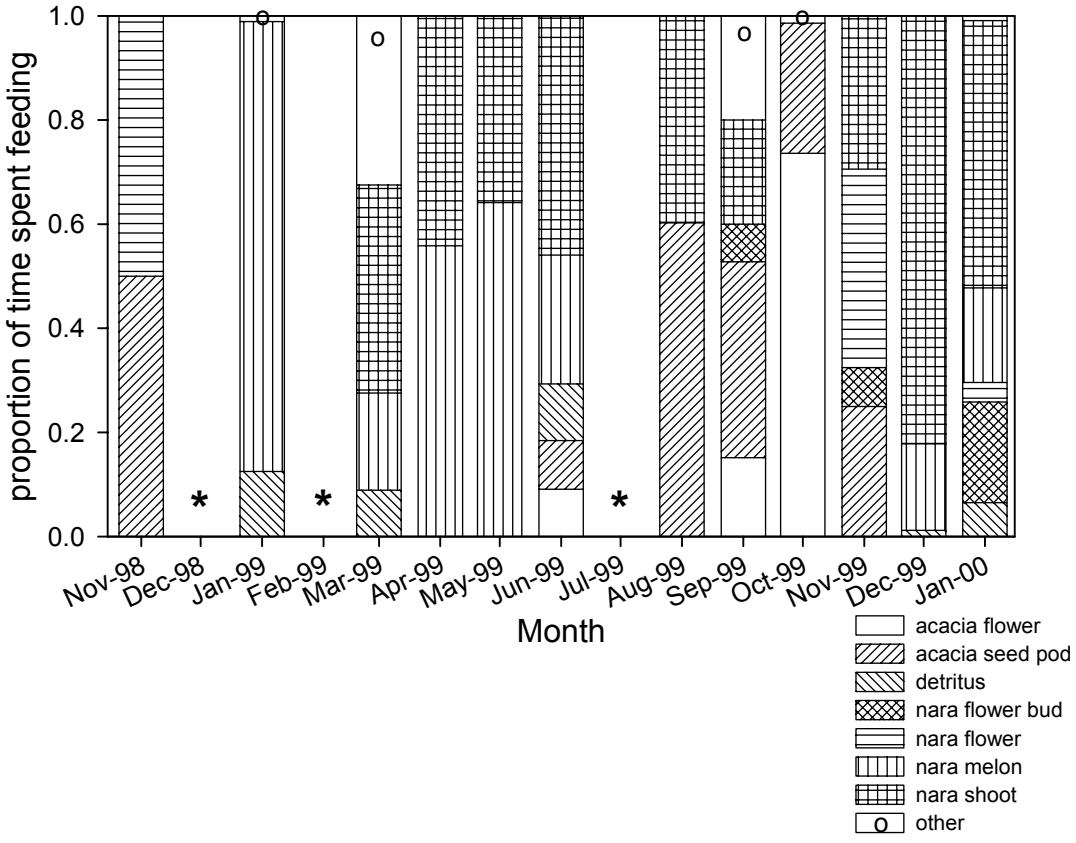


Figure IV-19: Seasonal changes in the use of selected food items in hummock V-4. Proportion of time spent feeding in a 10 min observation period. * no individuals observed.

As for animals living in hummocks V-2 and V-3, nara flowers were the most preferred food type for adult females, adult males and juveniles in hummock V-4

(Table IV-9). Adult females preferred nara flowers over nara melons, nara shoots were the least preferred item. Difference in rank preference were significant between food types (Friedman ANOVA: $\chi^2_{3,11}$=11.39, p<0.01). Adult males also preferred nara flowers over nara melons, and preferred nara shoots the least. Rank preference was significantly different between food types (Friedman ANOVA: $\chi^2_{3,24}$=14.34, p<0.01). Juveniles showed the same preferences as adult females and males, and the difference in preference was significant between food types (Friedman ANOVA: $\chi^2_{3,26}$=24.53, p<0.001). Within food types, preferences were not significant between adult females, adult males and juveniles (nara flower bud: Kruskal-Wallis test: $H_{2,61}$=1.62, NS; nara flower: Kruskal-Wallis test: $H_{2,61}$=0.53, NS; nara melon: Kruskal-Wallis test: $H_{2,61}$=0.50, NS; nara shoot: Kruskal-Wallis test: $H_{2,61}$=2.94, NS).

	female	male	juvenile
bud	0.45	0.08	-0.02
flower	**-0.73**	**-0.60**	**-0.67**
melon	-0.27	-0.23	-0.44
shoot	0.55	0.81	1.10

Table IV-9: Food preference: Average rank difference in food item usage in females (n=15), males (n=18) and juveniles (n=37) in hummock V-4. Bold print indicates most preferred food type.

Month	Buds	Flowers	Melons	Shoots
Nov-98	1.0	**-2.0**	-1.0	2.0
Dec-98 *				
Jan-99	1.0	0.0	**-3.0**	2.0
Feb-99 *				
Mar-99	1.0	**-1.0**	-0.7	0.7
Apr-99	0.4	**-0.7**	-0.4	0.7
May-99 *				
Jun-99	**-0.3**	**-0.3**	0.0	0.7
Jul-99 *				
Aug-99	1.0	0.0	**-1.0**	0.0
Sep-99	0.0	0.0	**-1.0**	1.0
Oct-99 *				
Nov-99	0.6	**-2.3**	0.5	1.1
Dec-99	0.1	**-0.9**	0.6	0.3
Jan-00	**-1.1**	-0.3	0.6	0.9

Table IV-10: Seasonal variation in diet preference in hummock V-4: Average rank difference in the preference of nara flower buds, flowers, melons and shoots. Data for all individuals pooled, # no nara products consumed, * no individual observed, ** single individual observed. Bold print indicates most preferred food type.

As with diet composition, animals displayed seasonal changes in the preference of the four food types. As in hummocks V-2 and V-3, nara flowers were the most preferred food type for most of the study period. Differences in preference were significant between months (nara flower: Kruskal-Wallis test: $H_{9,69}$=42.43, $p<0.001$). Nara melons were most preferred in January 1999 and again in August and September 1999 (winter and early spring). Preferences did change significantly between months (nara melon: Kruskal-Wallis test: $H_{9,69}$=33.74, $p<0.001$). Animals preferred nara flower buds most in January 2000, and nara shoots were the least preferred food type for all of the study period. Differences in preference were significant between months for both food types (nara flower bud: Kruskal-Wallis test: $H_{9,69}$=43.91, $p<0.001$; nara shoot: Kruskal-Wallis test: $H_{9,69}$=19.83, $p<0.05$).

Overall, acacia seedpods were consumed in the highest proportion in hummock V-1, and differences in proportion of acacia seedpods in the diet were significant between hummocks (Kruskal-Wallis test: $H_{3.268}$=50.11, $p<0.001$). Dry plant material was also consumed in the highest proportion by animals inhabiting hummock V-1, and differences in proportion in diet were significant between hummocks (Kruskal-Wallis test: $H_{3.268}$=35.67, $p<0.001$). Animals in both hummock V-2 and V-3 consumed nara flower buds in the highest proportion, and the difference was significant between hummocks (Kruskal-Wallis test: $H_{3.268}$=128.08, $p<0.001$). Nara flowers were consumed in the lowest proportion in hummock V-3, the differences between hummocks were significant (Kruskal-Wallis test: $H_{3.268}$=11.66, $p<0.01$). Animals inhabiting hummock V-4 consumed nara melons in a significantly higher proportion than those living in hummock V-1 (Mann-Whitney U-test: U=945.0, N_1=33, N_2=89, $p<0.01$). Nara shoots contributed most to the diet of animals inhabiting hummock V-4, the difference in proportion was significantly different between hummocks (Kruskal-Wallis test: $H_{3.268}$=31.27, $p<0.001$)

Differences in preference for nara flower buds were not significant between hummocks (Kruskal-Wallis test: $H_{3.204}$=2.01, NS), while nara flowers were least preferred by animals inhabiting hummock V-1 (Kruskal-Wallis test: $H_{3.204}$=13.33, $p<0.01$). Nara melons were significantly more preferred by animals living in hummock V-1 than by those living in hummock V-4 (Mann-Whitney U-test: U=511.5, N_1=17, N_2=61, $p<0.001$). Nara shoots were the least preferred food type in hummock V-4, the difference of preference was significant between hummocks (Kruskal-Wallis test: $H_{3.204}$=19.25, $p<0.001$).

Predation

Predation in the area was negligible, as the number and density of possible predators was very low, though exact data on the abundance of these predators are not available. All possible predators of *Rhabdomys* that were observed at the study site are listed in Table IV-11. Other possible predators that were not encountered during the course of the study, but are common in the Namib Desert, are the Cape cobra, *Naja nivea*, and the puff adder, *Bitis arietans*. Both species did rarely occur around the research centre, as it was practice to capture these snakes as soon as they were encountered near the station, and then to transfer them to areas 5 – 10 km away. The Fiscal Shrike, *Lanius collaris*, and the Namib Sand Snake, *Psammophis leightoni namibensis*, posed a threat to juveniles and nestlings respectively. Hughes et al. (1994) included the sidewinding adder, *Bitis perinqueyi*, in their list of possible predators of small mammals in the Namib Desert. This species was not observed at the study site, but was encountered regularly in the dune fields of the southern Namib.

Species	Daily Activity	Residency Status	Predator Age Class	Number encountered	Remarks
Aves					
Lanius collaris (Fiscal Shrike)	diurnal	resident	adult immature	2 (1 pair) 1 (1999)	frequently seen perching on nara and acacia
Melierax canorus (Pale Chanting Goshawk)	diurnal	resident	adult	1	infrequently seen perching on nara and acacia
Falco tinnunculus (Rock (Common) Kestrel	diurnal	resident	adult immature	2 (1 pair) 3 (2000)	left area in 1997, returned in 2000
Tyto alba (Barn Owl)	nocturnal	resident	adult	2 - 5	frequently seen and heard
Bubo africanus (Spotted Eagle Owl)	nocturnal	nomadic	adult	1	infrequently seen and heard in riverbed
Mammalia					
Herpestes sanguineus (Slender Mongoose)	diurnal / crepusc.	resident	adult	1	infrequently seen in river- bed and adjacent vegetation
Ictonyx striatus (Striped Polecat)	nocturnal	resident	adult	1 - 3	tracks frequently seen around Research Station
Reptilia					
Psammophis leightoni (Namib Sand Snake)	diurnal	resident?	adult	1	observed once in nara

Table IV-11: List of possible predators of *Rhabdomys pumilio* observed at the study site.

Direct predatory acts on *Rhabdomys* were never observed, but one juvenile was found dead with beak marks in October 1998. Another juvenile that was first trapped in March 1999, had a very short tail, and it was assumed that the fiscal shrike, *Lanius collaris*, caught both individuals. In those occurrences, when fiscal shrikes where

observed in the study area, adults (n=7) and one older juvenile showed no reaction to the presence of the (calling) bird and continued with their current activity. On four occasions, juveniles that were in close proximities of adults did not change their behaviour in response to a fiscal shrike being seen or heard. The one juvenile, though, who was foraging in the proximity of an older sibling, froze when the bird landed on the nara plant where both were foraging at that time.

ii.) Population Demography

Body size

Adult male *Rhabdomys* captured in the Namib Desert weighed on average 48.9±1.36g (N=80), and had an average head-body length of 8.5±0.10 cm (N=80), (Table IV-12). Adult non-pregnant females were lighter and smaller than the males, weighing 44.9±0.76g (N=80), and had a head-body length of 8.2±0.06 cm (N=80), (Table IV-13). Males were significantly heavier (Mann-Whitney U-test: U=2621.0, N_1=80, N_2=82, $p<0.05$) and larger (Mann-Whitney U-test: U=2582.0, N_1=80, N_2=82, $p<0.05$) than the females, indicating sexual dimorphism in the species. The tail was significantly longer than head-body length in both sexes (females: Wilcoxon Matched Pairs test: T=33.0, N=83, $p<0.001$; males: Wilcoxon Matched Pairs test: T=74.0, N=74, $p<0.001$).

	unit	Mean	StdDev	Min	Max	N
Mass	g	48.9	1.36	22.0	76.0	80
HB	cm	8.5	0.10	6.5	10.0	80
T	cm	10.0	0.09	7.0	12.0	80
TL	cm	18.5	0.16	15.0	22.0	80
HF	mm	25.7	0.15	20.0	27.0	80

Table IV-12: Mean body mass and size of adult male *Rhabdomys pumilio*. Mass: body mass, HB: head–body length, T: tail length, TL: total length, HF: hind foot length.

	unit	Mean	StdDev	Min	Max	N
Mass	g	44.9	0.76	32.0	64.0	82
HB	cm	8.2	0.06	7.0	9.0	82
T	cm	9.9	0.09	7.0	12.0	82
TL	cm	18.0	0.12	15.0	21.0	82
HF	mm	24.4	0.12	21.0	26.0	82

Table IV-13: Mean body mass and size of adult non-pregnant female *Rhabdomys pumilio*. Mass: body mass, HB: head–body length, T: tail length, TL: total length, HF: hind foot length.

MNA and Population structure

The minimum number of animals (MNA) present in hummock V-1 was estimated to be between 5 to 10 individuals. The Jolly Seber estimate gave a maximum N_i = 23±12 individuals for June/July 1999, and a minimum N_i=5 (Table IV-14). The Jolly-Seber estimate was significantly higher than the MNA estimate (Chi-Square test: χ^2_{11}=31.93, $p<0.001$). Survival rates in the population varied between 0.286±0.000, in

December 1998, and 1.186±0.566 for April/May 1999. New individuals, either juveniles or immigrating adults, were coming into the population throughout the year.

	MNA	N_i	SE N_i	M_i	ϕ_i	SE ϕ_i	B_i	SE B_i
Oct-98	6				0.667			
Nov-98	6	6	0	4.00	0.833	0.000	2	0
Dec-98	7	7	0	5.00	0.286	0.000	3	-
Jan-99	7	5	-	2.00	0.629	0.117	6	3
Feb-99	10	9	2	4.40	0.762	0.123	2	2
Mar-99	7	9	2	6.40	0.714	0.070	3	1
Apr/May-99	8	9	0	6.00	1.186	0.566	12	20
Jun/Jul-99	8	23	12	10.67	0.372	0.150	5	6
Aug-99	5	14	5	6.20	0.893	0.327	5	8
Sep-99	9	18	7	10.00	0.453	0.134	3	3
Oct-99	7	11	2	6.80	0.556	0.068	5	0
Nov-99	5	11	-	6.00	0.500	0.000	2	0
Dec-99	4	7	0	6.00				
Jan-00	6							

Table IV-14: Krebs' MNA, Jolly-Seber population estimate N_i, estimated number of marked population M_i, survival rate ϕ_i, number of new additions to the population B_i and corresponding Standard Errors (SE) for hummock V-1. -: values could not be calculated.

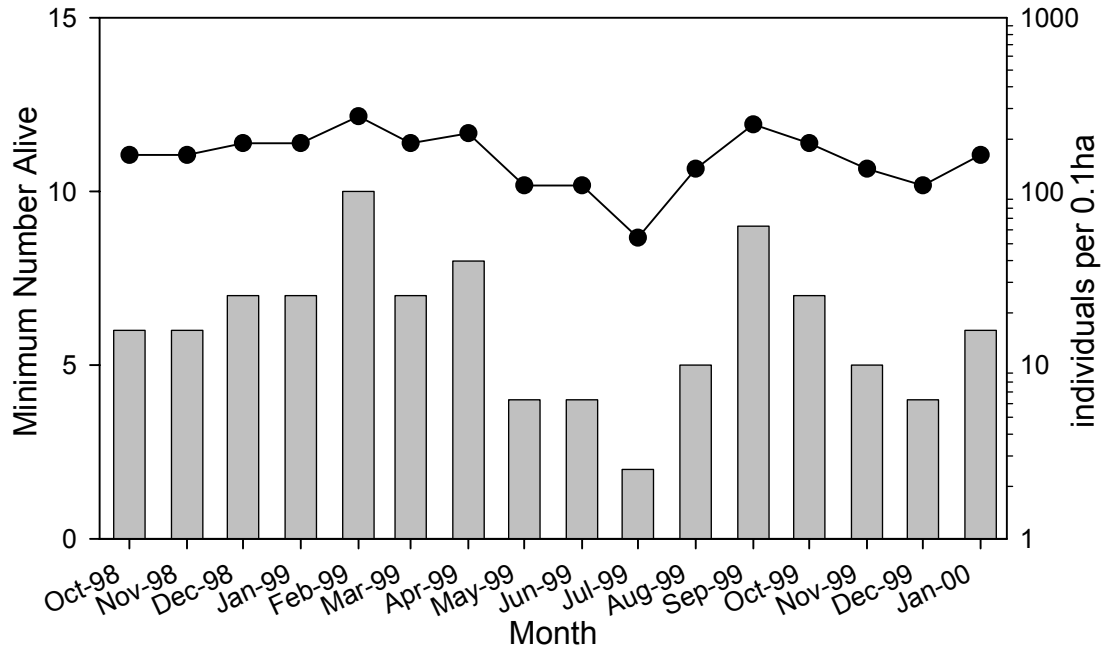


Figure IV-20: Fluctuations in MNA and population density per 0.1ha in hummock V-1.

Population density in this hummock was very high; a peak density of 216 individuals per 0.1ha was reached in February 1999 (Figure IV-20). Population declines from May onwards, and density dropped to its lowest point of 54 individuals

per 0.1ha in July 1999. The population started rising again in September, due to immigration. In the first half of the study period, between November 1998 and June 1999, more males than females were found to be living in this hummock (Figure IV-21). From August 1999, the relation was reversed, more females than males were captured and observed to be in the population. The sex ratio in V-1 was significantly different from 1:1 (Chi-square test: χ^2_{13}=25.07, p<0.05).

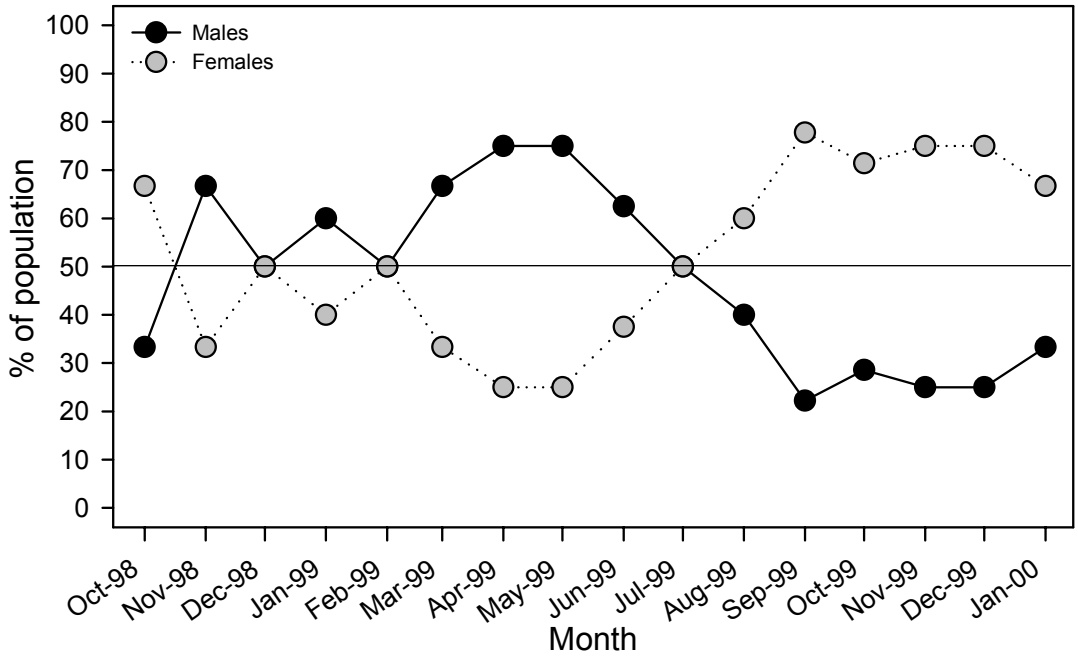


Figure IV-21: Changes in sex ratio in hummock V-1.

In hummock V-2, MNA in the population was estimated to be between 22 individuals at its peak in February 1999 and 5 individuals at its lowest point in October 1999 (Table IV-15). The Jolly-Seber estimate was very similar to the MNA estimate, and gave a zenith of 25±4 individuals in Feburary 1999, and the lowest estimate for October 1999, 8±0 individuals . The differences in population size estimate between MNA and Jolly-Seber were not significant (Chi-square test: χ^2_{12}=12.50, NS). Survival rates ranged from 0.300±0.0 in March 1999 to 1.157±0.085 for June/July 1999. New individuals were added to the population mainly between December 1998 and February 1999, and between September and November 1999.

Population density in V-2 was considerably lower than in hummock V-1, the highest population density was 86 individuals per 0.1ha in January 1999. Density declined from February 1999 until October 1999, when the population density was lowest at 19 individuals per 0.1ha (Figure IV-22).

	MNA	N_i	SE N_i	M_i	ϕ_i	SE ϕ_i	B_i	SE B_i
Oct-98	21				0.579			
Nov-98	16	19	1	11.00	0.984	0.144	-1	-
Dec-98	17	18	2	19.67	0.428	0.066	12	-
Jan-99	22	20	2	8.00	0.725	0.114	11	7
Feb-99	20	25	4	15.22	0.474	0.049	8	1
Mar-99	13	20	2	11.00	0.300	0.000	3	-
Apr-99	10	9	0	6.00	0.778	0.000	3	0
May-99	9	10	0	7.00	0.889	0.033	0	0
Jun/Jul-99	8	9	0	8.89	1.157	0.085	0	0
Aug-99	8	10	1	10.29	0.996	0.193	1	1
Sep-99	9	11	2	10.25	0.444	0.074	3	0
Oct-99	9	8	0	5.00	0.750	0.000	6	-
Nov-99	5	12	2	6.00	0.660	0.077	13	5
Dec-99	6	21	3	8.58				
Jan-00	13							

Table IV-15: Krebs' MNA, Jolly-Seber population estimate N_i, estimated number of marked population M_i, survival rate ϕ_i, number of new additions to the population B_i and corresponding Standard Errors (SE) for V-2. –: values could not be calculated.

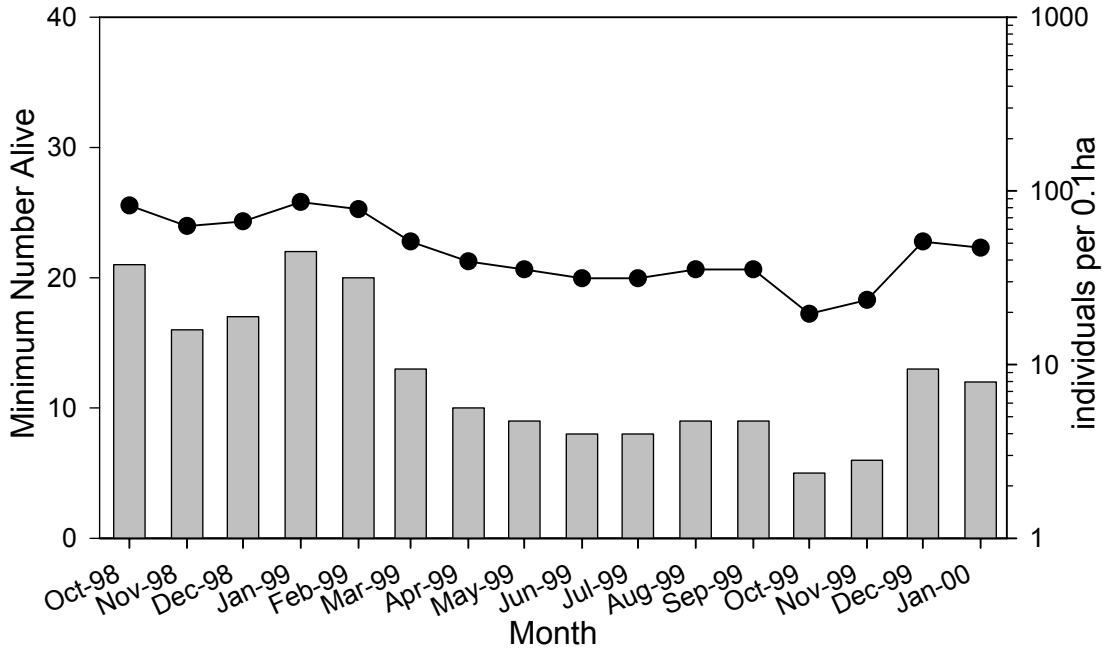


Figure IV-22: Fluctuations in MNA and population density per 0.1ha in hummock V-2.

Until September 1999, more males than females were present in the population. In October and November, the sex ratio was 1:1, and in the last two months of study, more males than females were found in the population. The sex ratio in hummock V-2 was not significantly different from 1:1 (Chi-square test: χ^2_{13}=17.17, NS).

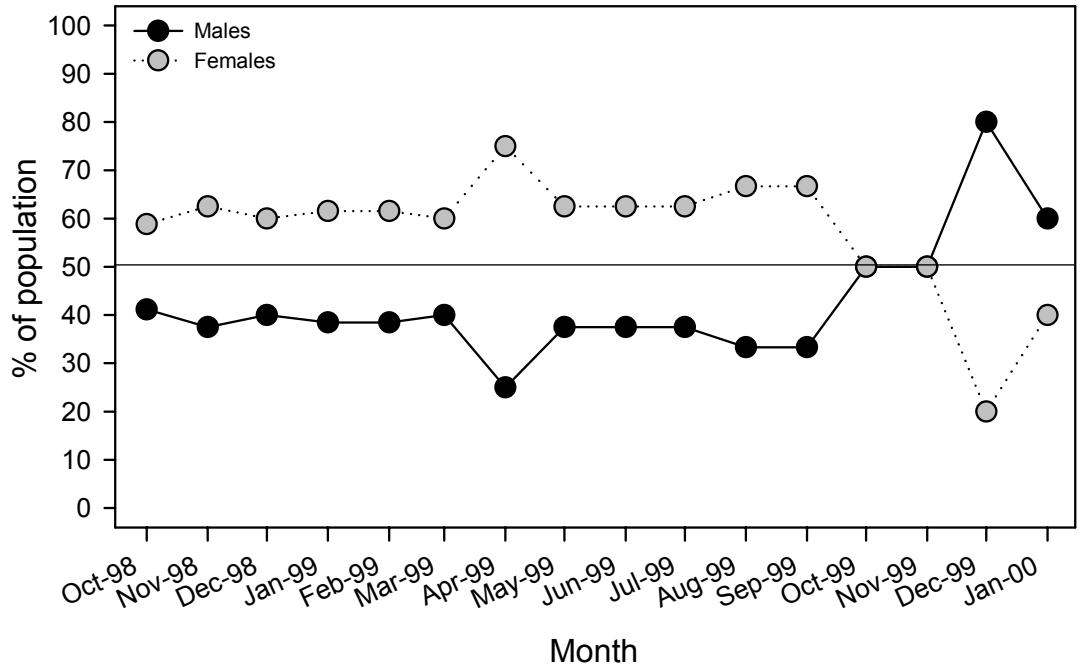


Figure IV-23: Changes in sex ratio in hummock V-2.

The population in hummock V-3 reached its peak between January and March 1999, MNA for that period was estimated to be 13 individuals. Only two animals were found to be living in this hummock in October 1998, at the beginning of the study period (Table IV-16).

	MNA	N_i	SE N_i	M_i	ϕ_i	SE ϕ_i	B_i	SE B_i
Oct-98	2				1.000			
Nov-98	3	3	0	2.00	0.867	0.358	9	9
Dec-98	9	12	7	2.60	0.671	0.116	7	7
Jan-99	13	15	2	6.44	0.739	0.084	4	3
Feb-99	13	15	2	10.67	0.859	0.164	3	3
Mar-99	12	16	3	12.60	0.529	0.185	9	10
Apr/May-99	9	17	8	8.25	0.571	0.122	1	4
Jun/Jul-99	8	11	0	7.00	0.494	0.076	7	3
Aug-99	6	12	2	5.43	0.700	0.051	0	2
Sep-99	5	8	0	8.00	0.625	0.000	0	0
Oct-99	4	5	0	5.00	0.800	0.000	2	0
Nov-99	6	6	0	4.00	0.500	0.000	2	0
Dec-99	4	5	1	3.00				
Jan-00	7							

Table IV-16: Krebs' MNA, Jolly-Seber population estimate N_i, estimated number of marked population M_i, survival rate ϕ_i, number of new additions to the population B_i and corresponding Standard Errors (SE) for hummock V-3.

The Jolly-Seber estimates for this population were slightly higher than the MNA estimates; a population peak was calculated at 17±8 individuals in April/May 1999. These differences between the population estimates were not significant (Chi-square test: χ^2_{11}=11.39, NS). Survival rate ranged between 0.494±0.076 in June/July 1999 and 0.867±0.358 in November 1999. New animals were recruited into the population in all months with exception of August and September 1999.

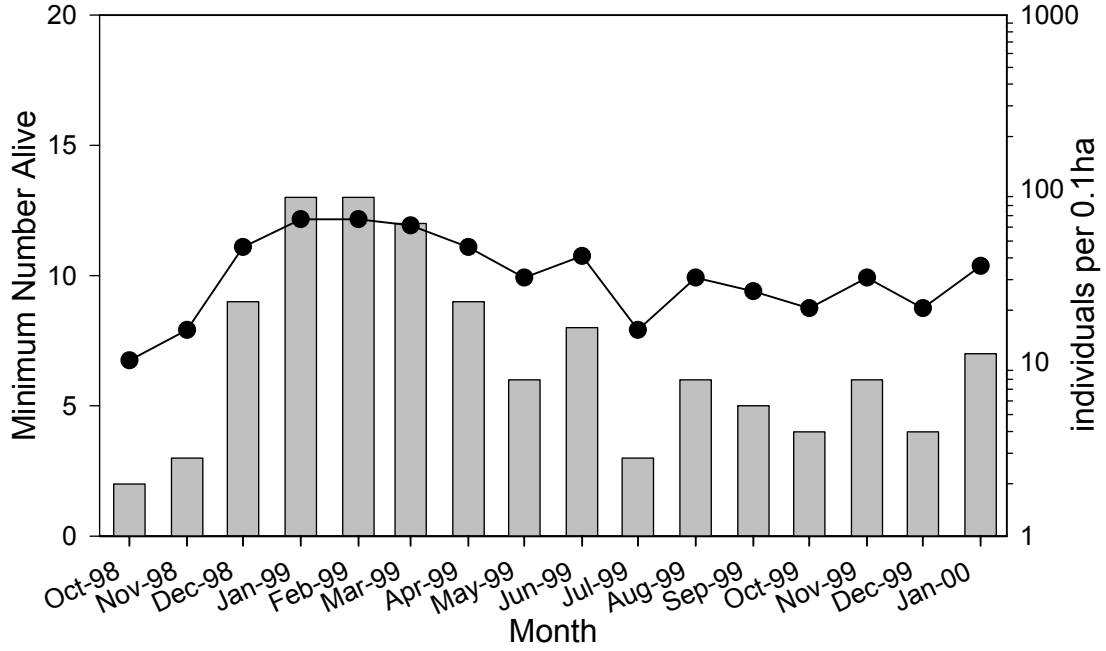


Figure IV-24: Fluctuations in MNA and population density per 0.1ha in hummock V-3.

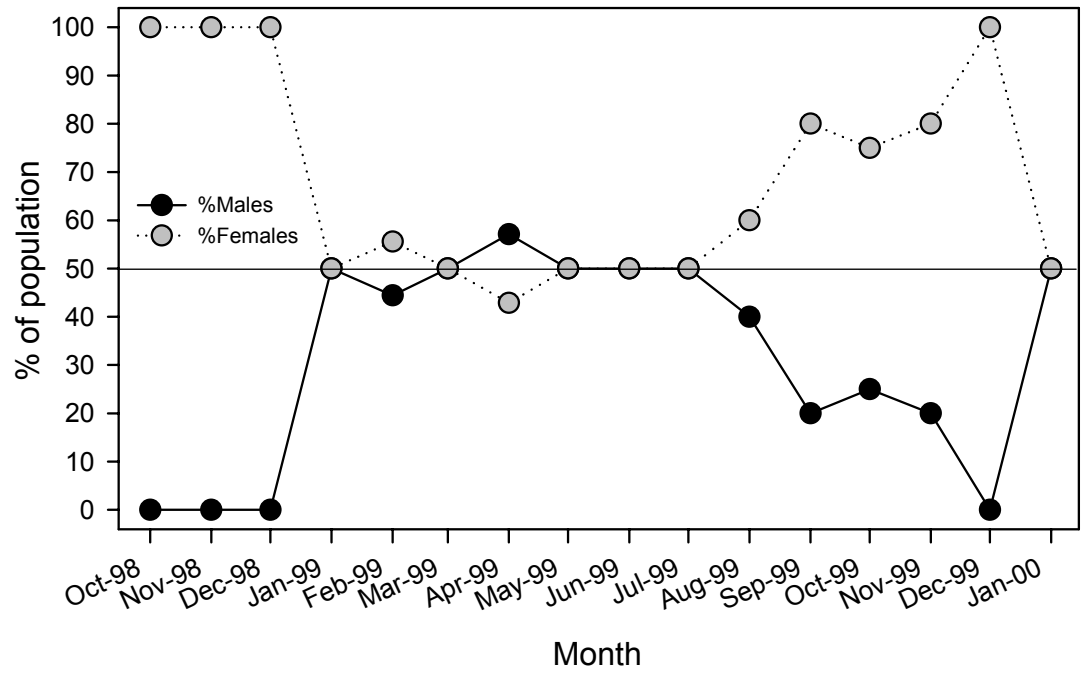


Figure IV-25: Changes in sex ratio in hummock V-3.

Population density showed a similar pattern to hummock V-2, and was highest in January 1999 with 67 individuals per 0.1ha (Figure IV-24). Population density declines from February 1999, and reaches its lowest point in October 1999, at 20 individuals per 0.1ha.

Sex ratio in hummock V-3 was rather variable (Figure IV-25). In the first three months of the study, only females were caught in this hummock. Between January 1999 and July 1999, the sex ratio was 1:1; after that, considerably more females than males were present in the population, indicating that the males dispersed, while the females stayed in the hummock. The sex ratio in hummock V-3 was significantly different from 1:1 (Chi-square test: $\chi^2_{13}=21.40$, $p<0.1$).

In hummock V-4, MNA was estimated between 6 individuals for December 1998 and 26 individuals for March and April 1999 (Table IV-17). Population size estimated with the Jolly-Seber Method was very similar to the MNA estimate. Despite this, differences between MNA and Jolly-Seber estimate were significant (Chi-square test: $\chi^2_{12}=26.42$, $p<0.01$).

	MNA	N_i	SE N_i	M_i	ϕ_i	SE ϕ_i	B_i	SE B_i
Nov-98	15				0.769			
Dec-98	6	20	22	10.00	0.348	0.249	8	6
Jan-99	19	15	3	4.18	0.987	0.161	7	6
Feb-99	24	22	4	14.00	0.527	0.076	11	4
Mar-99	26	23	2	10.54	0.726	0.093	9	5
Apr-99	26	26	4	15.64	0.685	0.147	-2	2
May-99	19	16	3	16.20	0.556	0.111	2	0
Jun-99	18	11	0	9.00	0.364	0.000	14	2
Jul-99	17	18	2	4.00	1.038	0.062	5	3
Aug-99	21	24	2	18.69	0.663	0.102	6	4
Sep-99	21	22	3	15.71	0.368	0.039	11	-
Oct-99	23	19	2	8.00	0.406	0.019	3	1
Nov-99	20	11	1	8.11	0.983	0.129	17	8
Dec-99	34	28	4	10.92				
Jan-00	22							

Table IV-17: Krebs' MNA, Jolly-Seber population estimate N_i, estimated number of marked population M_i, survival rate ϕ_i, number of new additions to the population B_i and corresponding Standard Errors (SE) for V-4. -: values could not be calculated.

Survival rates in V-4 ranged between 0.348±0.249 in December 1998 and 1.038±0.062 in July 1999. New animals were recruited into the population throughout

the study period, only in April was the number of new additions negative, indicating emigration of individuals.

Population density in hummock V-4 was slightly lower than population density in hummocks V-2 and V-3 (Figure IV-26). The lowest population density was found in October 1999, at 12 individuals per 0.1ha and the highest in December 1999 with 69 individuals per 0.1ha. The population density in V-4 showed a similar decline to the populations in hummock V-2 and V-3, but started rising again from August 1999.

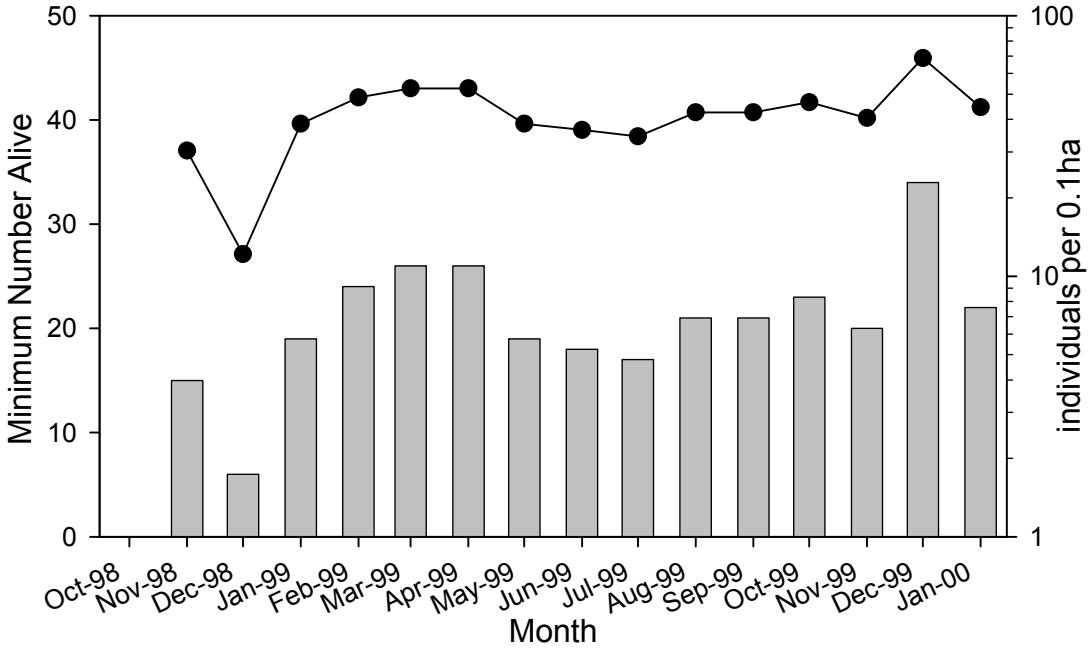


Figure IV-26: Fluctuations in MNA and population density per 0.1ha in hummock V-4.

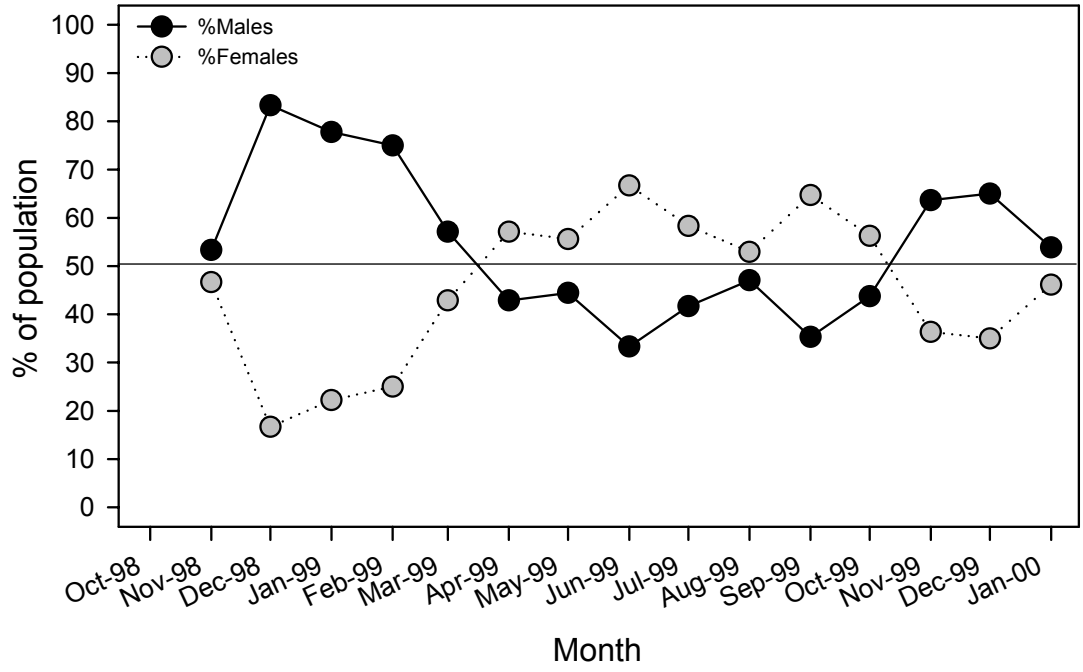


Figure IV-27: Changes in sex ratio in hummock V-4.

The change in sex ratio follows a similar pattern to hummock V-3, although the role of the sexes were reversed (Figure IV-27). From November 1998 to March 1999, and again from November 1999 until January 2000, more males than females were found in the population. Between April and October 1999 this was reversed, more females than males were captured. The sex ratio in hummock V-4 was, as in hummock V-1, significantly different from 1:1 (Chi-square test: $\chi^2_{13}=89.34$, $p<0.001$).

Using the MNA method, population size in hummock V-7 was estimated to range from 1 to 5 individuals (Table IV-18), the Jolly-Seber method gave similar results. As in hummock V-4, despite the similarities in the population estimates, differences in the estimates between methods were significant (Chi-square test: $\chi^2_9=289.85$, $p<0.001$). Survival rate ranged from 0.500±0.250 in January 1999 to 1.000±0.0 for June/July 1999. New animals were added to the population mainly between April and September 1999.

	MNA	N_i	SE N_i	M_i	ϕ_i	SE ϕ_i	B_i	SE B_i
Dec-98	5				0.600			
Jan-99	3	5	4	3.00	0.500	0.250	-1	0
Feb-99	2	2	0	2.00	-	-	-	-
Mar-99	2	-	-	-	-	-	-	-
Apr/May-99	1	1	0	1.00	1.000	0.000	2	2
Jun/Jul-99	5	3	-	1.00	0.750	0.000	2	1
Aug-99	4	4	0	3.00	0.500	0.000	1	20
Sep-99	3	3	0	2.00	0.500	0.000	1	6
Oct-99	1	2	-	1.00	-	-	-	-
Nov-99	3	-	-	-	-	-	-	-
Dec-99	3	-	-	-				-
Jan-00	6							

Table IV-18: Krebs' MNA, Jolly-Seber population estimate N_i, estimated number of marked population M_i, survival rate ϕ_i, number of new additions to the population B_i and corresponding Standard Errors (SE) for V-7. -:values could not be calculated.

Population density in hummock V-7 was very low, and lowest of all hummocks studied. Density ranges between 3 individuals per 0.1ha in April and May 1999 and 17 individuals per 0.1ha in January 2000. The population density declined until May 1999, and rose after that until a peak was reached in July 1999. From there, population density dropped again, to another low in October 1999.

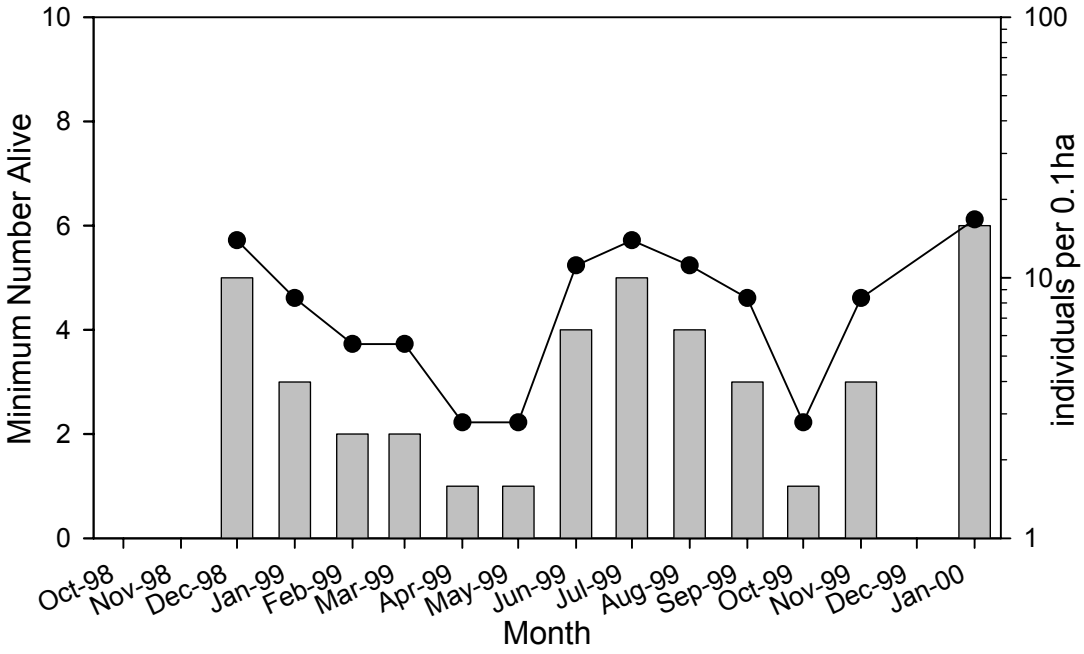


Figure IV-28: Fluctuations in MNA and population density per 0.1ha in hummock V-7.

Apart from September and October 1999, males were the dominant sex in hummock V-7 (Figure IV-29), and females were rarely caught. Despite the differences in the numbers of males and females caught, the sex ratio was not significantly different from 1:1 (Chi-square test: χ^2_{12}=8.83, NS).

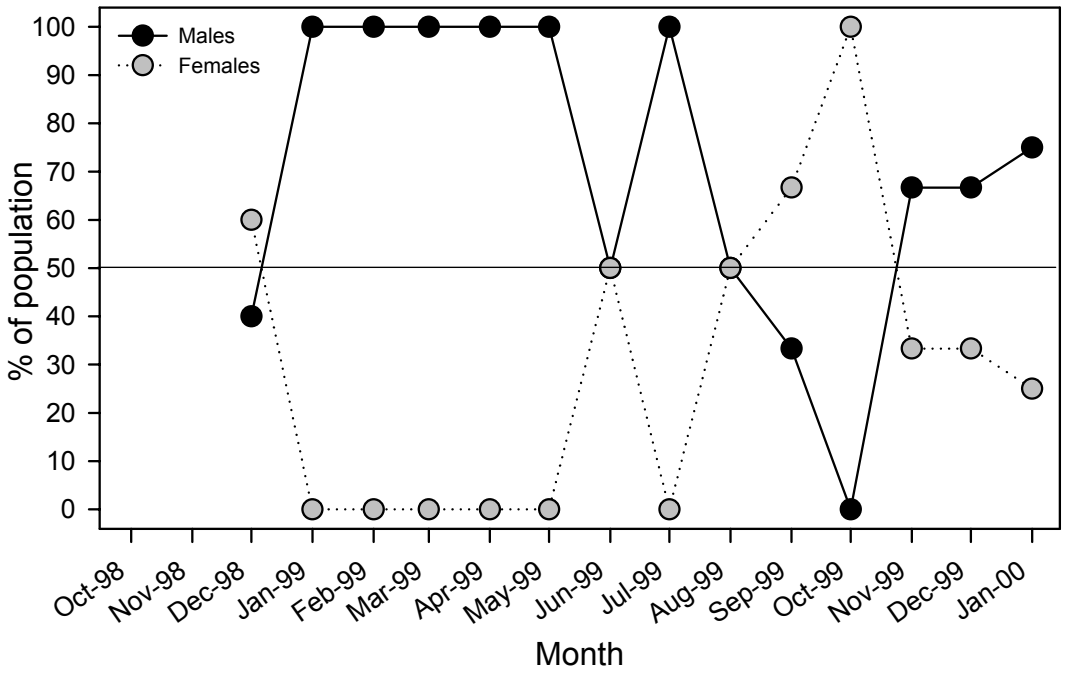


Figure IV-29: Changes in sex ratio in hummock V-7.

MNA in hummock V-8 was estimated to be between 2 and 6 individuals (Table IV-19). The Jolly-Seber method gave population estimates up to 9±5 individuals in

October 1999. The differences between the MNA and Jolly-Seber population estimates were significant (Chi-square test: χ^2_4=12.24, p<0.05). Survival rates in this hummock ranged from 0.267±0.084 in October 1999 to 2.250±1.186 in September 1999. New animals were recruited into the population from September to November 1999.

	MNA	N_i	SE N_i	M_i	ϕ_i	SE ϕ_i	B_i	SE B_i
Jul-99	4				0.750			
Aug-99	4	8	6	3.00	0.333	0.096	-1	0
Sep-99	2	2	0	2.00	2.250	1.186	5	0
Oct-99	2	9	5	4.50	0.267	0.084	1	0
Nov-99	6	3	0	2.00	1.000	0.000	2	0
Dec-99	2	5	1	3.00	0.000			
Jan-00	5							

Table IV-19: Krebs' MNA, Jolly-Seber population estimate N_i, estimated number of marked population M_i, survival rate ϕ_i, number of new additions to the population B_i and corresponding Standard Errors (SE) for V-8.

Population density in hummock V-8 was as high as population density in V-1, and showed similar fluctuations (Figure IV-30). Population density peaked in November 1999, with 214 individuals per 0.1ha, and was lowest in September and October 1999 with 71 individuals per 0.1ha.

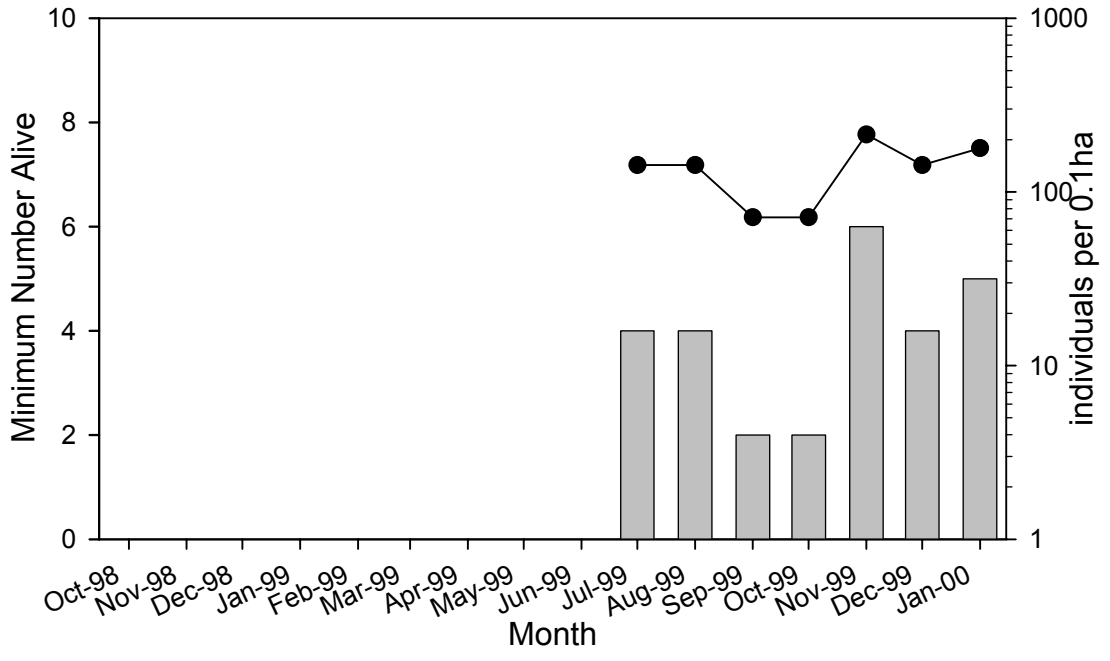


Figure IV-30: Fluctuations in MNA and population density per 0.1ha in hummock V-8.

Both sexes were equally represented in hummock V-8 throughout most of the trapping period (Figure IV-31), and the sex ratio in hummock V-8 was not significantly different from 1:1 (Chi-square test: χ^2_6=2.0, NS).

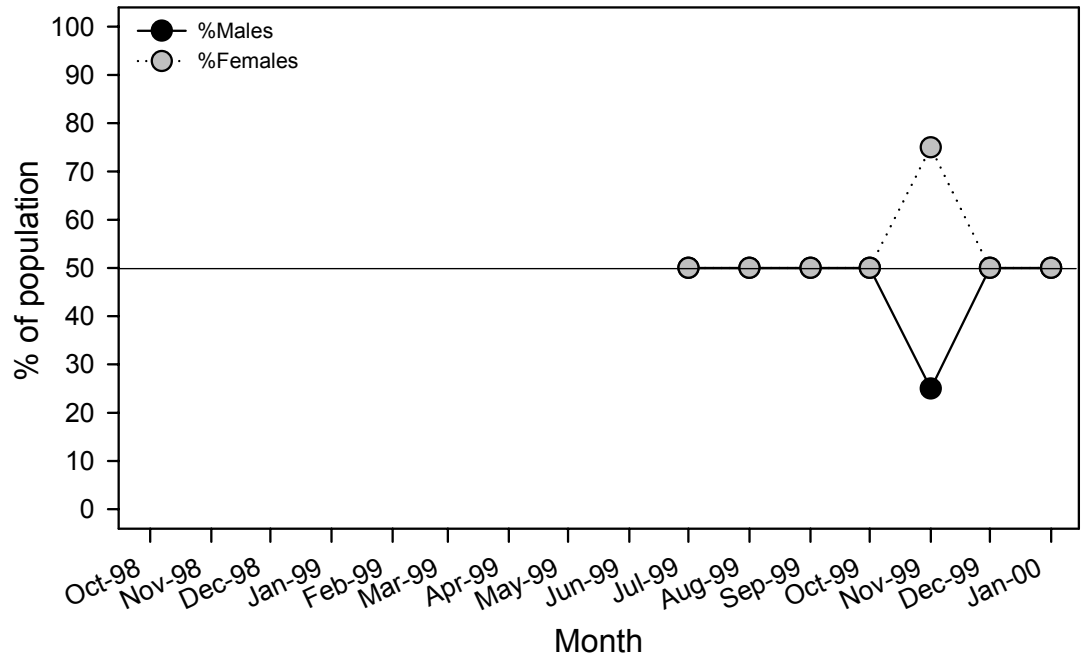


Figure IV-31: Changes in sex ratio in hummock V-8.

The MNA method gave a population estimate between one (in October 1999) and 9 individuals (in January 2000) for hummock V-9 (Table IV-20). The Jolly-Seber estimate was considerably higher where it could be calculated, and the maximum number of individuals was 14 according to this method. Differences in the population estimate between methods were significant (Chi-square test: χ^2_4=199.49, p<0.001). Survival rates varied between 0.438±0.321 and 0.57±0.084 in October and November. New Individuals were added to the population in October 1999 only.

	MNA	N_i	SE N_i	M_i	ϕ_i	SE ϕ_i	B_i	SE B_i
Jul-99	2				-			
Aug-99	3	-	-	-	-	-	-	-
Sep-99	2	-	-	-	-	-	-	-
Oct-99	1	3	-	1.00	0.438	0.321	13	0
Nov-99	5	14	-	1.75	0.571	0.084	-4	0
Dec-99	5	4	0	5.00	0.000			
Jan-00	9							

Table IV-20: Krebs' MNA, Jolly-Seber population estimate N_i, estimated number of marked population M_i, survival rate ϕ_i, number of new additions to the population B_i and corresponding Standard Errors (SE) for V-9. -: values could not be calculated.

Population density in hummock V-9 was again rather low, but not as low as in hummock V-7 (Figure IV-32). Lowest population density was 4 individuals per 0.1ha in October 1999, and highest in January 2000, with 34 individuals per 0.1ha. Population density showed a marked increase towards the end of the study period, which is due to the high recruitment of juveniles into the population.

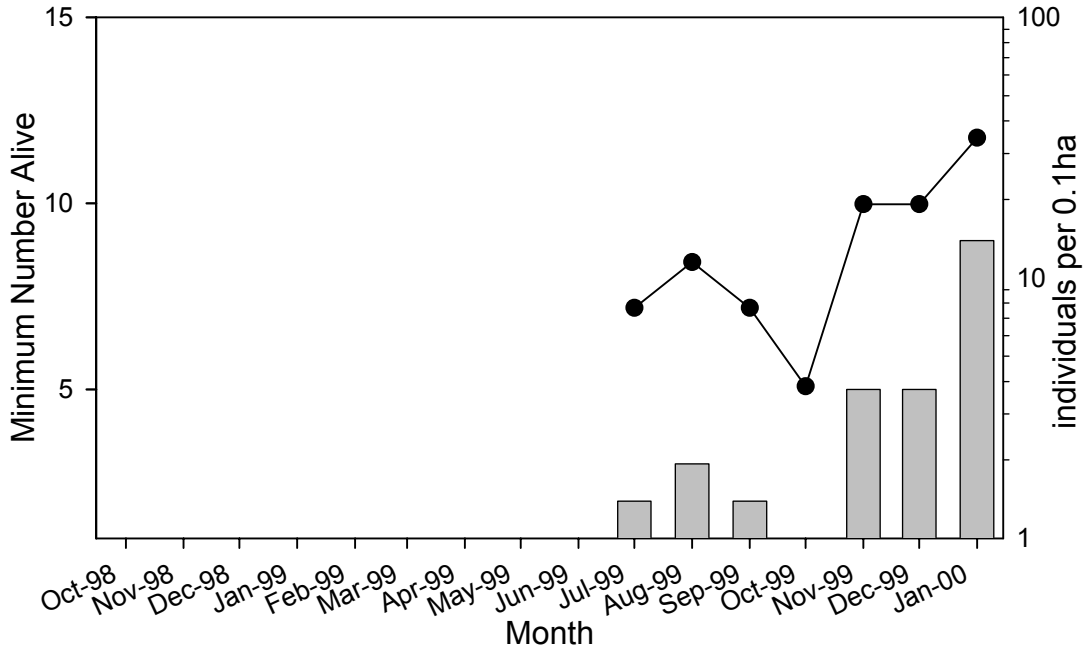


Figure IV-32: Fluctuations in MNA and population density per 0.1ha in hummock V-9.

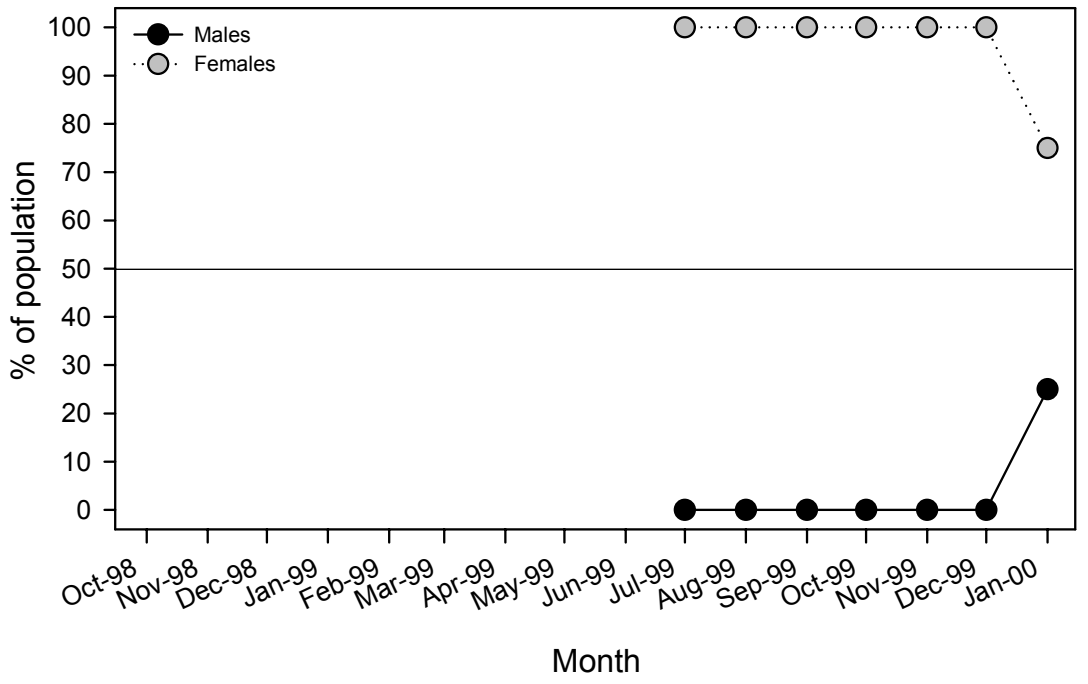


Figure IV-33: Changes in sex ratio in hummock V-9.

Females were the only inhabitants of hummock V-9; no males were captured in this population until the very last trapping session in January 2000 (Figure IV-33). Therefore, the sex ratio was significantly different from 1:1 (Chi-square test: χ^2_6=21.0, p<0.001).

The two smallest hummocks, hummock V-1 (37m^2) and V-8 (27m^2) had the highest population density of the hummocks. The nara plants forming these hummocks were also very dense. The two hummocks with the lowest population densities, V-7 and V-9, were of larger size (359m^2 and 261m^2), but the sand hummocks were only partially covered by the nara plant, leaving open sandy patches, which are generally avoided by *Rhabdomys*.

Survival from first capture

The average length of survival from first capture did differ between the populations studied. Females survived longest in hummock V-2, and lifespan recorded was shortest in hummock V-8 (Kruskal-Wallis test: $H_{6,121}$=17.16, p<0.01). Lifespan of males was found to be longest in hummock V-3, and shortest in hummock V-4 (Kruskal-Wallis test: $H_{5,95}$=11.41, p<0.05).

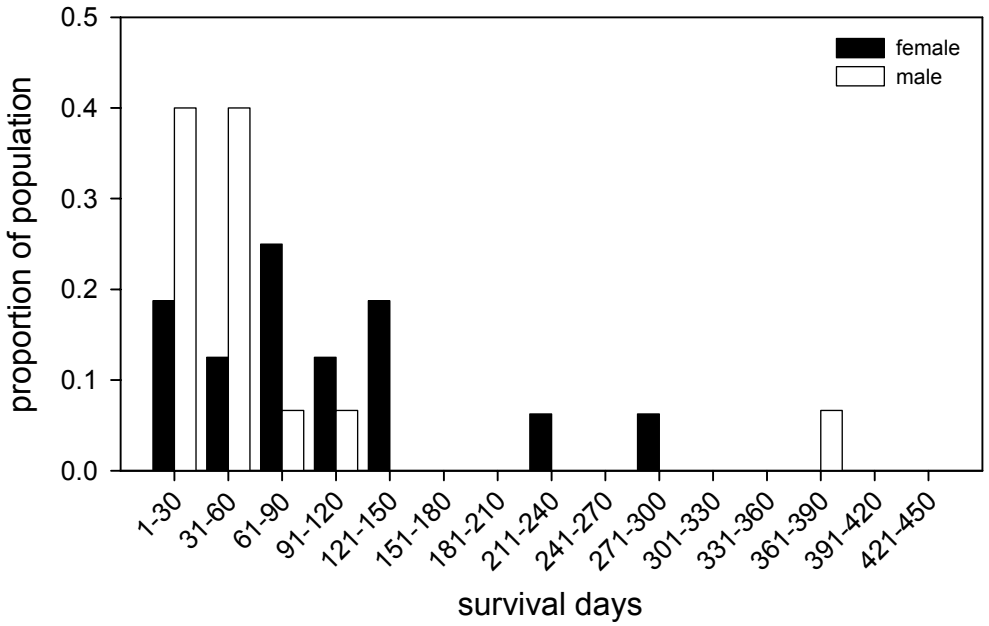


Figure IV-34: Length of survival after first capture: Proportion of females (n=16) and males (n=15) present in the population for a specific number of days in hummock V-1.

In hummock V-1, females survived on average 96.9±76.9 days (N=16), after first capture, the lifespan of males was 56.1±97.1 (N=15). This was significantly shorter than the lifespan of females (Mann-Whitney U-test: U=58.5, N_1=16, N_2=15, p<0.05).

43.8% of the females survived for 3 months or longer in the population, while only 13.3% of the males did so (Figure IV-34).

Females inhabiting hummock V-2 were found to have a lifespan of 97.2±92.4 days (N=34) after being captured for the first time. This is only slightly shorter than the average length of survival of 105.9±112.4 days (N=19) for the males living in V-2 (Mann-Whitney U-test: U=322.5, N_1=34, N_2=19, NS). In both sexes, a third of the individuals (38.2% and 31.6% respectively) were found to be alive in the population for more than 3 months (Figure IV-35).

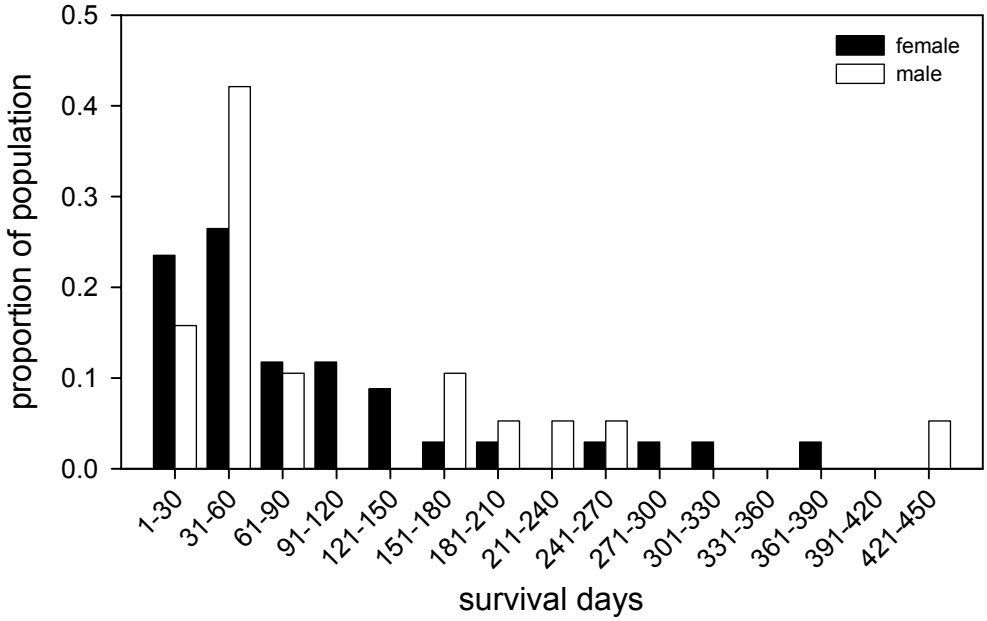


Figure IV-35: Length of survival after first capture: Proportion of females (n=34) and males (n=19) present in the population for a specific number of days in hummock V-2.

Of the population inhabiting hummock V-3, females survived for an average of 94.8±97.0 days (N=17) after first capture, which is shorter than the average lifespan of the males of 133.9±129.8 days (N=10), but not significantly so (Mann-Whitney U-test: U=71.0, N_1=17, N_2=10, NS). In this population, 35.3% of the females and 50% of the males survived for 3 months or longer (Figure IV-36).

Animals of both sexes living in hummock V-4 had a shorter lifespan from first capture than animals caught in hummock V-1, V-2 and V-3. Females survived for an average of 56.4±61.2 days (N=36), while the males were found in the population for an average of 51.5±47.6 days (N=43), only slightly shorter than the females (Mann-Whitney U-test: U=74.7, N_1=36, N_2=43, NS). Only a sixth of both females and males (16.7% and 16.3% respectively) were found to be alive after 3 months or more in this population (Figure IV-37).

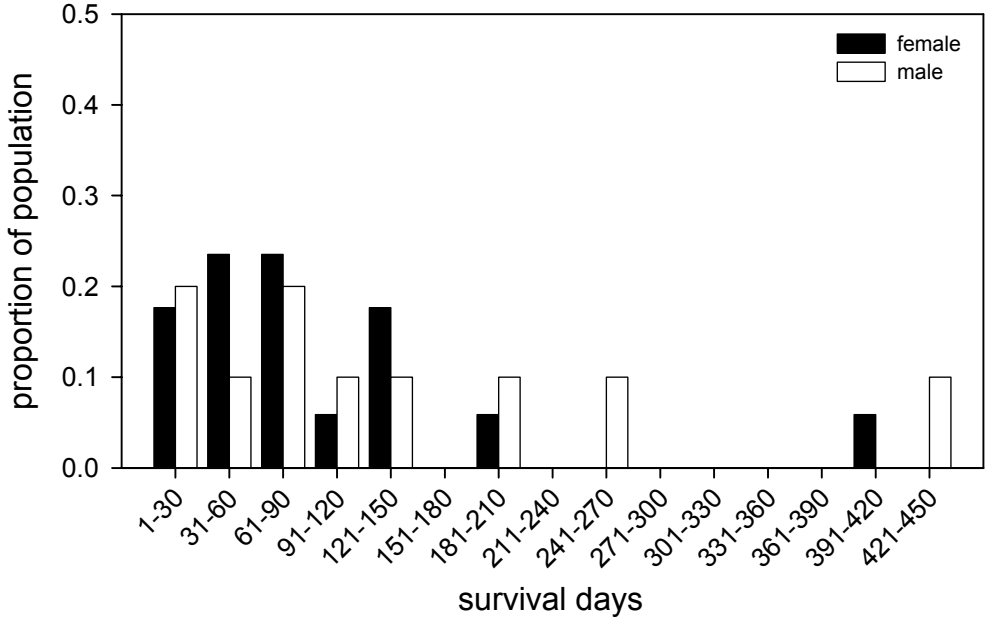


Figure IV-36: Length of survival after first capture: Proportion of females (n=17) and males (n=10) present in the population for a specific number of days in hummock V-3.

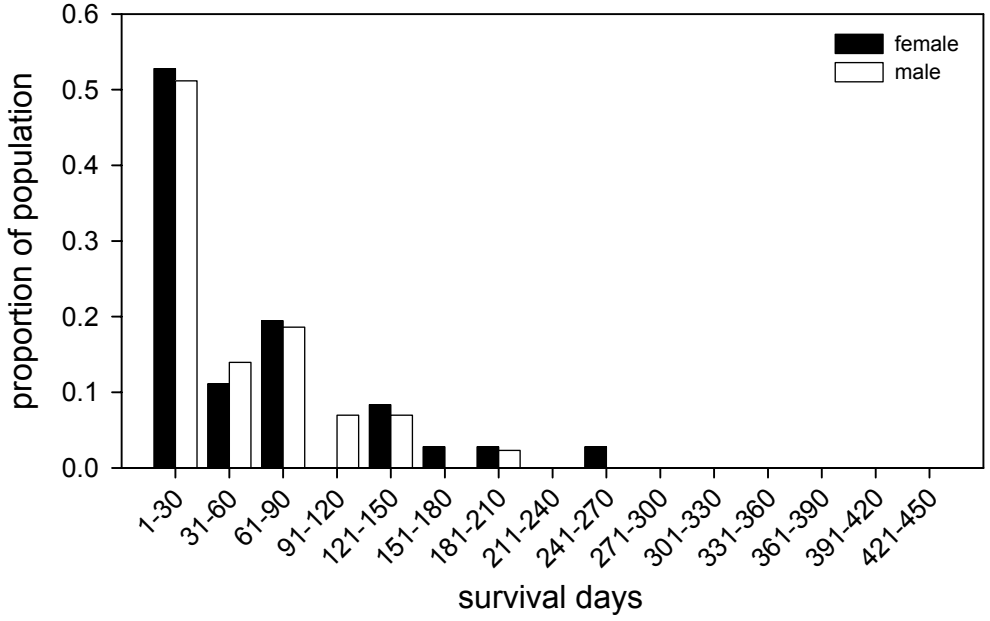


Figure IV-37: Length of survival after first capture: Proportion of females (n=36) and males (n=43) present in the population for a specific number of days in hummock V-4.

Average length of survival differed greatly between females and males inhabiting hummock V-7, although this was not significant (Mann-Whitney U-test: U=4.5, $N_1=N_2=4$, NS). Females had an average lifespan of 38.3±43.9 days (N=4) after first capture, while the males survived on average for 105.3±112.2 days (N=4) after first capture. This is reflected also reflected in the proportion of individuals found in the population for 3 months or more – 25% of the females (N=1) and 50% of the males (N=2) respectively (Figure IV-38).

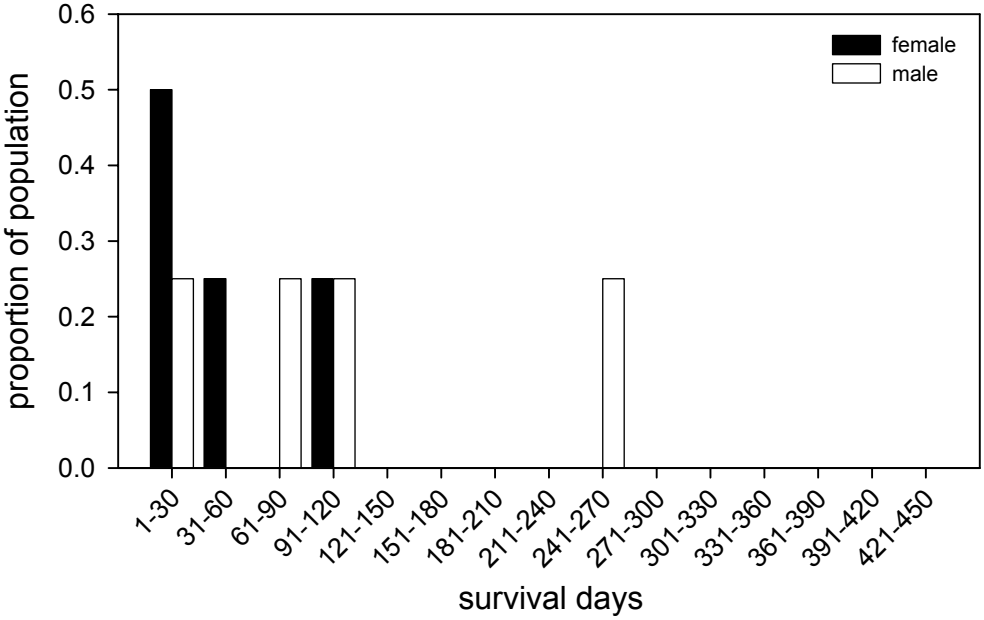


Figure IV-38: Length of survival after first capture: Proportion of females (n=4) and males (n=4) present in the population for a specific number of days in hummock V-7.

A similar discrepancy in the average lifespan after first captured between females and males could be documented in hummock V-8; the difference was also not significant in this case (Mann-Whitney U-test: U=13.5, N_1=4, N_2=4, NS). Females (N=7) survived for an average 25.9±57.3 days after first capture, which is about half of the average length of survival of 55.0±96.9 days for the males (N=4). A single female (14.3%) was found to be alive in the population for more than three months, while two males (50%) survived for 3 months or longer (Figure IV-39).

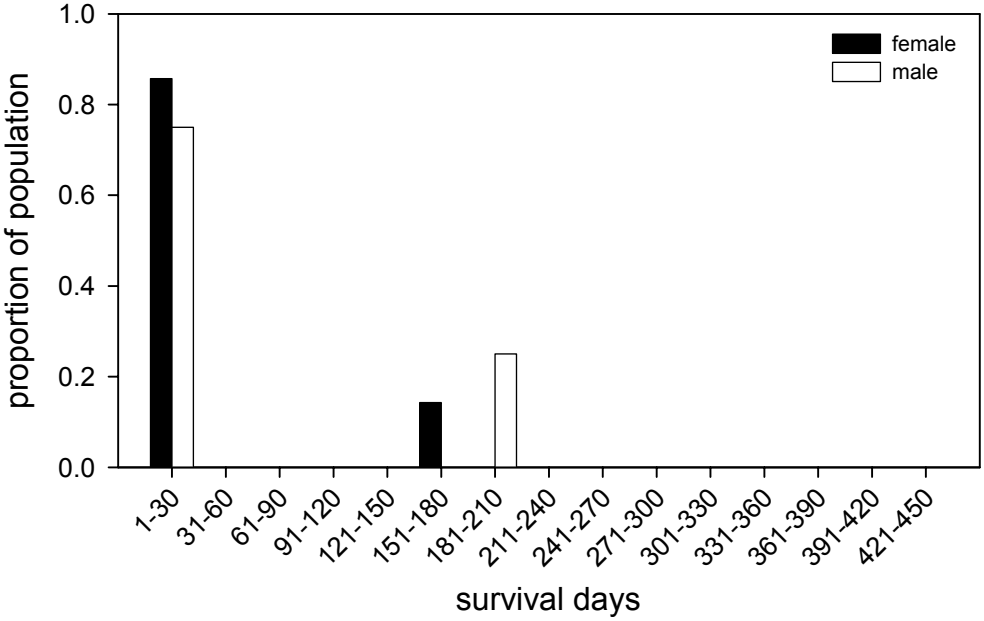


Figure IV-39: Length of survival after first capture: Proportion of females (n=7) and males (n=4) present in the population for a specific number of days in hummock V-8.

In hummock V-9, average length of survival after first capture could only determined for females, as the single male found to be present in the population was only trapped in the last trapping session of the study. Females survived for an average of 71.7±61.5 days (N=7) after capture. Of these seven females, only one was found to be alive in the population for more than 3 months (Figure IV-40).

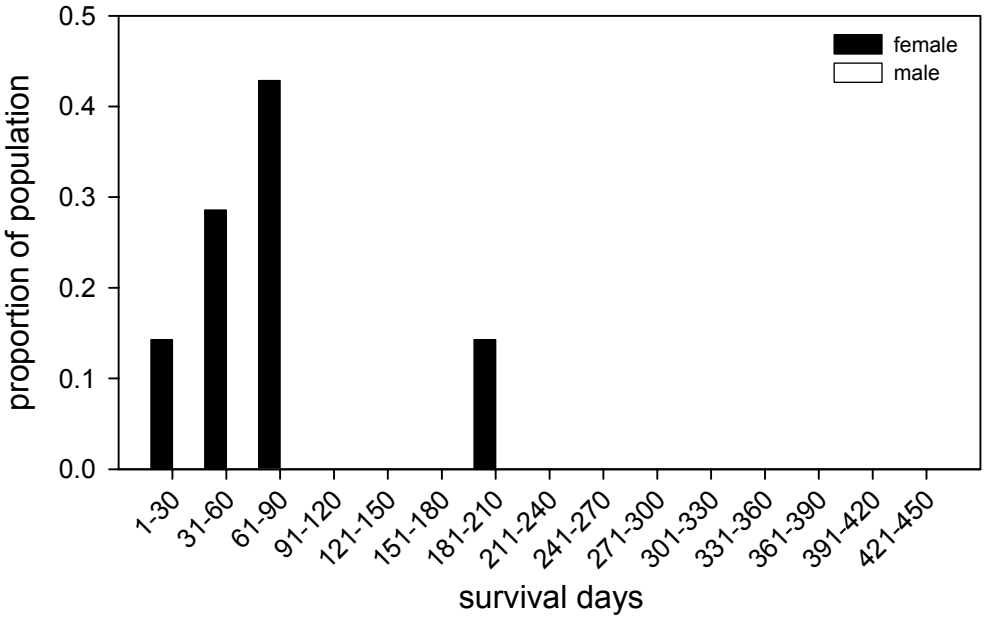


Figure IV-40: Length of survival after first capture: Proportion of females (n=7) present in the population for a specific number of days in hummock V-9. The only male was captured in the last trapping session of the study and therefore not considered.

0.93% of the population, i.e. 3 individuals (2♂, 1♀), survived for longer than a year. These individuals had a life span of 14 to 15 months after first capture in the population.

iii.) Reproduction

(i) Physiology

Sexual Maturity

In hummock V-1, reproductively active females and males were significantly heavier than the non-reproductively active animals of the same sex (Table IV-21), (females: Mann-Whitney U test: U=22.5, N_1=8, N_2=20, p<0.01; males: Mann-Whitney U test: U=0.0, N_1=9, N_2=5, p<0.01). The smallest female found to be sexually mature in this hummock had a body mass of 40g, the smallest male a body mass of 31g. Overall, body mass between sexually mature males and females did not differ significantly. (Mann-Whitney U test: U=30.5, N_1=9, N_2=8, NS).

sex	reproductive Status	mass (g)	N
female	perforate	52.6 ± 6.07	8
	imperforate	36.9 ± 13.96	20
male	scrotal	49.4 ± 11.07	9
	abdominal	17.6 ± 4.93	5

Table IV-21: Sexual Maturity: body mass of sexually mature and immature females and males in hummock V-1. Means ± SD.

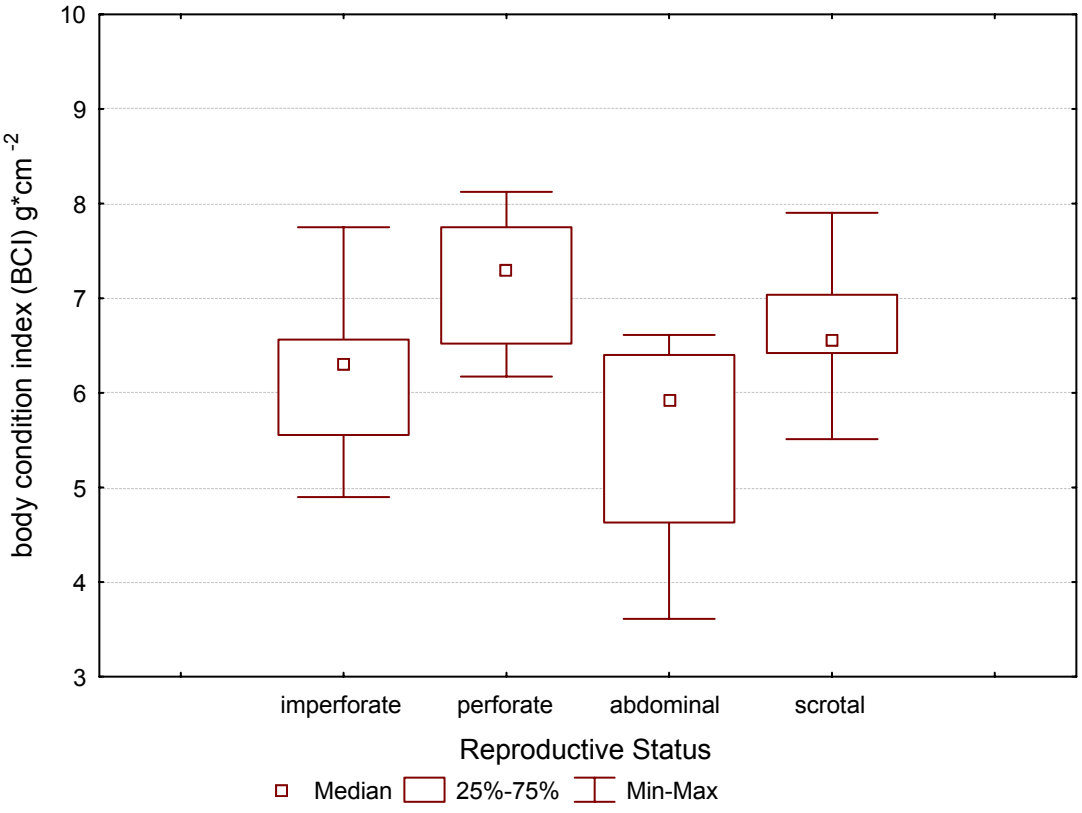


Figure IV-41: Sexual maturity: body condition index (BCI) of imperforate non-pregnant females (N=8), perforate non-pregnant females (N=19) and of males with abdominal (N=5), and scrotal testes (N=9) in hummock V-1.

Both sexually mature females and males had a significantly higher body condition index than sexually immature females and males (females: Mann-Whitney U test: U=31.5, N_1=8, N_2=19, p<0.05; males: Mann-Whitney U test: U=8.0, N_1=9, N_2=5, p<0.1), (Figure IV-41). The lowest body condition index (BCI) for a reproductively active female in this hummock was 6.2g*cm^{-2}, for the males the BCI was 5.5g*cm^{-2}. Seventy percent (N=5) of the males with a BCI between 6.0 and 6.9g*cm^{-2} were sexually mature, while only 23% of the females in the same BCI class were reproductively active. All males (N=3) with a BCI over 7.0g*cm^{-2} were reproductively active, while only 62.5% of the females with a similar BCI were sexually mature. As body mass, body condition index did not differ significantly between reproductively active males and females (Mann-Whitney U test: U=23.0, N_1=9, N_2=8, NS).

As in hummock V-1, sexually mature females with a perforate vagina were significantly heavier that immature females (Mann-Whitney U test: U=161.5, N_1=18, N_2=31, p<0.05), (Table IV-22). Reproductively active males were also significantly heavier that non-reproductive males (Mann-Whitney U test: U=0.0, N_1=12, N_2=7, P<0.001). The smallest female to attain sexual maturity in this hummock weighed 34g, as much as the smallest sexually mature male. Body mass did not differ significantly between sexually mature males and females (Mann-Whitney U test: U=71.0, N_1=12, N_2=18, NS).

sex	Reproductive Status	mass (g)	N
female	perforate	45.8 ± 6.67	18
	imperforate	35.4 ± 14.47	31
male	scrotal	53.0 ± 13.56	12
	abdominal	14.36 ± 6.59	7

Table IV-22: Sexual Maturity: body mass of sexually mature and immature females and males in hummock V-2. Means ± SD.

In contrast to the difference in body mass, the body condition index was not significantly different between reproductively active and non-reproductive animals (Figure IV-42), (females: Mann-Whitney U test: U=235.5, N_1=18, N_2=31, NS; males: Mann-Whitney U test: U=28.0, N_1=12, N_2=7, NS). The lowest BCI for a reproductively active male was 5.0g*cm^{-2}, for the females, this value was only slightly higher, at 5.2g*cm^{-2}. As in hummock V-1, all males with a body condition index of at least 7.0g*cm^{-2} were reproductively active, while only 38.5% of the females with a similar BCI were sexually mature. There were no significant

differences in the body condition index of reproductively active males and females (Mann-Whitney U test: U=86.0, N_1=12, N_2=18, NS).

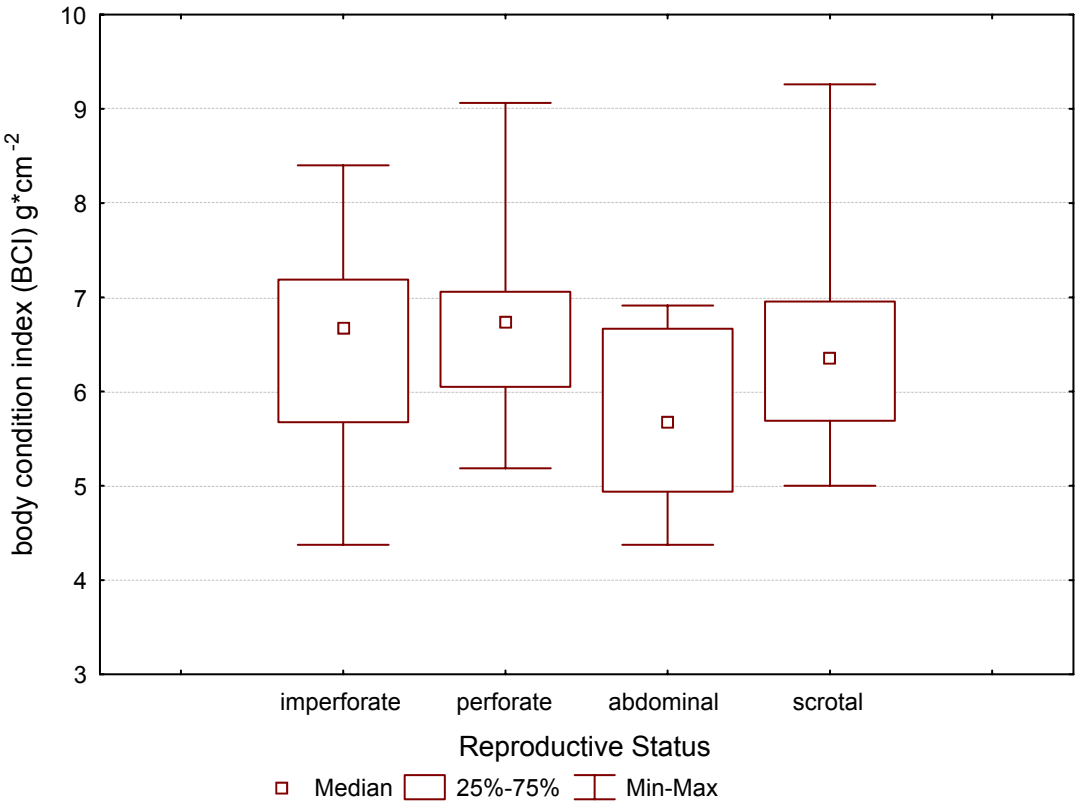


Figure IV-42: Sexual Maturity: body condition index (BCI) vs. reproductive status in imperforate (N=31) or perforate (N=18) non-pregnant females and males with abdominal (N=7) or scrotal (N=12) testes in hummock V-2.

In hummock V-3, reproductively active females were, as in the previous hummocks, significantly heavier that non-reproductive females (Mann-Whitney U test: U=17.0, N1=6, N2=22, p<0.01), (Table IV-23). Sexually mature males were also significantly heavier than immature males (Mann-Whitney U test: U=10.5, N_1=7, N_2=8, p<0.05). The smallest sexually mature females in this hummock weighed 42g, nine grammes more than the smallest reproductively active male found, which weighed 33g. Difference in the body mass of sexually mature males and females were not significant (Mann-Whitney U test: U=18.0, N_1=7, N_2=6, NS).

sex	Reproductive Status	mass (g)	N
female	perforate	47.0 ± 3.89	6
	imperforate	36.3 ± 9.08	22
male	scrotal	53.6 ± 17.48	7
	abdominal	32.5 ± 10.64	8

Table IV-23: Sexual Maturity: body mass of sexually mature and immature females and males in hummock V-3. Means ± SD.

As in hummock V-2, body condition index was not significantly different between sexually mature and immature females, despite the difference in body mass (Mann-Whitney U test: 65.5, N_1=6, N_2=22, NS), (Figure IV-43). The same holds true for the males in this hummock, where there were no significant differences between reproductively active and non-reproductive males (Mann-Whitney U test: U=14.0, N_1=7, N_2=8, NS). The BCI of the smallest sexually mature female was at 6.3g*cm^{-2} considerably higher than the BCI of 5.2g*cm^{-2} of the smallest male found to be reproductively active. As in the two previous hummocks, all males with a BCI higher than 7.0g*cm^{-2} living in this hummock were found to be reproductively active, while only twenty percent of the females (N=2) were sexually mature. The differences in body condition index between reproductively active males and females were not significant (Mann-Whitney U test: U=16.0, N_1=7, N_2=6, NS).

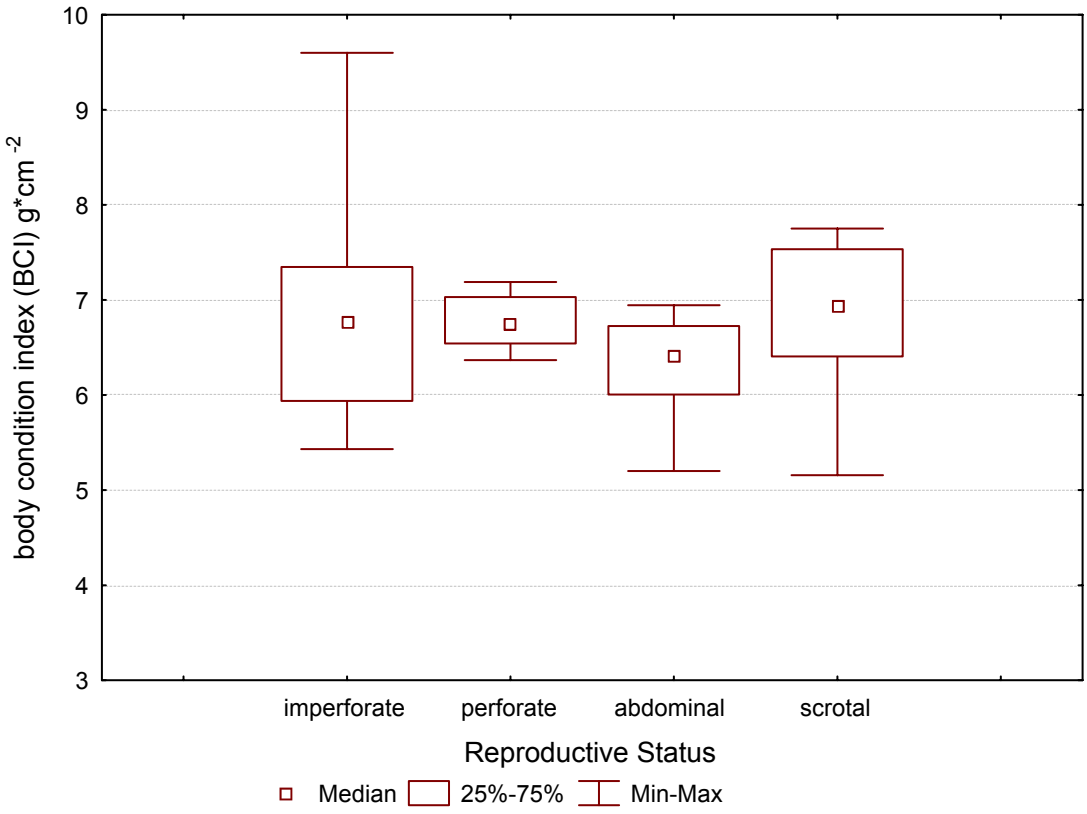


Figure IV-43: Sexual Maturity: body condition index (BCI) vs. reproductive status in imperforate (N=22) or perforate (N=6) non-pregnant females and males with abdominal (N=8) or scrotal (N=7) testes in hummock V-3.

In hummock V-4, sexually mature individuals of both sexes were significantly heavier than non-reproductive animals of the same sex (females: Mann-Whitney U test: U=65.0, N_1=12, N_2=29, p<0.01; males: Mann-Whitney U test: U=64.0, N_1=39, N_2=26, p<0.001), (Table IV-24). The smallest sexually mature female in this

hummock weighed 34g, the smallest reproductively active male 30g. Overall, the difference in body mass between sexually mature females and males was only marginally significant (Mann-Whitney U test: U=144.5, N_1=38, N_2=128, p<0.1).

sex	Reproductive Status	mass (g)	N
female	perforate	44.3 ± 8.92	12
	imperforate	29.8 ± 14.1	29
male	scrotal	52.5 ± 13.45	39
	abdominal	26.1 ± 11.16	26

Table IV-24: Sexual Maturity: body mass of sexually mature and immature females and males in hummock V-4. Means ± SD.

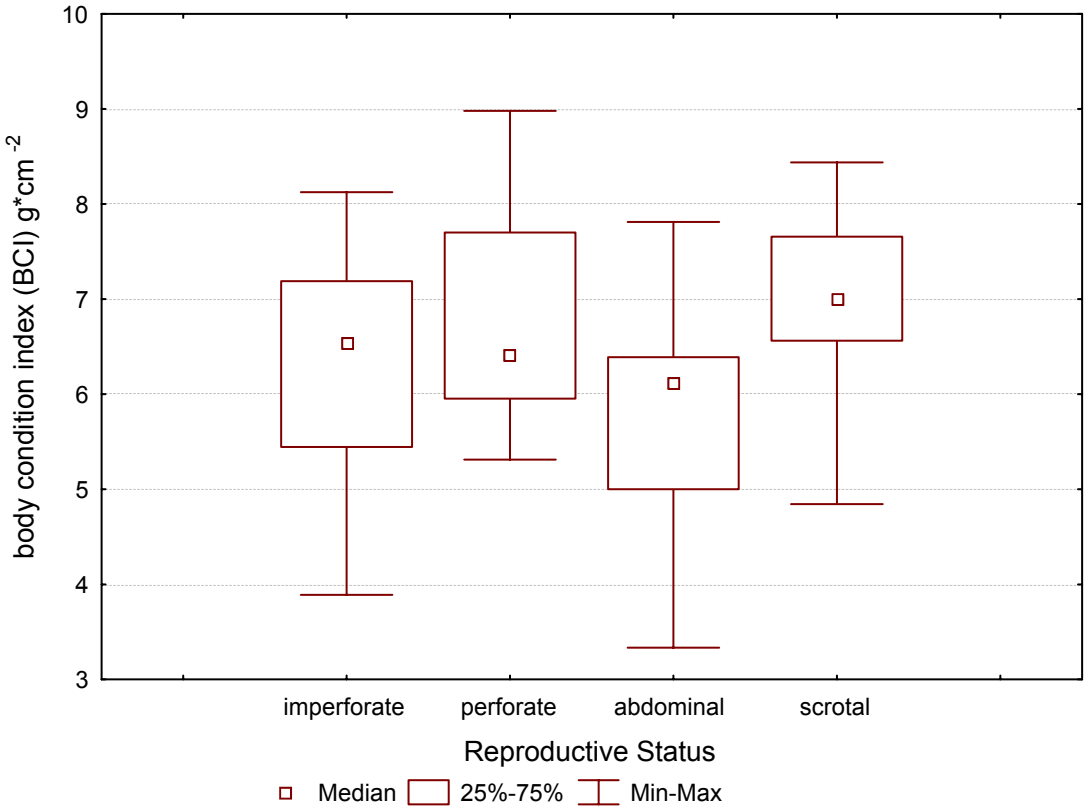


Figure IV-44: Sexual Maturity: body condition index (BCI) vs. reproductive status in imperforate (N=29) or perforate (N=12) non-pregnant females and males with abdominal (N=26) or scrotal (N=39) testes in hummock V-4.

Despite the significant difference in body mass, body condition index of sexually mature females did not differ significantly of the BCI of immature females (Mann-Whitney U test: U=133.0, N_1=12, N_2=29, NS), while reproductively active males were significantly heavier than non-reproductive males (Mann-Whitney U test: U=196.5, N_1=39, N_2=26, p<0.001), (Figure IV-44). The smallest male to become reproductively active in this hummock had a rather low body condition index of 4.8g*cm^{-2}, while the smallest female captured had a BCI of 5.3g*cm^{-2}. Of the males with a BCI of

7.0g*cm^{-2} and above, only 90.0% were found to be sexually mature, and only 40% of the females with a BCI above 7.0g*cm^{-2} were reproductively active. Body condition index between reproductively active males and females did not differ significantly (Mann-Whitney U test: U=201.0, N_1=38, N_2=128, NS).

In contrast to the previously discussed hummocks, reproductively active females living in hummock V-7 were not significantly heavier than the non-reproductive females of this hummock (Mann-Whitney U test: U=11.5, N_1=3, N_2=2, NS), (Table IV-25). The difference in body mass between sexually mature and immature males was only marginally significant (Mann-Whitney U test: U=1.0, N_1=10, N_2=3, $p<0.1$). The smallest of all males to become sexually mature was caught in this hummock; he weighed 22g. The smallest female to become reproductively active in V-7 weighed 37g. The difference in body mass between reproductively active males and females was not significant (Mann-Whitney U test: U=20.5, N_1=9, N_2=5, NS).

sex	Reproductive Status	mass (g)	N
female	perforate	48.6 ± 6.99	5
	imperforate	40.0 ± 18.73	3
male	scrotal	47.5 ± 15.73	10
	abdominal	23.0 ± 5.66	2

Table IV-25: Sexual Maturity: body mass of sexually mature and immature females and males in hummock V-7. Means ± SD.

The difference in body condition index between reproductively active and non-reproductive individuals was also not significant (females: Mann-Whitney U test: U=7.5, N_1=5, N_2=3, NS; males: Mann-Whitney U test: U=6.0, N_1=10. N_2=2, NS), (Figure IV-45). The smallest male to attain sexual maturity had a comparably high body condition index of 5.2g*cm^{-2}, the BCI of the smallest female was 6.0g*cm^{-2}. All males with a BCI of 7.0g*cm^{-2} and above were reproductively active, while only 50% of the females with a similar BCI were sexually mature. Body condition index between sexually mature males and females did not differ significantly (Mann-Whitney U test: U=14.0, N_1=9, N_2=5, NS)

Reproductively active females inhabiting hummock V-8 were also heavier than non-reproductive females, but not significantly so (Mann-Whitney U test: U=1.0, N_1=2. N_2=7, NS), (Table IV-26). The smallest reproductively active male caught in this hummock weighed 47g, the smallest sexually mature female 49g. The differences in body mass between reproductively active males and females were not significant (Mann-Whitney U test: U=2.0, N_1=9, N_2=2, NS).

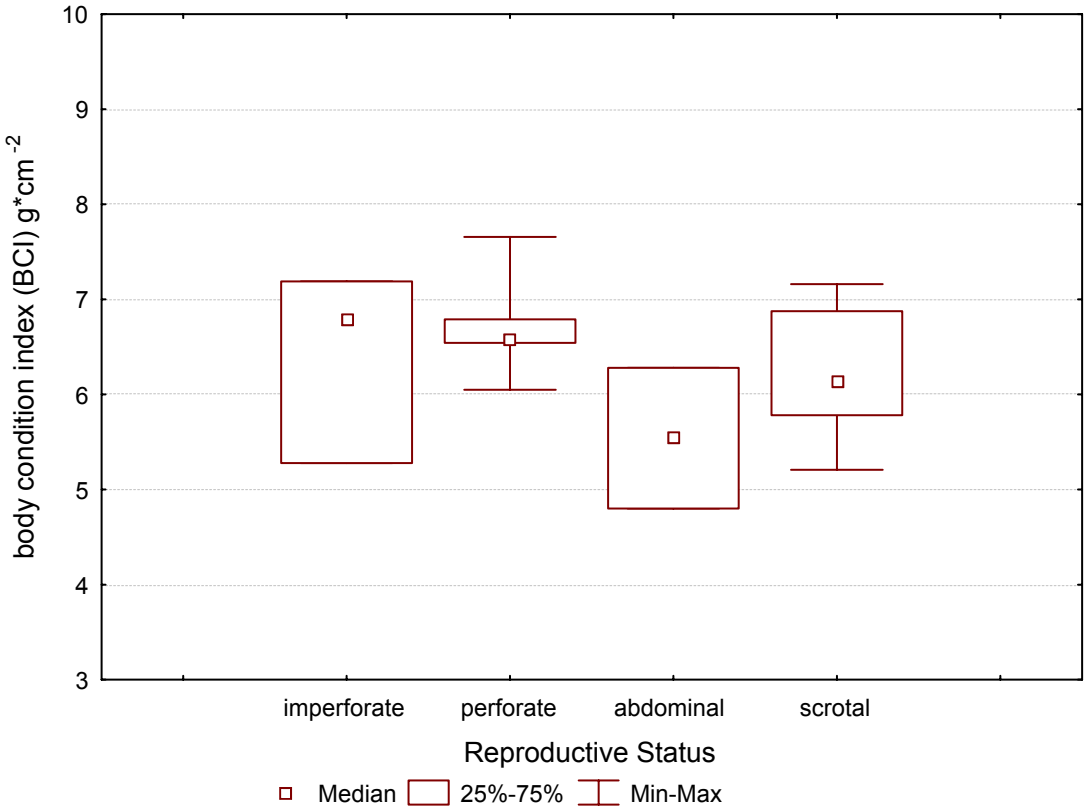


Figure IV-45: Sexual Maturity: body condition index (BCI) vs. reproductive status in imperforate (N=3) or perforate (N=5) non-pregnant females and males with abdominal (N=2) or scrotal (N=10) testes in hummock V-7.

sex	Reproductive Status	mass (g)	N
female	perforate	51.5 ± 3.54	2
	imperforate	35.6 ± 11.77	7
male	scrotal	62.7 ± 13.65	3
	abdominal	13.0	1

Table IV-26: Sexual Maturity: body mass of sexually mature and immature females and males in hummock V-7. Means ± SD.

The body condition index of sexually mature females was also not significantly higher than the BCI of non-reproductive females (Mann-Whitney U test: U=2.0, N_1=2, N_2=7, NS), (Figure IV-46). Body condition index of the smallest sexually mature female was calculated to be 7.5g*cm^{-2}, which is slightly higher than the BCI of the smallest reproductively active male of 7.3g*cm^{-2}. All males with a BCI higher than 7.0g*cm^{-2} were sexually mature, while the same held true for only 66% of the females. The differences in body condition index of sexually mature males and females were not significant (Mann-Whitney U test: U=2.0, N_1=9, N_2=2, NS).

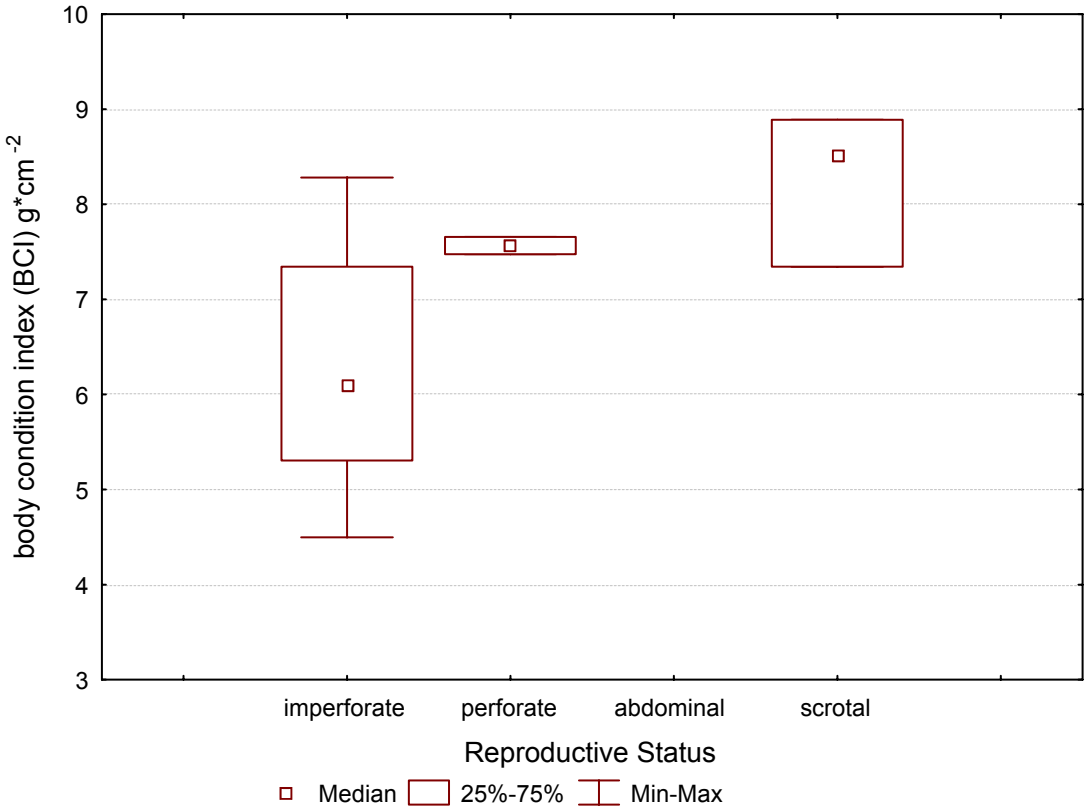


Figure IV-46: Sexual Maturity: body condition index (BCI) vs. reproductive status in imperforate (N=7) or perforate (N=2) non-pregnant females and males scrotal (N=2) testes in hummock V-8.

Sexually mature females inhabiting hummock V-9 were significantly heavier than immature females of the same hummock (Mann-Whitney U test: U=0.5, N_1=2, N_2=3, $p<0.05$), (Table IV-27). The smallest sexually mature female caught weighed 45g.

sex	Reproductive Status	mass (g)	N
female	**perforate**	45.5 ± 0.71	2
	imperforate	31.0 ± 10.25	8
male	**scrotal**	55.0	1
	abdominal		

Table IV-27: Sexual Maturity: body mass of sexually mature and immature females and males in hummock V-7. Means ± SD.

The difference in body condition index between reproductively active and non-reproductive females was also significant (Mann-Whitney U test: U=0.5, N_1=2, N_2=8, $p<0.05$), (Figure IV-47). The body condition index of the smallest sexually mature female was 7.0g*cm^{-2}, and 66% of the females with this body condition index or above were reproductively active.

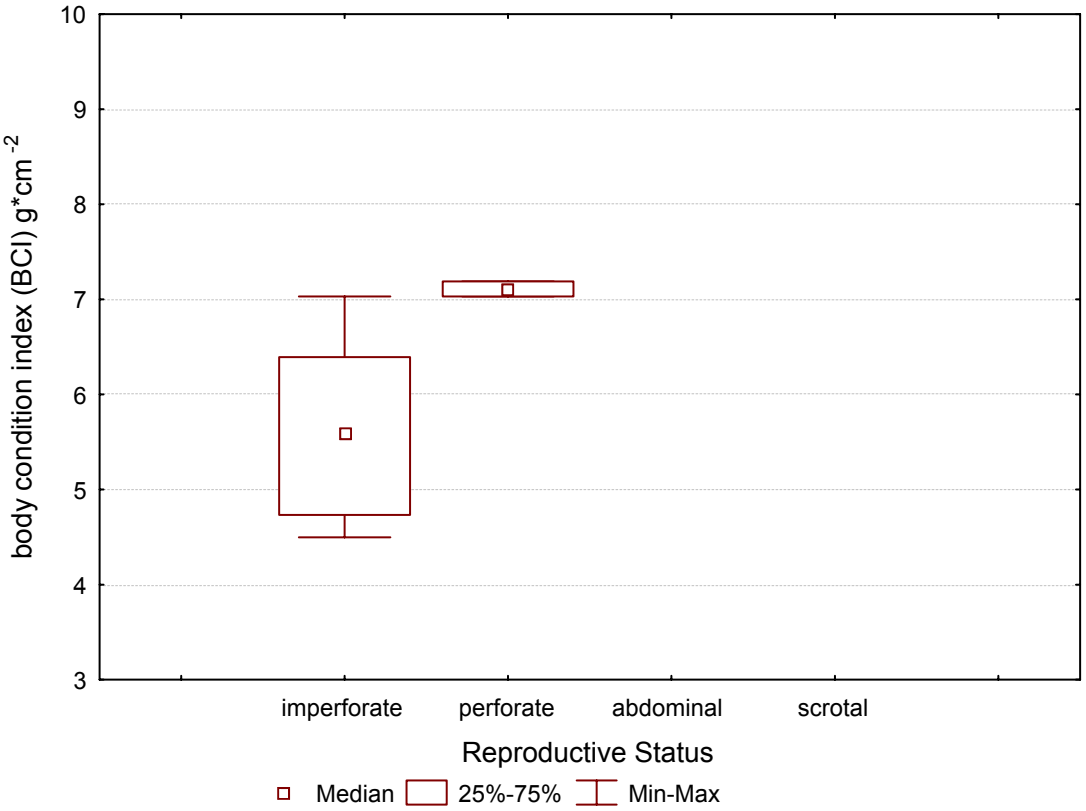


Figure IV-47: Sexual Maturity: body condition index (BCI) vs. reproductive status in imperforate (N=2) or perforate (N=8) non-pregnant females in hummock V-9.

There are no significant differences in body mass of sexually mature females between hummocks, (Kruskal-Wallis test: $H_{6,53}$=10.32, NS), and also no significant differences in body condition index between hummocks (Kruskal-Wallis test: $H_{6,53}$=5.38, NS). As in the females, the differences in body mass of sexually mature males of different hummocks are not significant (Kruskal-Wallis test: $H_{6,78}$ =3.56, NS), but differences in body condition index of reproductively active males were significant between hummocks (Kruskal-Wallis test: $H_{6,79}$=14.36, $p<0.05$).

As differences were not significant, data were pooled to obtain information on seasonal changes in body mass and body condition index of sexually mature females. The body mass of sexually mature females shows significant seasonal differences (Kruskal-Wallis test: $H_{12,53}$=22.65, $p<0.05$). Reproductively active females are lighter during the spring and summer months and heavier throughout autumn and winter (Figure IV-48). A similar pattern emerged in the seasonal change of body condition of sexually mature females, the body condition index was significantly different between months (Kruskal-Wallis test:$H_{12,53}$=22.65, $p<0.05$). Body condition index of reproductively active females was lower in spring and summer, and higher in the autumn and winter months (Figure IV-49).

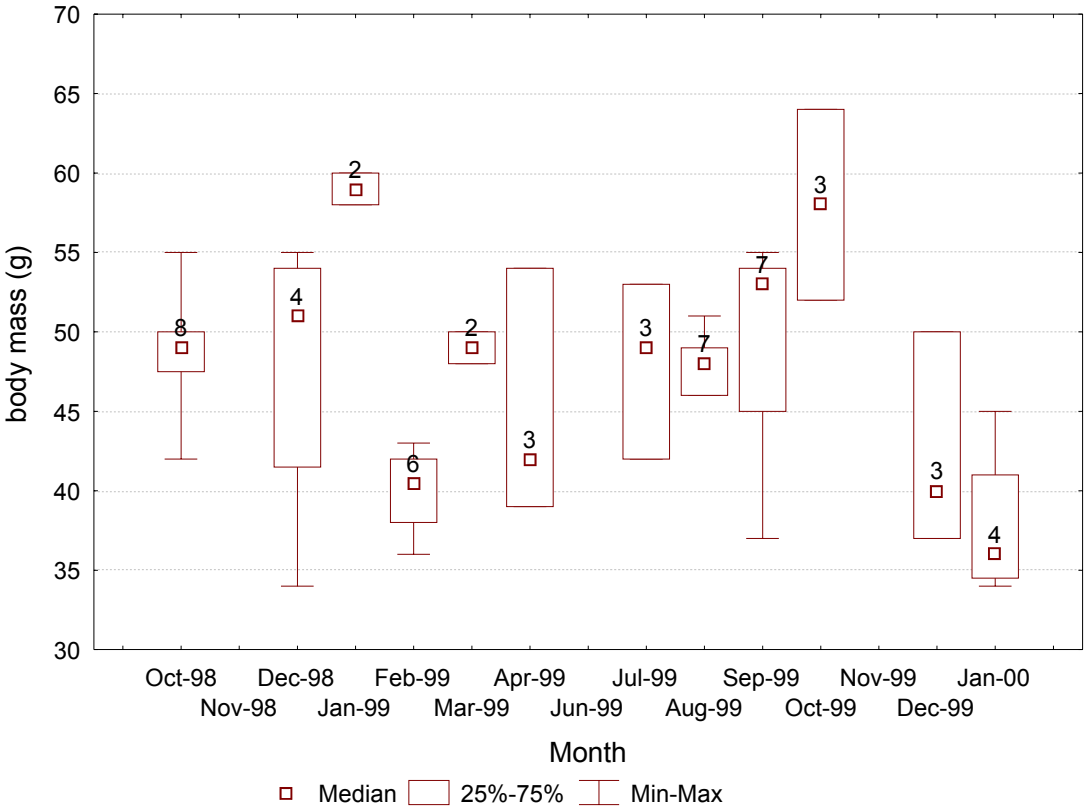


Figure IV-48: Sexual Maturity: Seasonal changes in body mass of sexually mature females. Point labels indicate number of individuals captured.

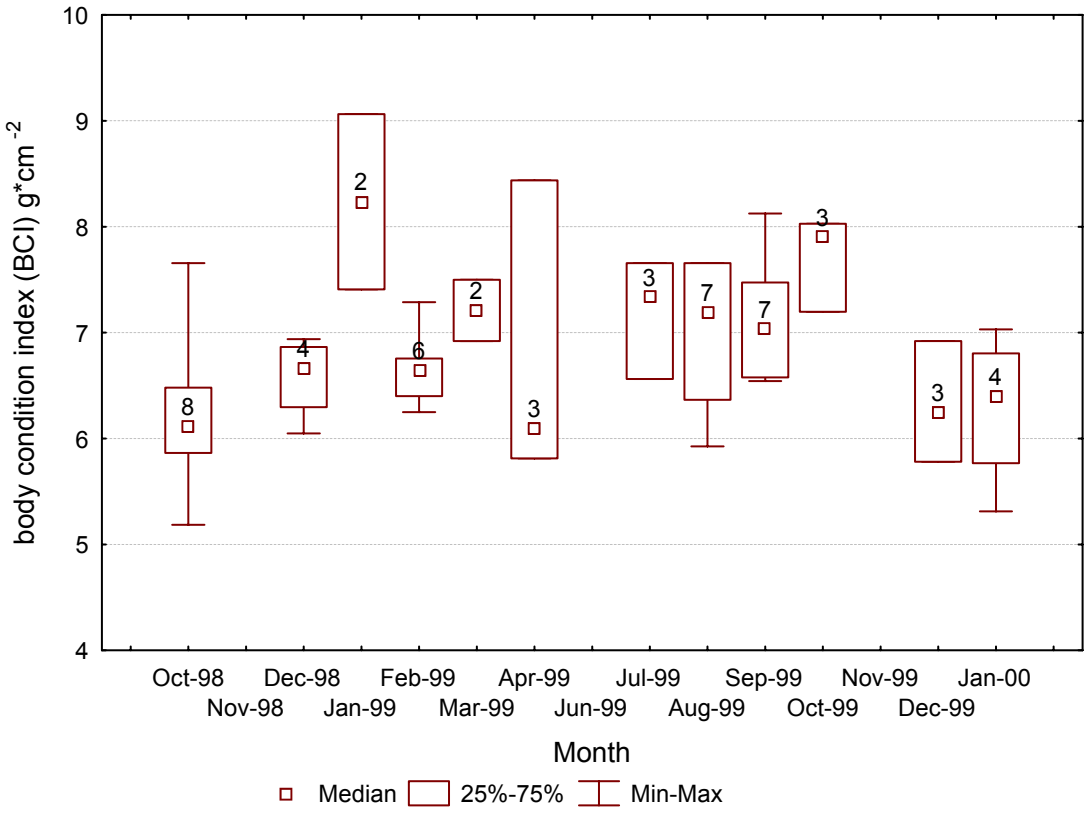


Figure IV-49: Sexual Maturity: Seasonal changes in body condition index of reproductively active females. Point labels indicate number of individuals captured.

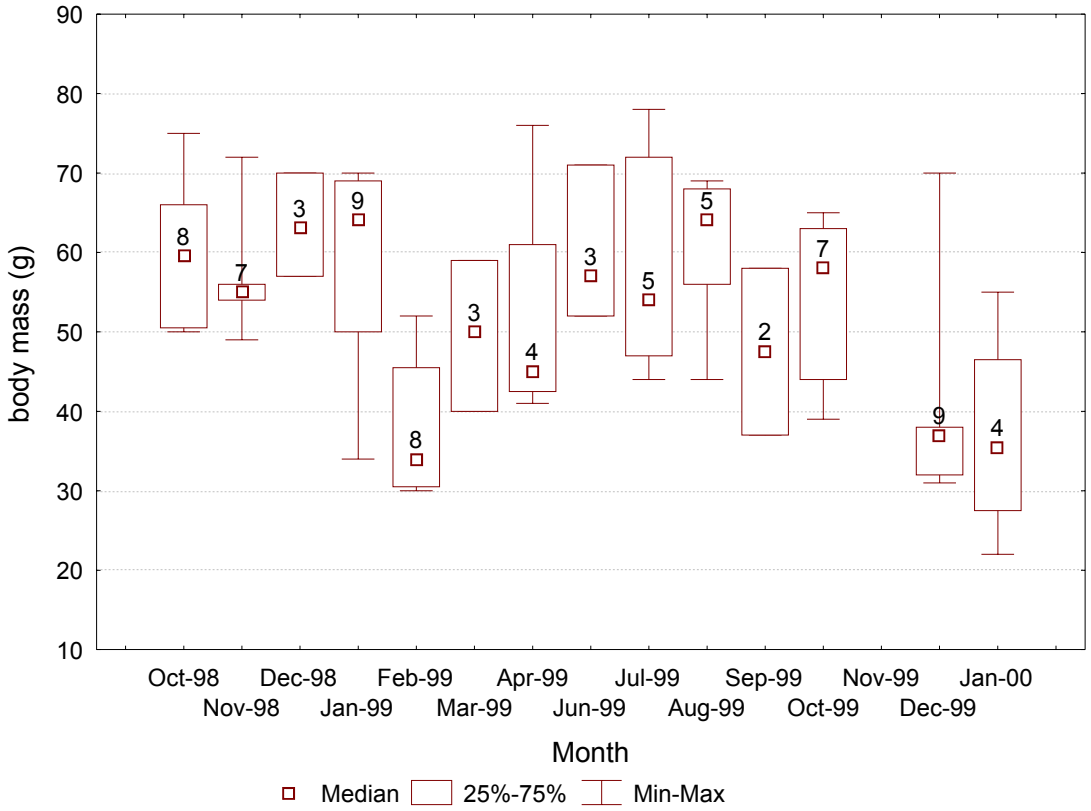


Figure IV-50: Sexual Maturity: Seasonal changes in body mass of sexually mature males. Point labels indicate number of individuals captured.

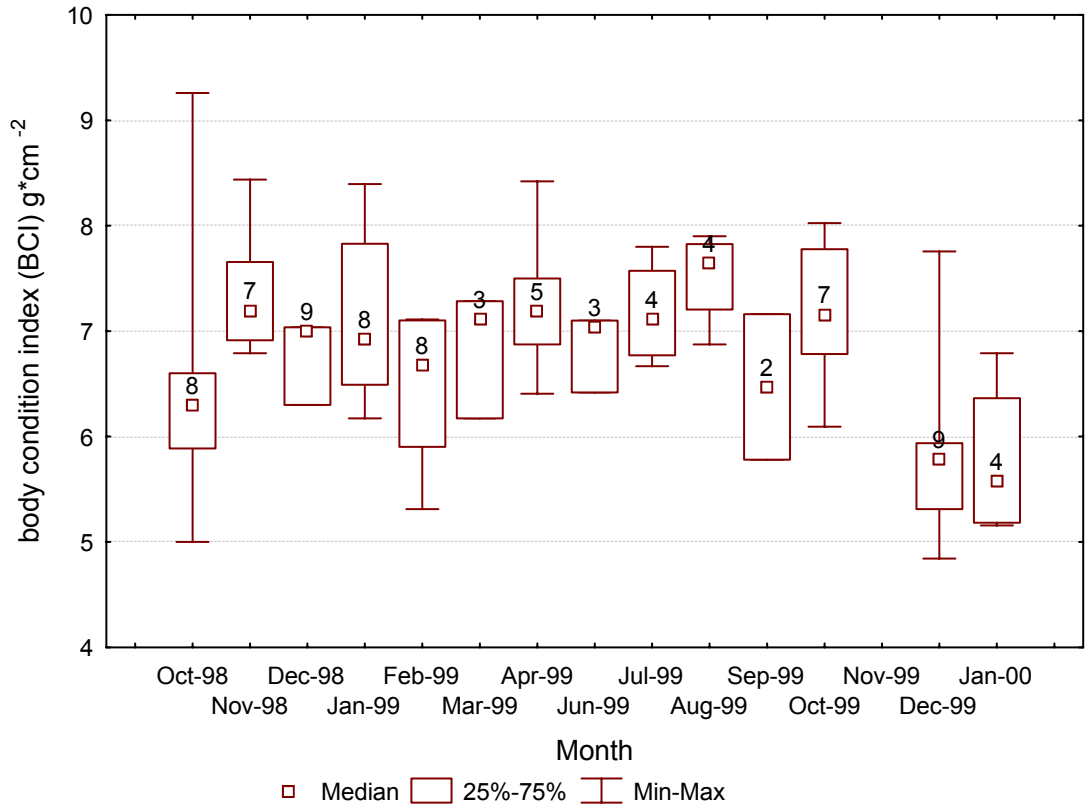


Figure IV-51: Sexual Maturity: Seasonal changes in body condition index of sexually mature males. Point labels indicate number of individuals captured.

As there were no differences in body mass of sexually mature males between hummocks, data of all hummocks were pooled to obtain information on seasonal changes in body mass. The body mass of reproductively active males does differ significantly between months (Kruskal-Wallis test: $H_{14,78}=33.05, p<0.01$). As in the females, sexually mature males are lighter during spring and summer, and heavier during the autumn and winter months (Figure IV-50).

To obtain information on seasonal differences in sexually mature males, data of hummocks V-1 to V-7 were pooled, and data for hummock V-8 not regarded, as males in this hummock had a significantly higher body condition index than the sexually mature males of the other hummocks. Again, there are significant differences in the body condition of reproductively active males between months (Kruskal-Wallis test: $H_{14,76}=28.77$, $p<0.05$). Sexually mature males captured during spring and summer months had lower body condition indices than males caught during autumn and winter (Figure IV-51).

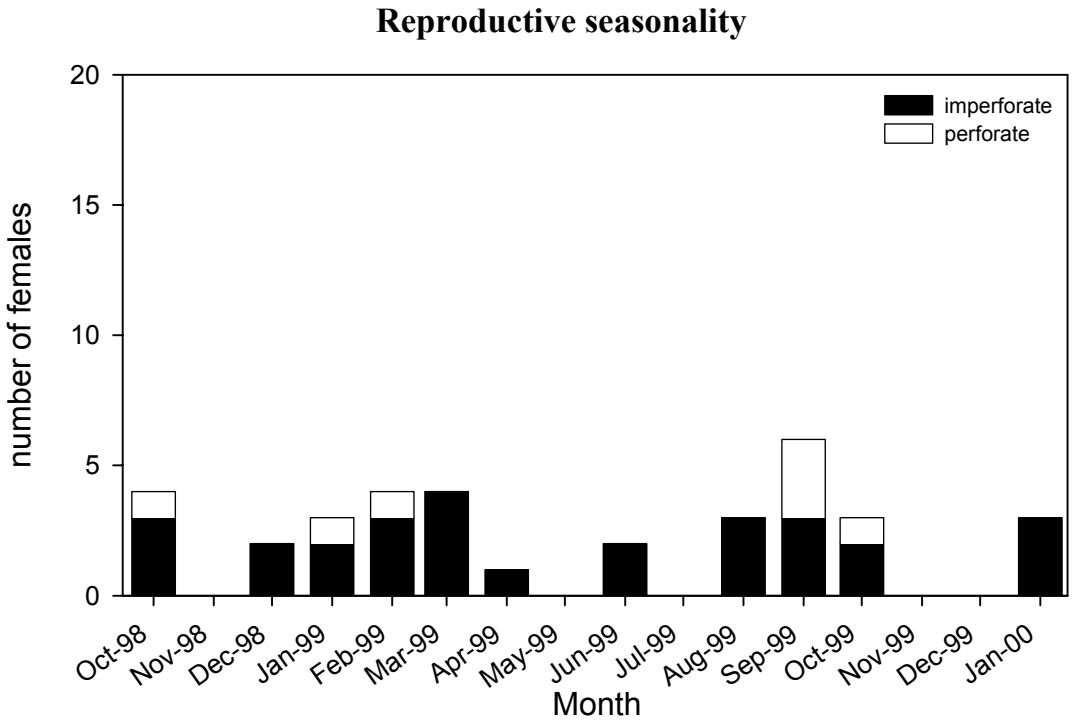


Figure IV-52: Reproductive seasonality: number of perforate and imperforate non-pregnant females captured in hummock V-1.

Reproductively active females were found in hummock V-1 only during the spring and summer months. No perforate, non-pregnant females were found in the population in the autumn or winter (Figure IV-52), while females with an imperforate vagina were present throughout the year. Both climate and resource availability had

an influence on reproductive activity. The number of perforate females was negatively related to mean ambient temperature the preceding month (Spearman rank correlation: rs=-0.641, N=11, $p<0.05$), and to the number of buds two months previously (Spearman rank correlation: rs=0.702, N=9, $p<0.05$).

Occurrences of pregnancy and lactation showed a similar pattern. Females were pregnant and/or lactating during the spring and summer months, while non-pregnant females were present throughout the year (Figure IV-53). Climate was found to have an influence on pregnancy and lactation; the number of pregnant females is positively correlated with relative humidity (Spearman rank correlation: rs=0.617, N=11, $p<0.05$), and the number of fog days two months previously (Spearman rank correlation: rs=0.657, N=11, $p<0.05$).

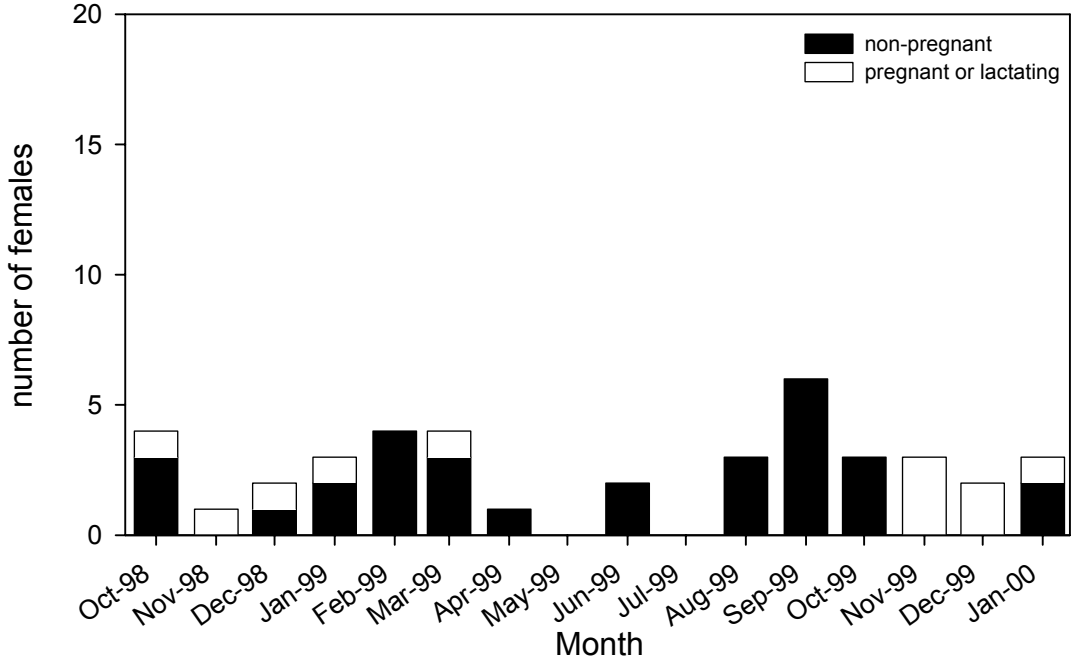


Figure IV-53: Reproductive seasonality: number of non-pregnant and pregnant or lactating females captured in hummock V-1.

The pattern was reversed for the reproductive activity of males. Males with scrotal testes were present in the population throughout the year, while males with abdominal testes were only found in the population during spring and summer (Figure IV-54). These were the young males born during this period. The males matured at the end of summer, and the testes descended. One single young male with abdominal testes was found in June 1999. In this case, the individual had not yet reached sexual maturity. Reproductive status in males was also influence by resource availability and climate. The number of males with scrotal testes was positively correlated with the number of nara flower buds available the previous month (Spearman rank correlation: rs=0.637,

N=11, p<0.05), and negatively correlated with absolute maximum temperature the previous month (Spearman rank correlation: rs=-0.850, N=11, p<0.001).

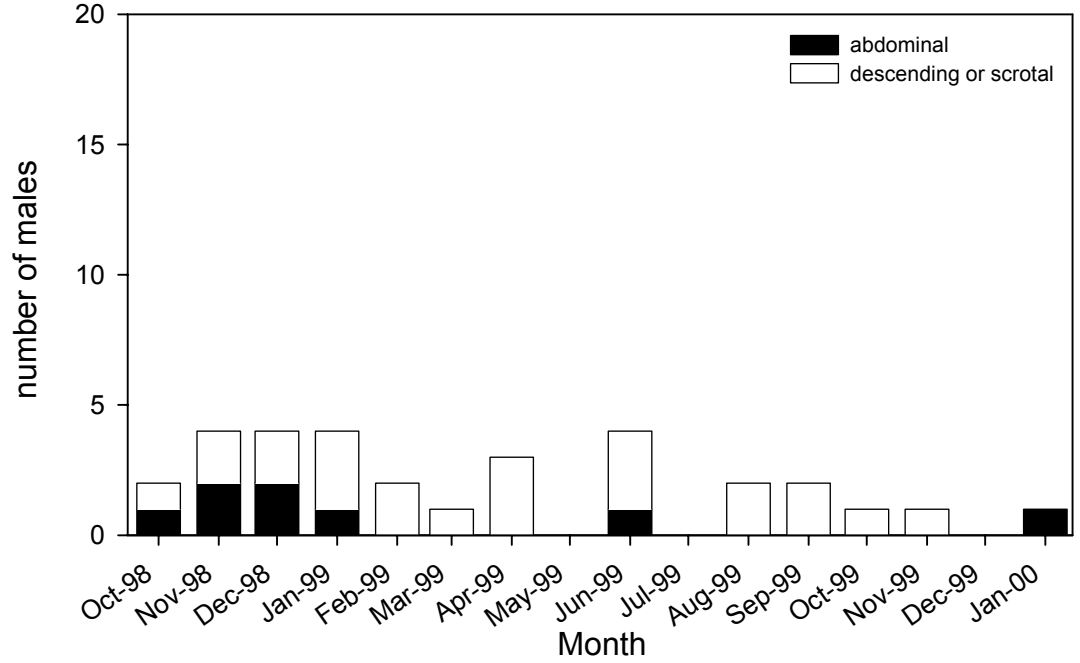


Figure IV-54: Reproductive seasonality: number of males with abdominal, descending and scrotal testes captured in hummock V-1.

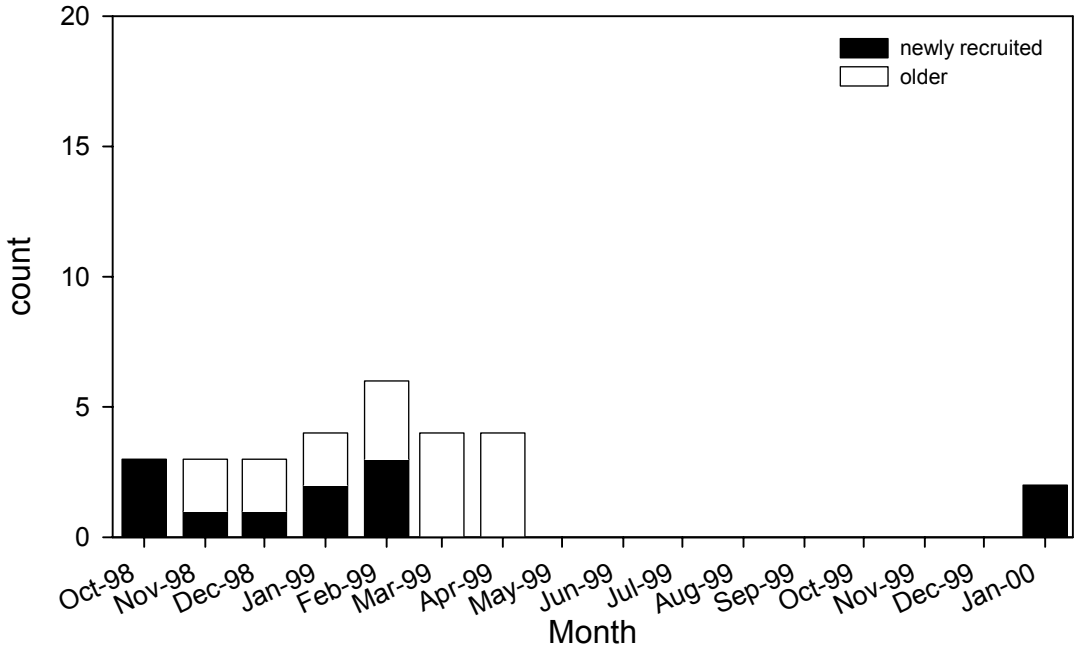


Figure IV-55: Reproductive seasonality: newly recruited juveniles and older juveniles present in hummock V-1.

Juveniles were present in the population between October 1998 and April 1999 and again in January 2000 (Figure IV-55). The females found pregnant in November apparently did not produce any offspring (see also pp.117). A number of climatic factors influenced juvenile recruitment. Number of juveniles in a month was

positively related with the number of fog days in the same month (Spearman rank correlation: rs=0.660, N=16, p<0.01), and relative humidity the same month (Spearman rank correlation: rs=0.567, N=16, p<0.05). This indicated that juveniles were born in the population during the cooler, wetter months.

The pattern of reproductive activity in hummock V-2 was similar to the pattern found in hummock V-1. Non-pregnant females with a perforate vagina were only trapped in the population during spring and summer (Figure IV-56), while non-perforate females were present throughout the year. Females became perforate at the end of winter, earlier than hummock V-1. Perforation in females was influenced by both resource availability and climate. The number of perforate females was positively related to the number of flowers available (Spearman rank correlation: rs=0.607, N=12, p<0.05), as well as to relative humidity the previous month (Spearman rank correlation: rs=0.623, N=13, p<0.01).

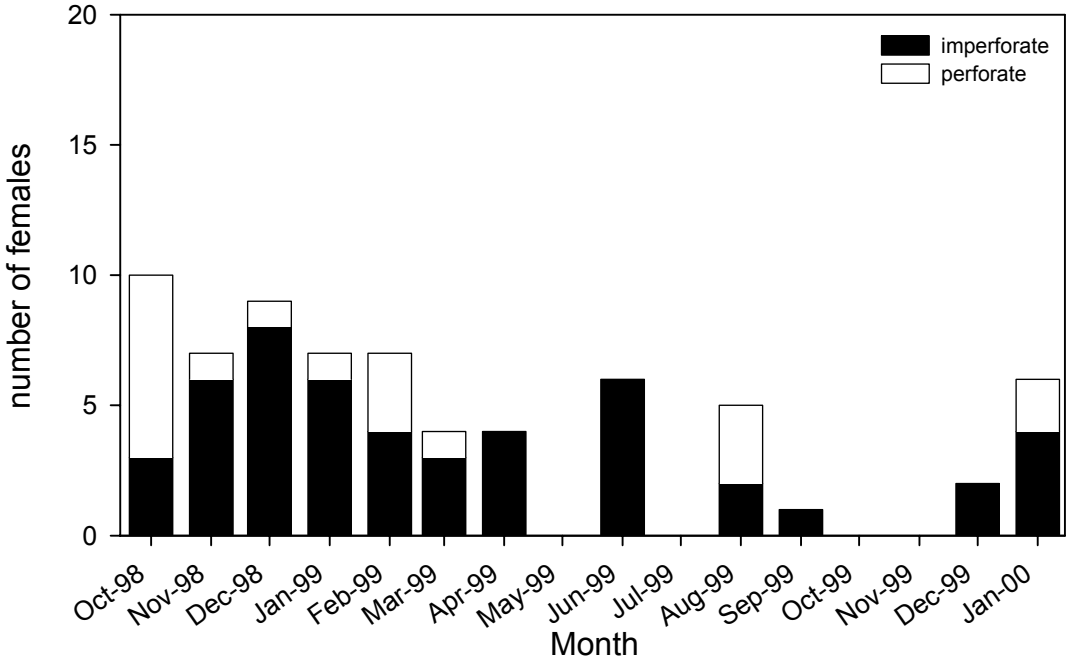


Figure IV-56: Reproductive seasonality: number of perforate and imperforate non-pregnant females captured in hummock V-2.

Pregnant and/or lactating females were also only present in the population during the spring and summer months (Figure IV-57). Occurrence of pregnancy and lactation was related to a number of resource and climatic factors. The number of pregnant females was positively related to the number of flowers available the previous month (Spearman rank correlation: rs=0.687, N=12, p<0.05), and the number of fog days in the previous month (Spearman rank correlation: rs=0.723, N=14, p<0.05). The number of pregnant and/or lactating females was also positively correlated with the

number of rain days in the previous month (Spearman rank correlation: rs=-0.542, N=14, $p<0.05$), and negatively related to mean ambient temperature two months previously (Spearman rank correlation: rs=-0.589, N=14, $p<0.05$).

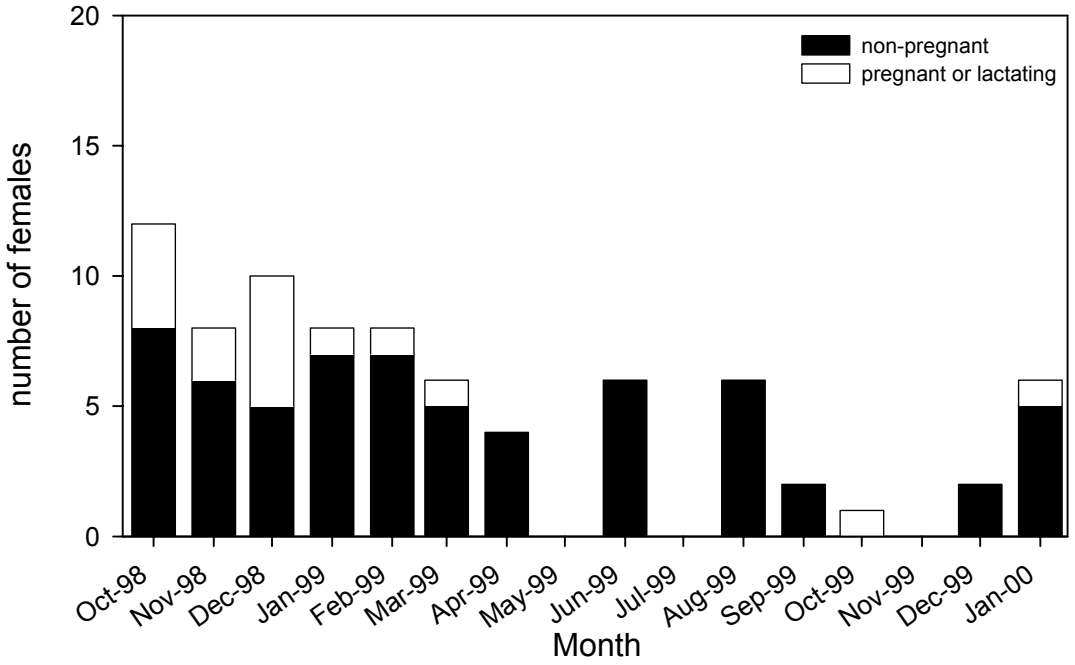


Figure IV-57: Reproductive seasonality: number of non-pregnant and pregnant or lactating females captured in hummock V-2.

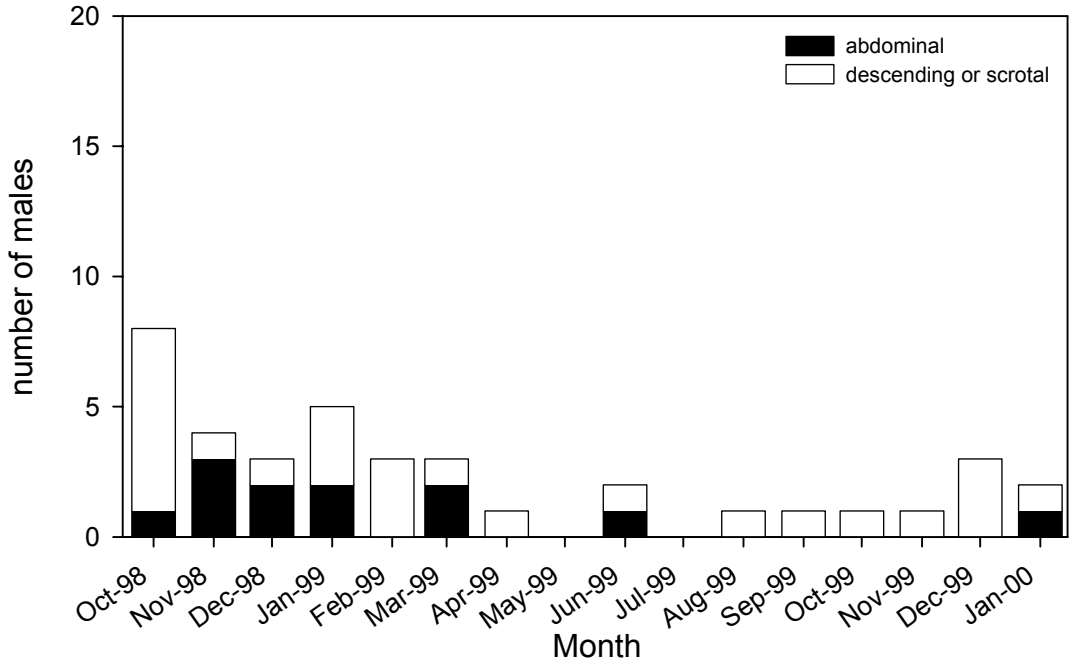


Figure IV-58: Reproductive seasonality: number of males with abdominal, descending and scrotal testes captured in hummock V-2.

As in hummock V-1, the reproductive activity of males showed the opposite pattern to the reproductive activity of females. Males with scrotal testes were present in the population throughout the year, while males with abdominal testes were only

found in spring and summer (Figure IV-58). Again, these were the males that were born during this period, and which had not matured yet. The male with abdominal testes caught in June 1999 was also a young male that had not yet matured. Reproductive activity of males was influence by resource availability and climatic factors. The number of with scrotal testes was positively related to the number of nara flowers available (Spearman rank correlation: rs=0.625, N=14, p<0.05), and number of nara flower buds available in the previous month (Spearman rank correlation: rs=0.606, N=13, p<0.05).

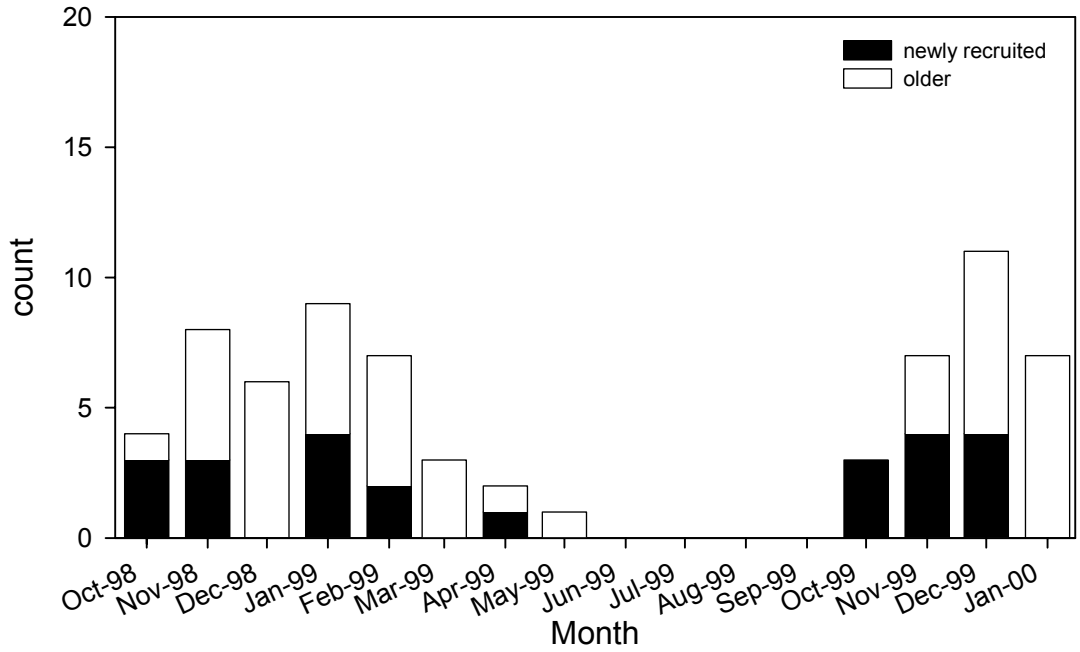


Figure IV-59: Reproductive seasonality: newly recruited juveniles and older juveniles present in hummock V-2.

In hummock V-2, juveniles were born from spring through to late summer; no juveniles were caught between June and September 1999 (Figure IV-59). Juvenile recruitment was related to a number of environmental factors. It was found that the number of juveniles was negatively correlated with the proportion of nara shoots in the diet of females one month previously (Spearman rank correlation: rs=-0.609, N=14, p<0.05). The number of juveniles in the population was positively correlated with the number of nara flowers available one month previously (Spearman rank correlation: rs=0.629, N=14, p<0.05) and to number of nara flowers available two months previously (Spearman rank correlation: rs=0.588, p<0.05). The number of juveniles per month was also positively related to the number of fog days (Spearman rank correlation: rs=0.597, N=16, p<0.05), and to relative humidity (Spearman rank correlation: rs=0.653, N=16, p<0.01). Number of juveniles per month was as well

positively correlated with mean ambient temperature (Spearman rank correlation: rs=0.538, N=16, p<0.05) and absolute minimum temperature (Spearman rank correlation: rs=0.729, N=16, p<0.01) in the corresponding months. The number of juveniles were also positively correlated to the number of fog days the previous month (Spearman rank correlation: rs=0.718, N=16, p<0.01), and the number of fog days two months previously (Spearman rank correlation: rs=0.708, N=16, p<0.01). In this hummock, juveniles were being born during the cooler, wetter months, and when good quality food was available.

The pattern of reproductive activity seen in hummocks V-1 and V-2 was repeated in hummock V-3. Non-pregnant females with a perforate vagina were found in the population during spring and summer, and females matured in late winter, as in hummock V-2 (Figure IV-60). Immature, i.e. imperforate females were present in the population throughout the year. No significant correlations were found between the number of perforate females and resource or climatic factors.

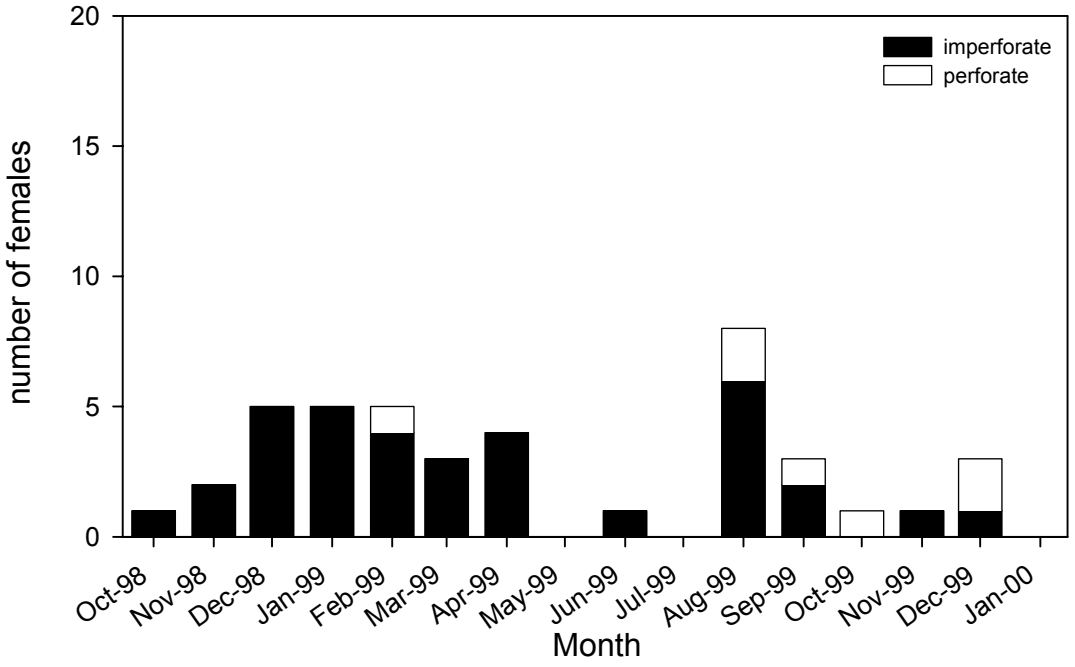


Figure IV-60: Reproductive seasonality: number of perforate and imperforate non-pregnant females captured in nara hummock V-3.

Pregnant or lactating females were present in the population only during spring, and not in summer, as in the other hummocks (Figure IV-61). Non-pregnant females were found throughout the year. Pregnancy and lactation were influence by resource and climatic factors. The number of pregnant females was positively correlated with the number of nara flower buds available (Spearman rank correlation: rs=0.775, N=14, p<0.01), and number of flowers two months previously (Spearman rank

correlation: rs=0.676, N=12, p<0.05). Furthermore, the number of pregnant and/or lactating females was positively related to the number of fog days per month (Spearman rank correlation: rs=0.658, N=14, p<0.05), and negatively correlated with absolute maximum temperature (Spearman rank correlation: rs=-0.565, N=14, p<0.05), and mean ambient temperature (Spearman rank correlation: rs=-0.609, N=14, p<0.05).

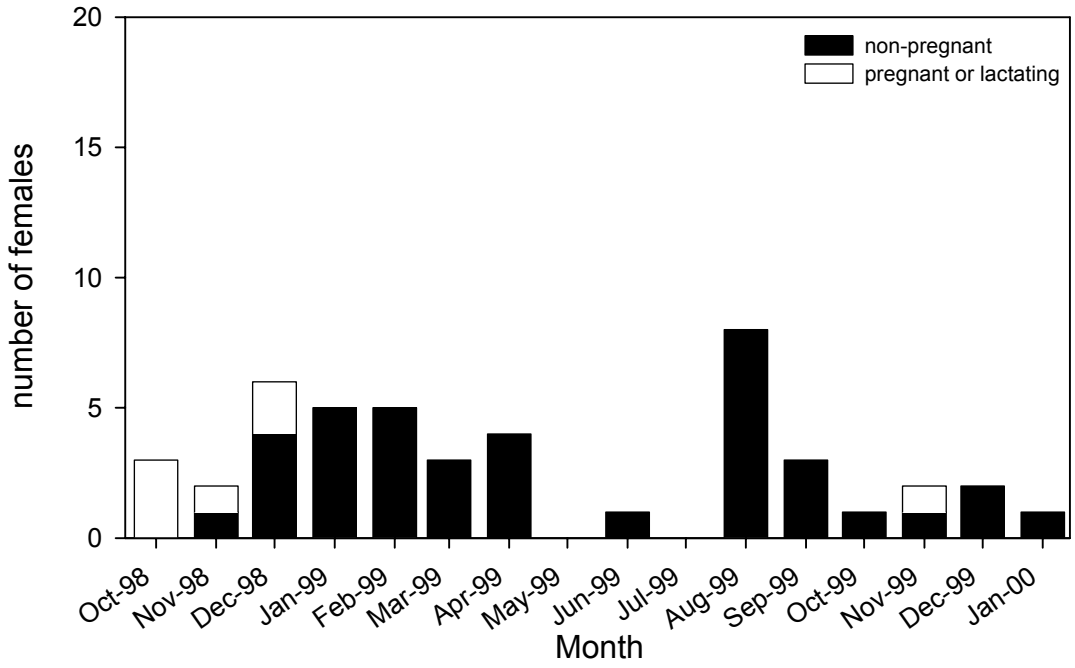


Figure IV-61: Reproductive seasonality: number of non-pregnant and pregnant or lactating females captured in hummock V-3.

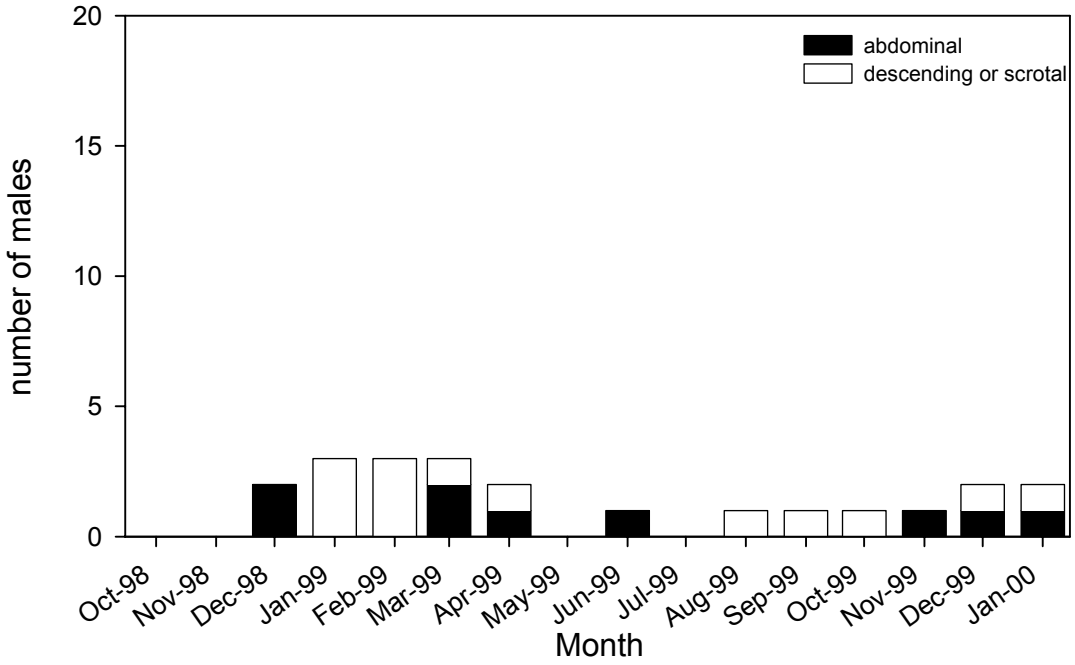


Figure IV-62: Reproductive seasonality: number of males with abdominal, descending and scrotal testes captured in hummock V-3.

Males with scrotal testes were trapped in hummock V-3 throughout the year (Figure IV-62), males with abdominal testes were found in the spring and summer months. As in hummocks V-1 and V-2, a single immature young male was caught in June 1999. The number of scrotal males in the population is positively correlated with absolute maximum temperature (Spearman rank correlation: $r_s=0.645$, $N=14$, $p<0.05$).

As in hummock V-2, juveniles were present in the population in the spring and summer months. No young were captured or observed between April and September 1999, the drier months (Figure IV-63). Resource availability and climatic factors were influencing juvenile recruitment; the number of juveniles present is positively correlated with the number of nara flower buds available two months previously (Spearman rank correlation: $r_s=0.777$, $N=13$, $p<0.01$). The number of juveniles is also positively correlated with relative humidity (Spearman rank correlation: $r_s=0.764$, $N=16$, $p<0.001$), mean ambient temperature ($r_s=0.602$, $N=16$, $p<0.05$), and absolute minimum temperature in the same months (Spearman rank correlation: $r_s=0.813$, $N=16$, $p<0.001$). Number of juveniles per month is also positively related to the number of fog days in the previous month (Spearman rank correlation: $r_s=0.665$, $N=16$, $p<0.01$) and the number of fog days two months previously (Spearman rank correlation: $r_s=0.712$, $p<0.01$). Juveniles were being born during the cooler wetter months, and when good quality food was available.

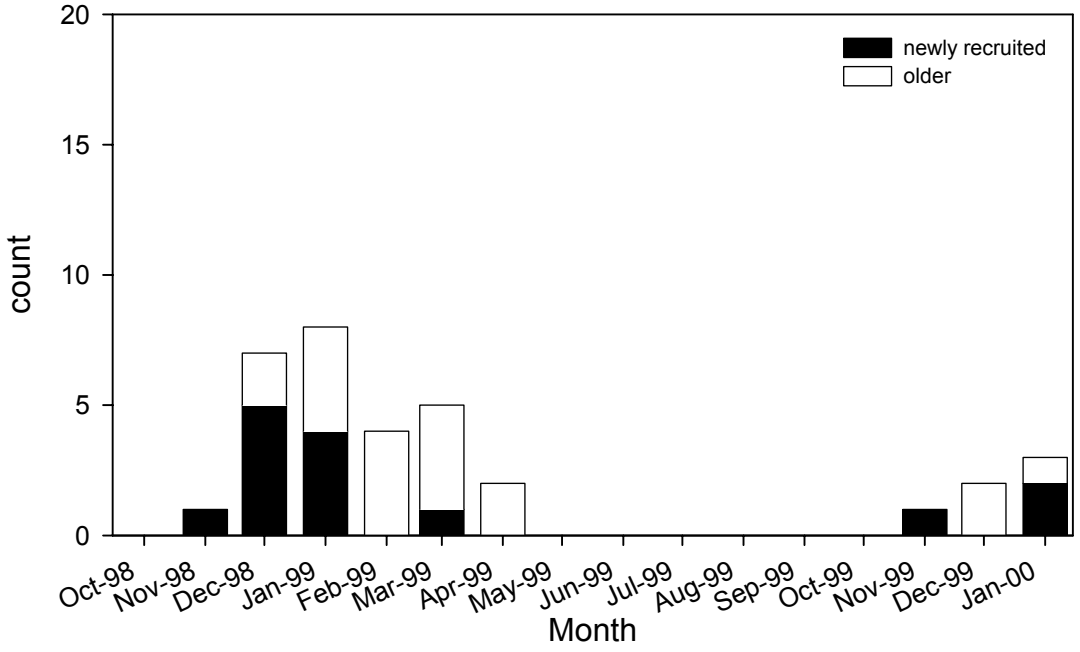


Figure IV-63: Reproductive seasonality: newly recruited juveniles and older juveniles present in hummock V-3

In nara hummock V-4, non-pregnant females with perforate vagina were present throughout the year (Figure IV-64), and were not only restricted to spring and summer, as in the hummocks discussed above. Imperforate females are also found throughout the study period. Occurrence of perforate females was influenced by resource availability; the number of perforate females was positively correlated with the number of nara shoots available in the previous month (Spearman rank correlation: $r_s=0.800$, $N=10$, $p<0.05$).

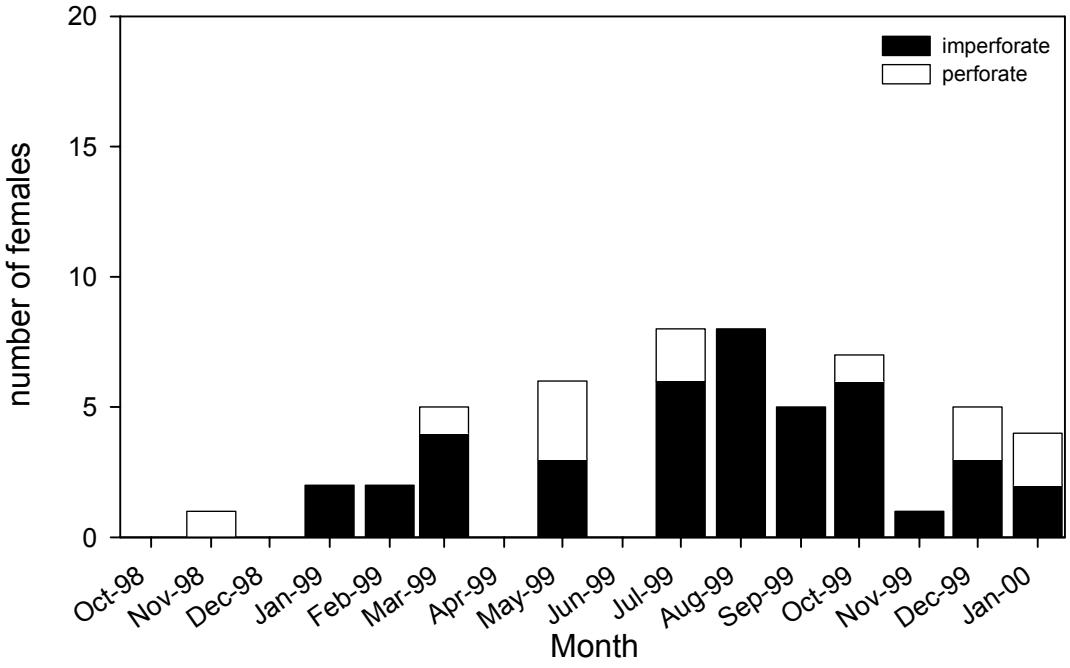


Figure IV-64: Reproductive seasonality: number of perforate and imperforate non-pregnant females captured in nara hummock V-4.

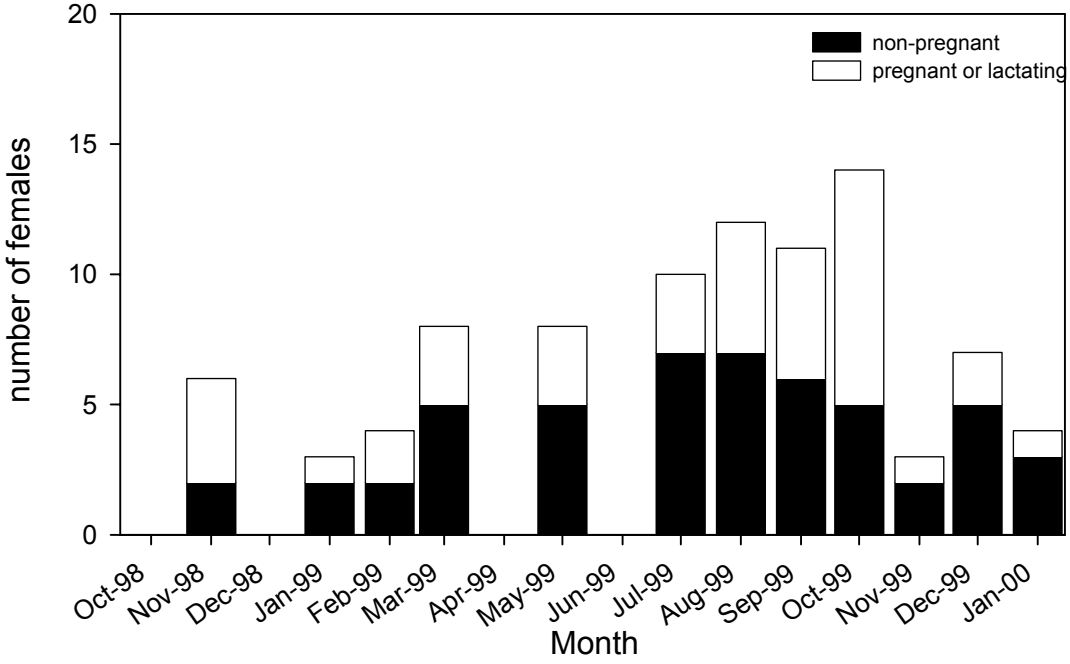


Figure IV-65: Reproductive seasonality: number of non-pregnant and pregnant or lactating females captured in hummock V-4.

Like the perforate females, pregnant and/or lactating females were captured in the population throughout the study period (Figure IV-65), and were also not restricted to spring and summer. The number of pregnant and/or lactating females was negatively related to the number nara melons the previous month (Spearman rank correlation: rs=-0.778, N=12, p<0.01)

As in the hummocks discussed previously, reproductively active males were present in the population throughout the study period (Figure IV-66). Males with abdominal testes were found during the winter months, indicating year-round recruitment. Reproductive activity in males was influence by resource and climatic factors. The number of scrotal males was positively correlated with the number of nara shoots available (Spearman rank correlation: rs=0.614, N=12, p<0.05), and was positively related to absolute minimum temperature (Spearman rank correlation: rs=0.702, N=12, p<0.05), relative humidity in the previous month (rs=0.596. N=12, p<0.05) and relative humidity two months previously (Spearman rank correlation: rs=0.663, N=12, p<0.05).

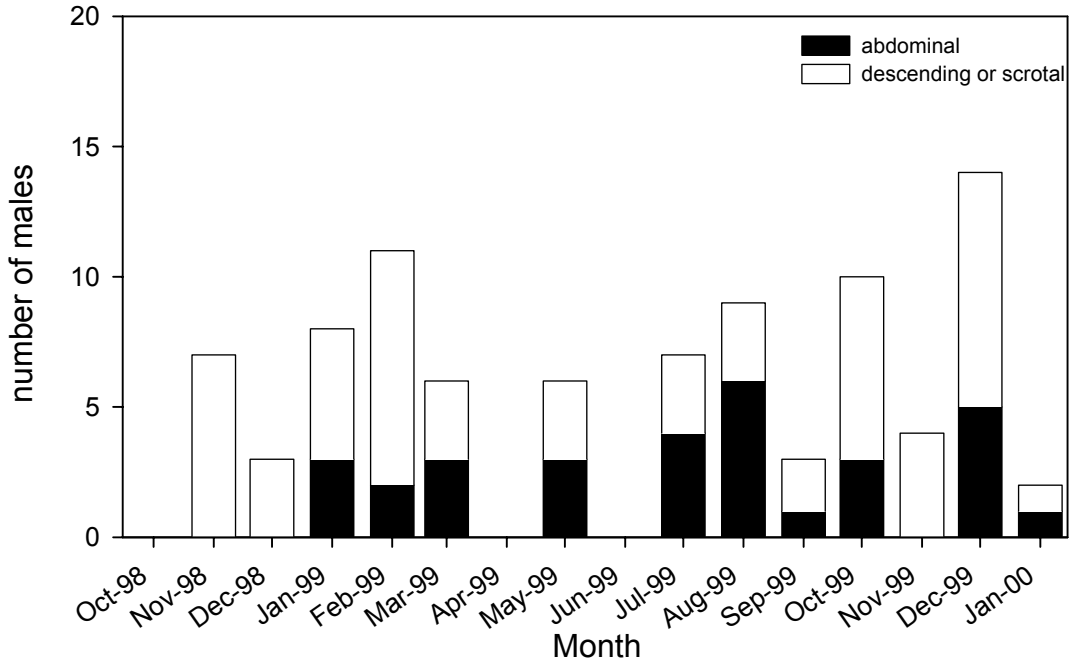


Figure IV-66: Reproductive seasonality: number of males with abdominal, descending and scrotal testes captured in hummock V-4.

In contrast to the above-discussed hummocks, juveniles were present in hummock V-4 throughout the study period, although the number of juveniles was lower between June and September 1999 (Figure IV-67). Juvenile recruitment was influenced by a number of environmental factors. The number of juveniles was negatively related to

the proportion of acacia seedpods in diet of adult females (Spearman rank correlation: rs=-0.800, N=11, p<0.01), but positively related to number of nara melons (Spearman rank correlation: rs=0.726, N=12, p<0.01) and number of nara shoots (Spearman rank correlation: rs=0.771, N=12, p<0.01) available in the same month. The number of juveniles per month was also positively correlated with the number of nara melons available in the previous month (Spearman rank correlation: rs=0.713, p<0.01), and number of number of nara flowers two months previously (Spearman rank correlation: rs=0.666, N=12, p<0.05). The number of juveniles was also positively related to the absolute minimum temperature in the same month (Spearman rank correlation: rs=0.669, N=13, p<0.05), the number of fog days in the previous month (Spearman rank correlation: rs=0.601, N=13, p<0.05) and the number of rain days two months previously (Spearman rank correlation: rs=0.618, N=13, p<0.05). Again, most of the juveniles were born in the cooler, wetter months, and those months with good quality food supply.

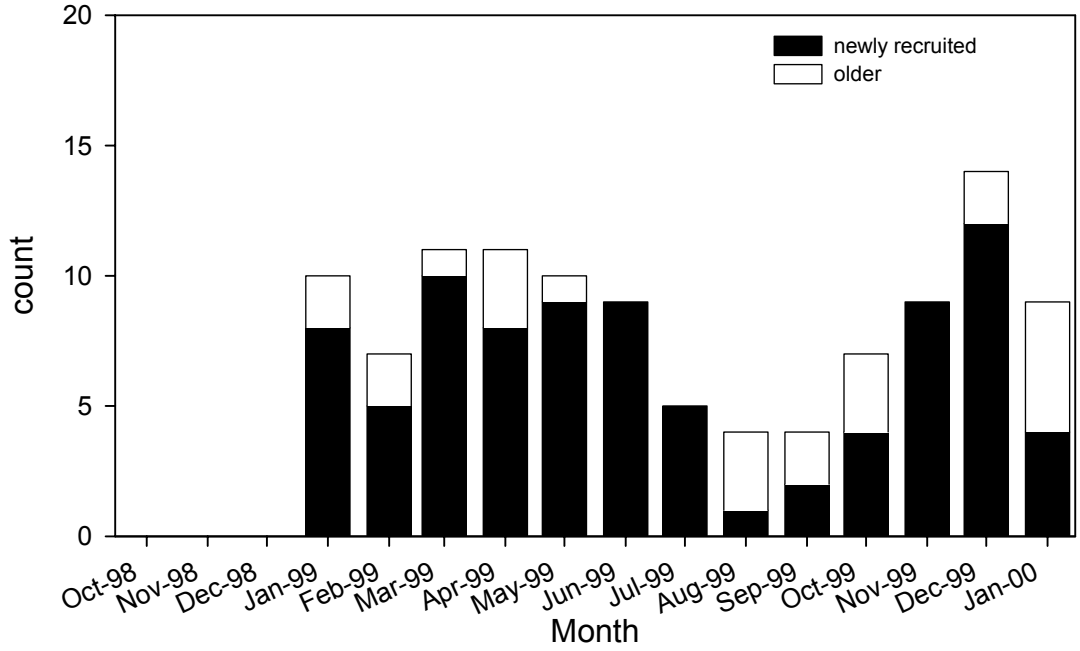


Figure IV-67: Reproductive seasonality: newly recruited juveniles and older juveniles present in hummock V-4.

In hummock V-7, perforate females were only captured during spring and summer (Figure IV-68), although the presence of juveniles in this hummock indicated that a reproductively active female must have been present in the winter months. One young imperforate female born in June 1999 was subsequently captured in spring. Reproductive activity in this hummock is mainly influence by resource availability, the number of perforate females is positively correlated with the number of nara

shoots available (Spearman rank correlation: rs=0.894, N=7, p<0.01), as well as the number of nara flower buds two months previously (Spearman rank correlation: rs=0.852, N=6, p<0.05) and the number of flowers two months previously (Spearman rank correlation: rs=0.853, N=6, p<0.05). Number of perforate females was also negatively correlated with mean ambient temperature two months previously (Spearman rank correlation: rs=-0.797, N=7, p<0.05).

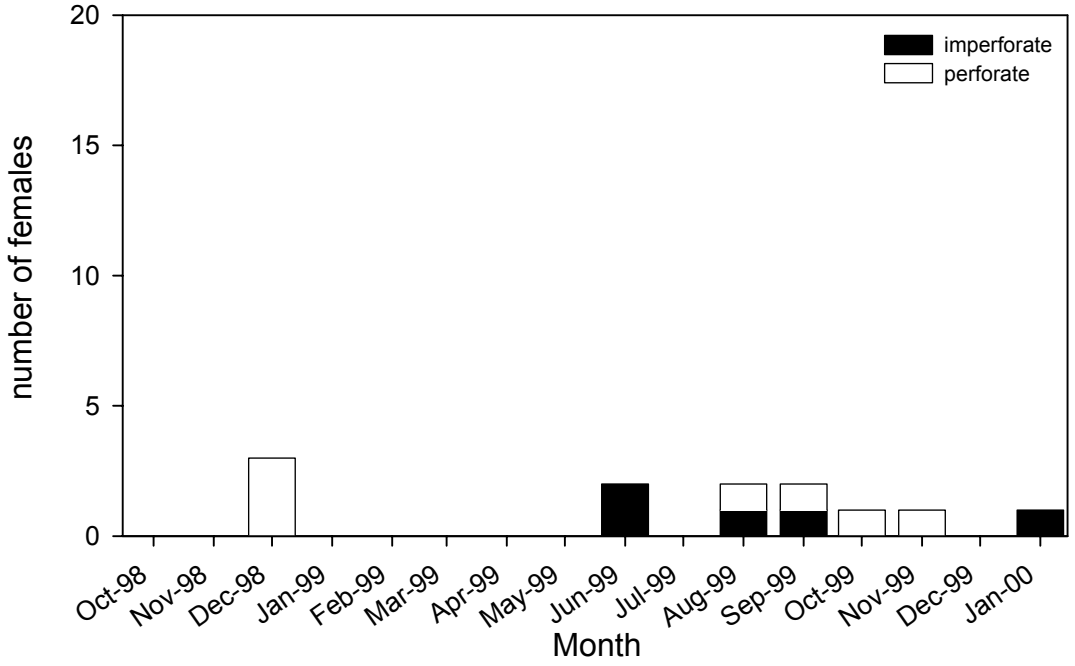


Figure IV-68: Reproductive seasonality: number of perforate and imperforate non-pregnant females captured in nara hummock V-7.

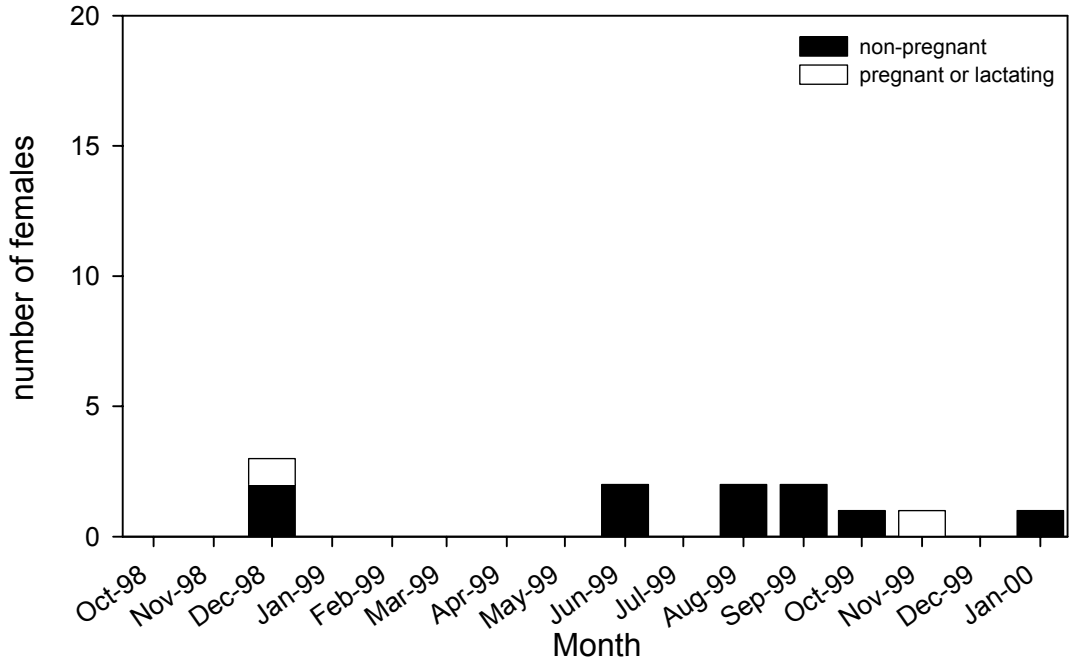


Figure IV-69: Reproductive seasonality: number of non-pregnant and pregnant or lactating females captured in hummock V-7.

Pregnant females were only found in two months of the study period, in summer (Figure IV-69). Reproductive activity was influenced by both resource and climatic factors. The number of pregnant females was negatively correlated with the number of nara flower buds available (Spearman rank correlation: rs=-0.787, N=7, $p<0.05$), and negatively related to the number of nara shoots available (Spearman rank correlation: rs=-0.802, N=7, $p<0.05$). The number of pregnant females was positively related to the number of fog days two months previously (Spearman rank correlation: rs=0.801, N=7, $p<0.05$) and to relative humidity two months previously (Spearman rank correlation: rs=0.802, N=7, $p<0.05$).

Males with scrotal testes were captured in hummock V-7 throughout the study period, immature males with abdominal testes were found in the population in winter and in summer (Figure IV-70). As in the other hummocks, reproductive activity of males was influenced by resource and climate factors. The number of scrotal males was negatively correlated with the number of nara flower buds available the previous month (Spearman rank correlation: rs=-0.781, N=8, $p<0.05$), and positively related to relative humidity (Spearman rank correlation: rs=0.738, N=11, $p<0.01$), absolute minimum temperature (Spearman rank correlation: rs=0.608, N=11, $p<0.05$), and the number of fog days in the previous month (Spearman rank correlation: rs=0.645, N=11, $p<0.05$).

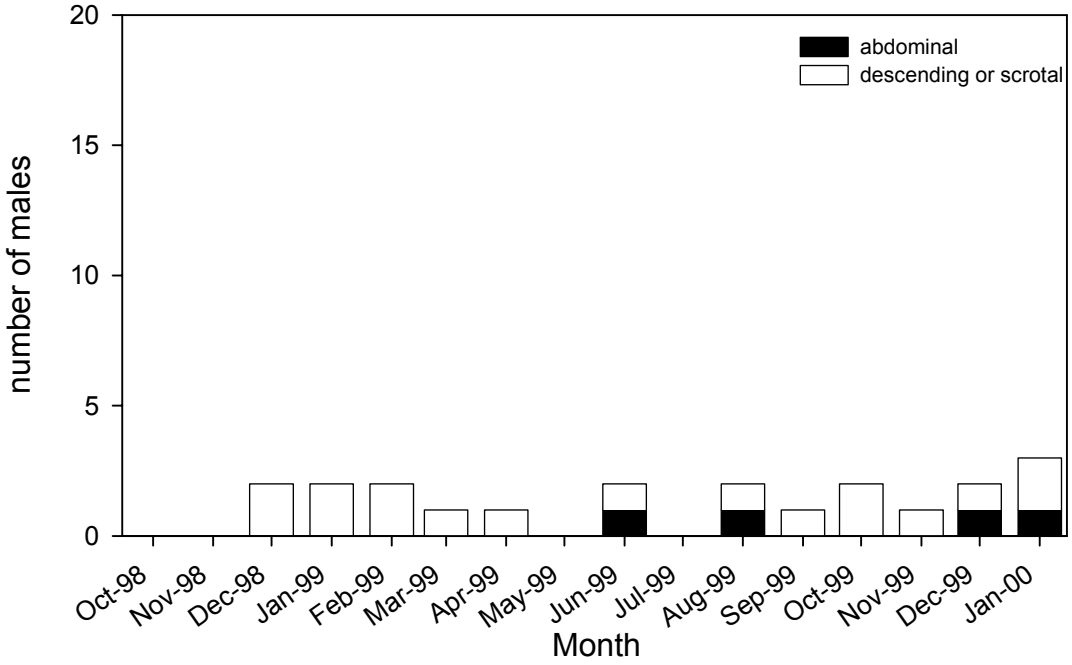


Figure IV-70: Reproductive seasonality: number of males with abdominal, descending and scrotal testes captured in hummock V-7.

In contrast to hummocks V-1, V-2 and V-3, juveniles were mainly captured during the dry winter months, from June to August 1999 (Figure IV-71). No correlations could be found between environmental factors and juvenile recruitment.

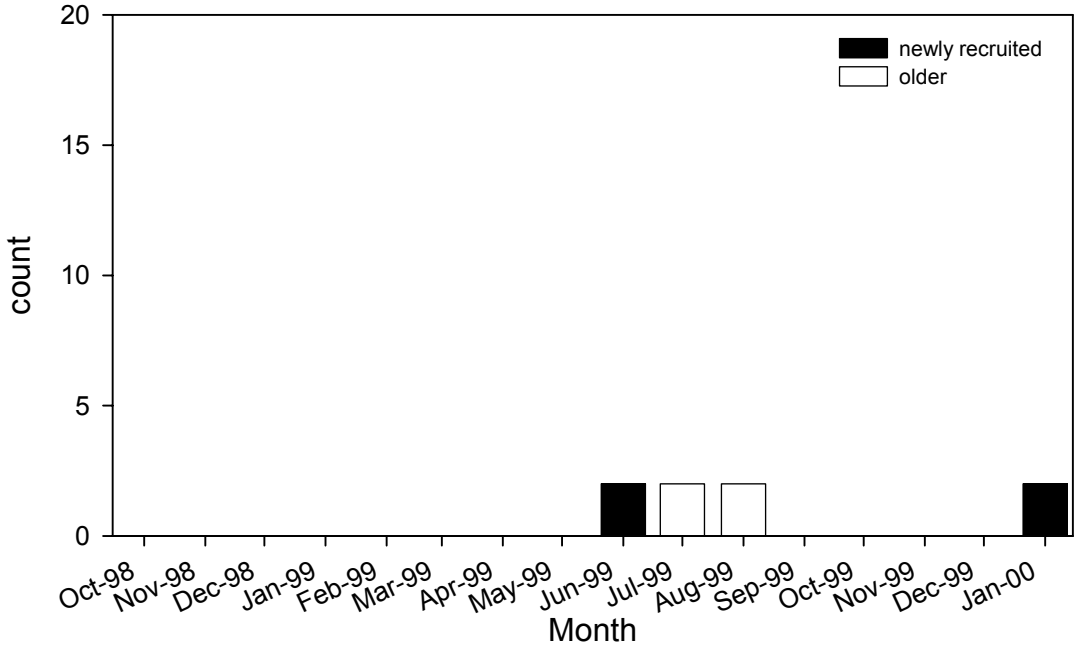


Figure IV-71: Reproductive seasonality: newly recruited juveniles and older juveniles present in hummock V-7.

In hummock V-8, reproductively active females were found from the start of the trapping in the winter months through to summer (Figure IV-72). Immature females were present during the same period. In this hummock, reproductive activity was related to climatic factors, the number of perforate females was positively correlated with mean ambient temperature (Spearman rank correlation: $r_s=0.926$, $N=6$, $p<0.01$).

Pregnant and/or lactating females were first trapped one month after the first female with a perforate vagina was captured, and were present throughout spring (Figure IV-73). Non-pregnant females were in the population for the duration of the trapping. Pregnancy and/or lactation in females was related to resource and climatic factors. The number of pregnant females was positively correlated with the number of nara flowers (Spearman rank correlation: $r_s=0.814$, $N=6$, $p<0.05$), and positively related to the number of rain days (Spearman rank correlation: $r_s=0.876$, $N=6$, $p<0.05$) and negatively correlated with mean ambient temperature two months previously (Spearman rank correlation: $r_s=-0.926$, $N=6$, $p<0.01$).

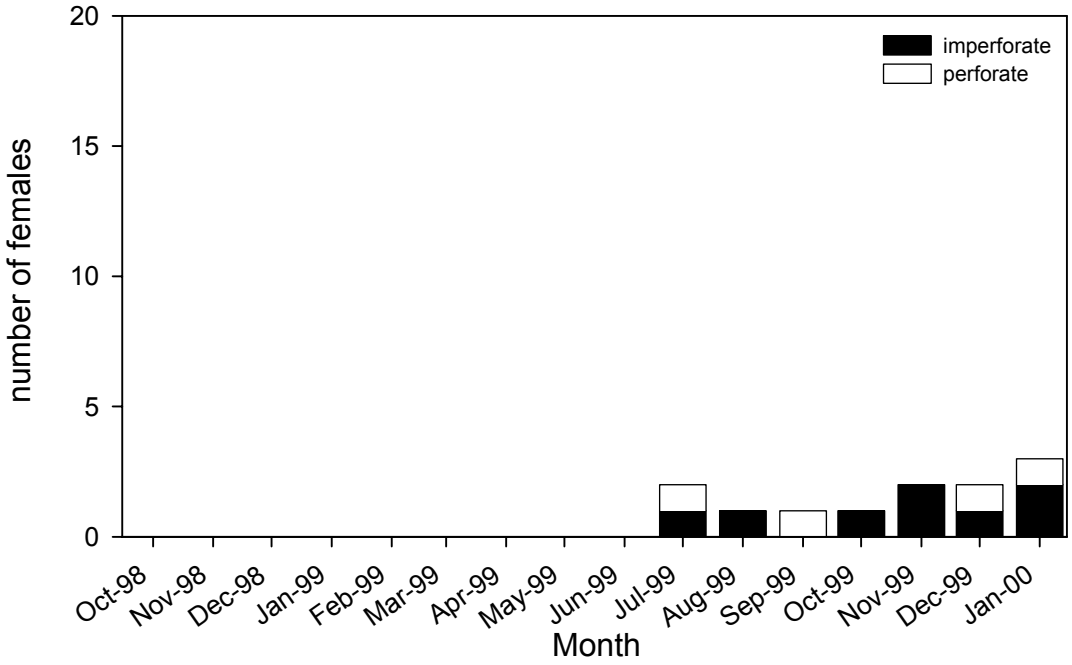


Figure IV-72: Reproductive seasonality: number of perforate and imperforate non-pregnant females in nara hummock V-8.

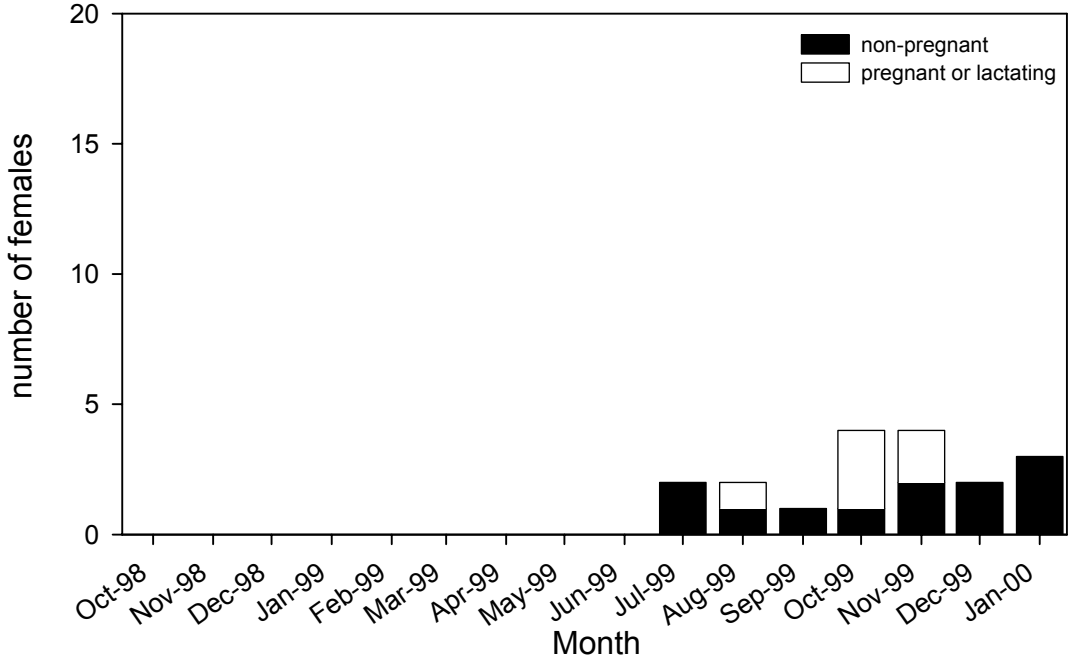


Figure IV-73: Reproductive seasonality: number of non-pregnant and pregnant or lactating females captured in hummock V-8.

Reproductively active males with scrotal testes were captured throughout the duration of the trapping period, while immature males with abdominal testes were only found in summer (Figure IV-74). No relation between the number of scrotal males and resource and climatic factors could be found.

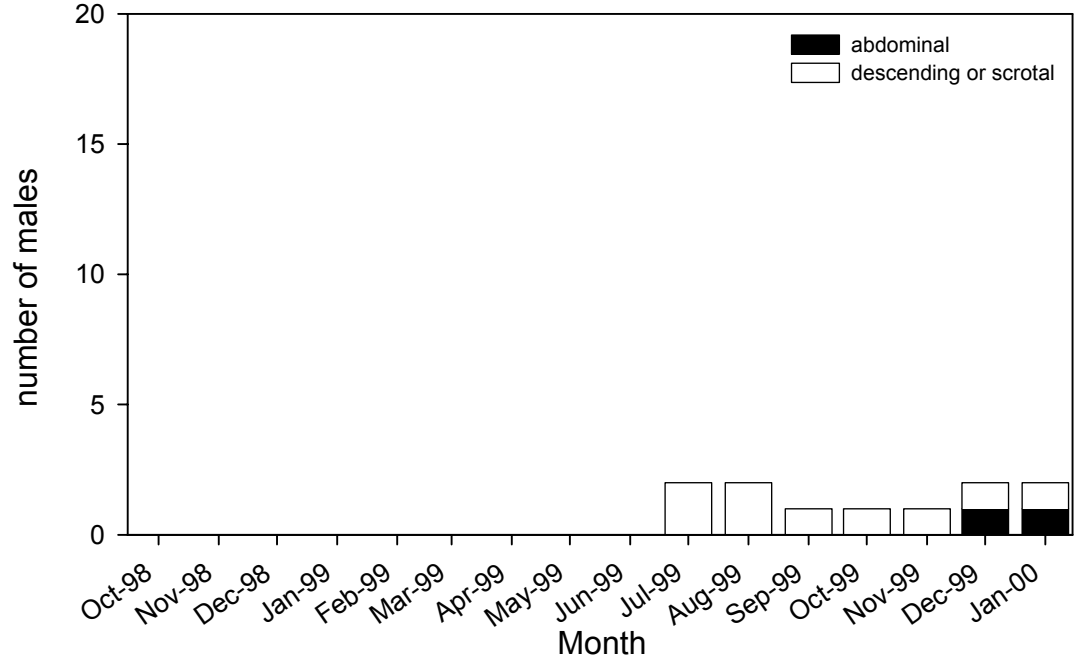


Figure IV-74: Reproductive seasonality: number of males with abdominal, descending and scrotal testes captured in hummock V-8.

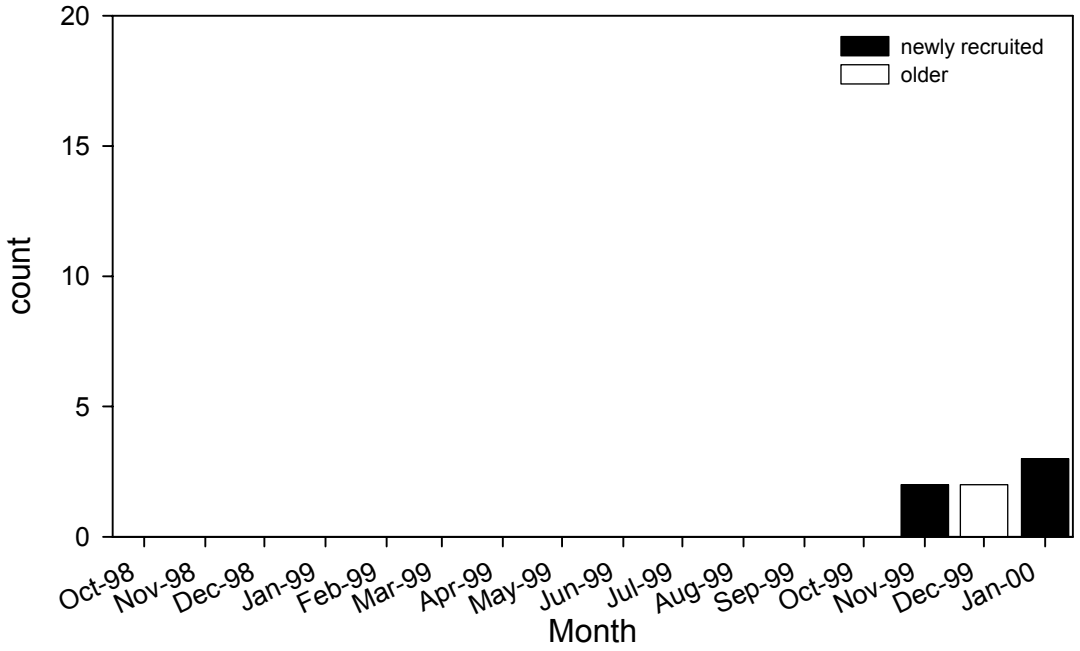


Figure IV-75: Reproductive seasonality: newly recruited juveniles and older juveniles present in hummock V-8.

Juveniles were captured in this hummock only in spring and early summer (November 1999 onwards, Figure IV-75). Recruitment was influenced by a number of environmental factors, the number of juveniles was negatively correlated with the number of nara buds available in the same month (Spearman rank correlation: r_s=-0.791, N=7, $p<0.05$). Furthermore, number of juveniles was positively related to relative humidity (r_s=0.790, N=7. $p<0.05$) and absolute minimum temperature

(Spearman rank correlation: rs=0.790, N=7, p<0.05), in the previous month, and the number of fog days at two months previously (Spearman rank correlation: rs=0.805, N=7, p<0.05). As in the other hummocks, juveniles were being born during the cooler wetter months and during periods with good quality food availability.

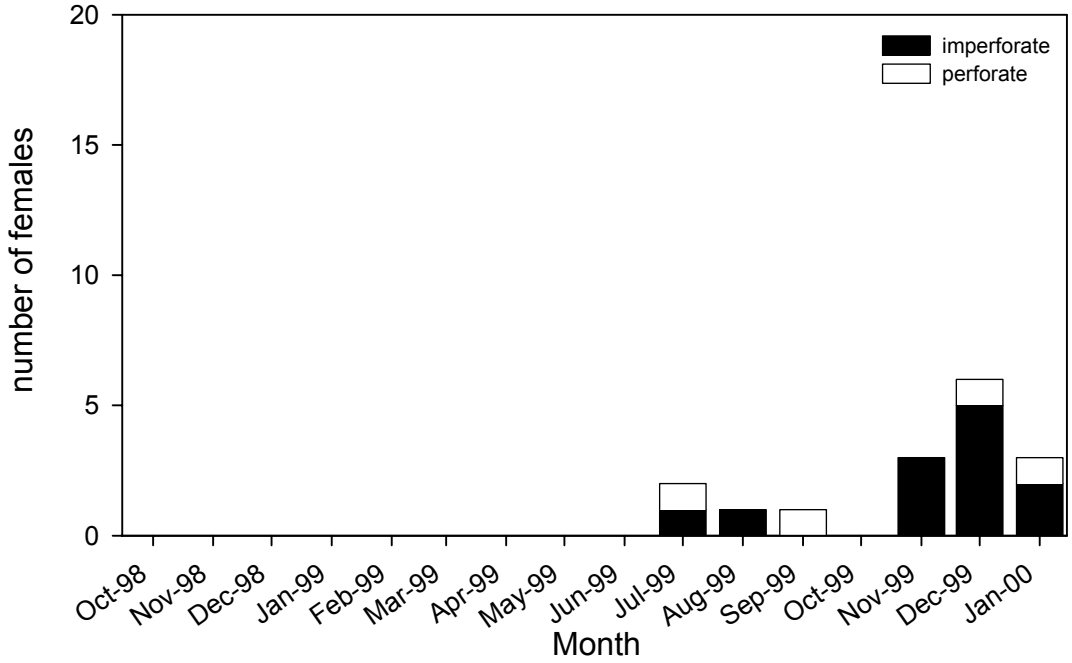


Figure IV-76: Reproductive seasonality: number of perforate and imperforate non-pregnant females in nara hummock V-9.

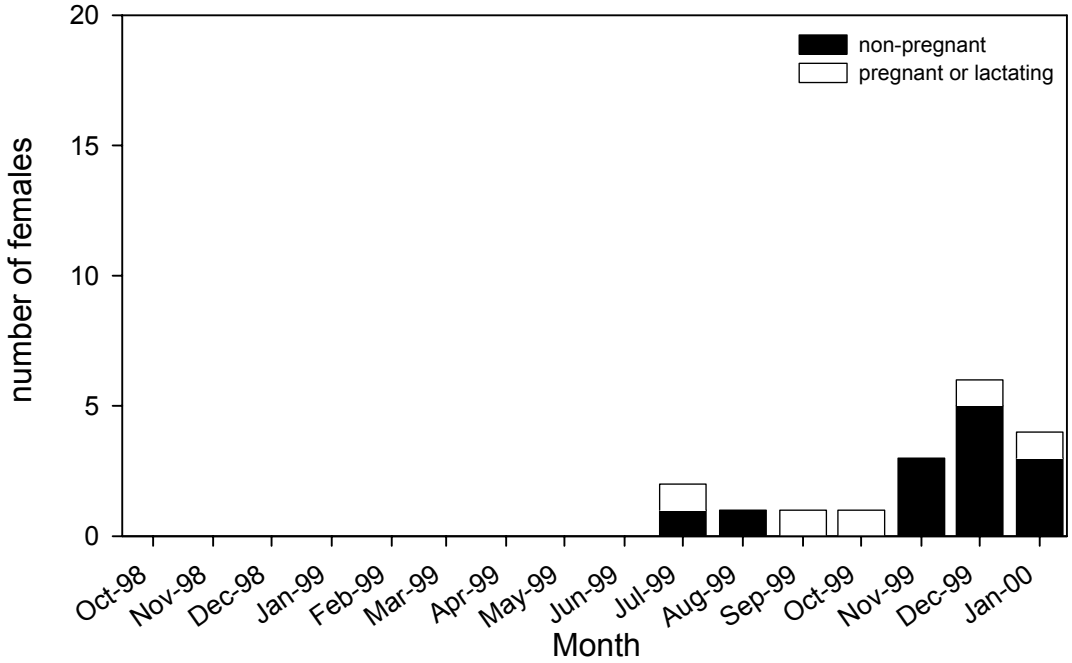


Figure IV-77: Reproductive seasonality: number of non-pregnant and pregnant or lactating females captured in hummock V-9.

As in hummock V-8, females with perforate vaginas were captured in hummock V-9 from the beginning of the trapping in the winter months (Figure IV-76).

Immature females were present in winter and in summer. No relations between the number of perforate females and resource or climatic factors could be found.

Pregnant and/or lactating females were captured in this population from winter through to the summer months (Figure IV-77). Non-pregnant females were found in winter and summer, but not in spring. As with the perforate females, no relation could be found between the number of pregnant and/or lactating females and resource and climatic factors.

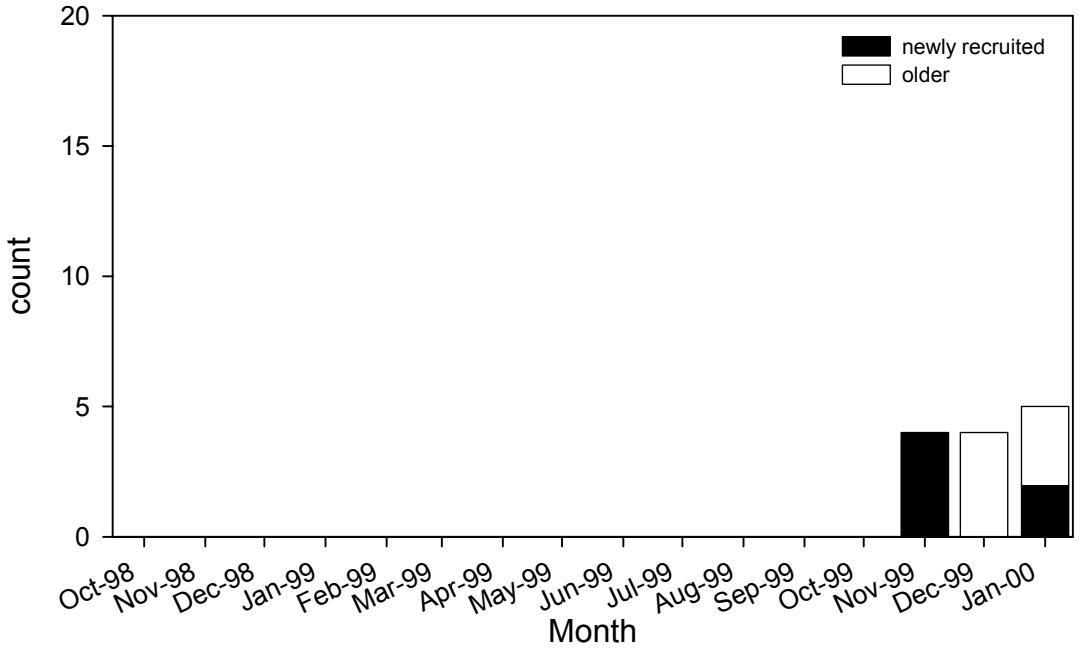


Figure IV-78: Reproductive seasonality: newly recruited juveniles and older juveniles present in hummock V-9.

Juveniles were captured in this hummock during the same period as in hummock V-8, from November 1999 onwards (Figure IV-78). No correlations between juvenile recruitment and environmental factors could be found.

Fecundity

Of 106 adult females captured, only 45 were diagnosed as being pregnant or lactating, and of which only 33 were known to produce offspring. Average litter size in the Namib Desert was estimated at 1.9±0.86 young per litter (N=68), (Table IV-28). The smallest and most often observed litter size was one young per litter, the largest litter size was four young per litter (Figure IV-79). Average number of litters was 2.1±1.54 litters per female (N=33), (Table IV-28). More than fifty percent of the females observed gave birth to two litters; a quarter of the females had only one litter (Figure IV-80). Only six females gave birth to three or more litters.

Hummock	offspring per litter	litters per female	offspring per female	n (females)	n (litters)	n (offspring)
V-1	2.4 ± 0.53	2.5 ± 2.12	6.5 ± 6.36	2	5	13
V-2	2.1 ± 1.08	2.3 ± 1.03	5.5 ± 4.46	6	14	33
V-3	1.9 ± 1.02	1.8 ± 0.83	3.2 ± 1.79	5	9	16
V-4	2.0 ± 0.83	2.2 ± 2.2	4.8 ± 5.26	13	29	63
V-7	2.0 ± 1.0	1.7 ± 0.58	3.3 ± 2.3	3	5	10
V-8	1.2 ± 0.29	1.3 ± 0.58	1.7 ± 1.15	3	4	5
V-9	2.5 ± 2.12	2	5	1	2	5
all	1.9 ± 0.86	2.1 ± 1.54	4.4 ± 4.14	33	68	145

Table IV-28: Number of offspring per litter, Number of litters per female and Number of offspring per female for each of the hummocks studied. N=33 females, N=68 litters, N=145 offspring.

Litter size, number of litter per female and number of offspring per female were not significantly different between hummocks (offspring per litter: Kruskal-Wallis test: $H_{6,33}$=3.23, NS; number of litters per female: Kruskal-Wallis test: $H_{6,33}$=3.14, NS; number of offspring per female: Kruskal-Wallis test: $H_{6,33}$=3.33, NS). The number of young per litter did not change significantly over the study period (Kruskal-Wallis test: H17,68=13.85, NS), nevertheless, number of young born to a female was lower in winter (July and August 1999) than in the other months (Figure IV-82).

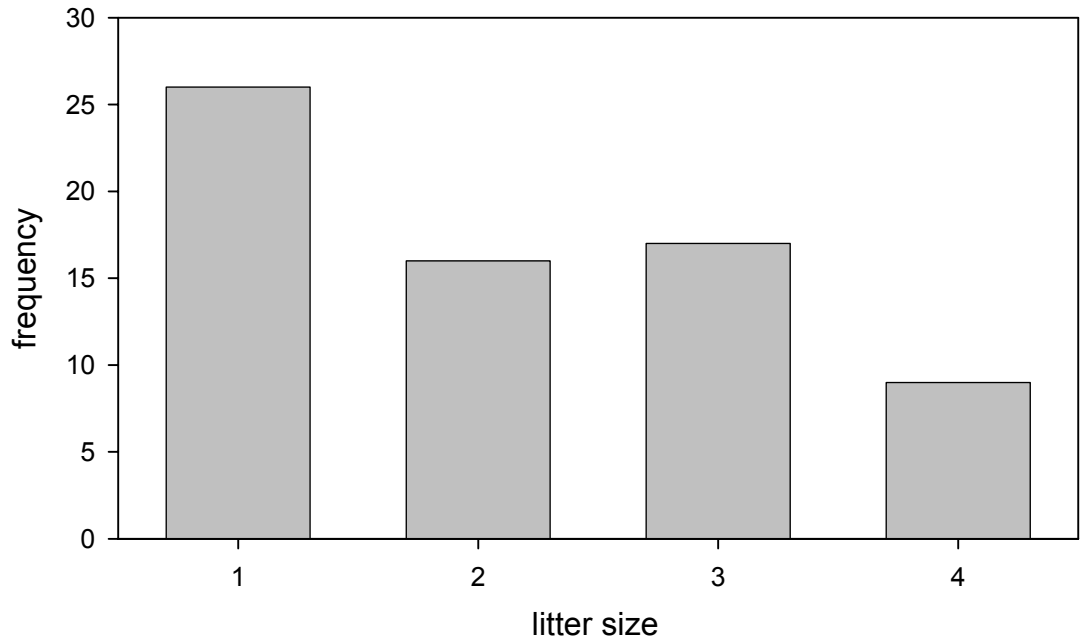


Figure IV-79: Frequency of litter sizes in *Rhabdomys* in the Namib Desert. N=68 litters, data for all hummocks pooled.

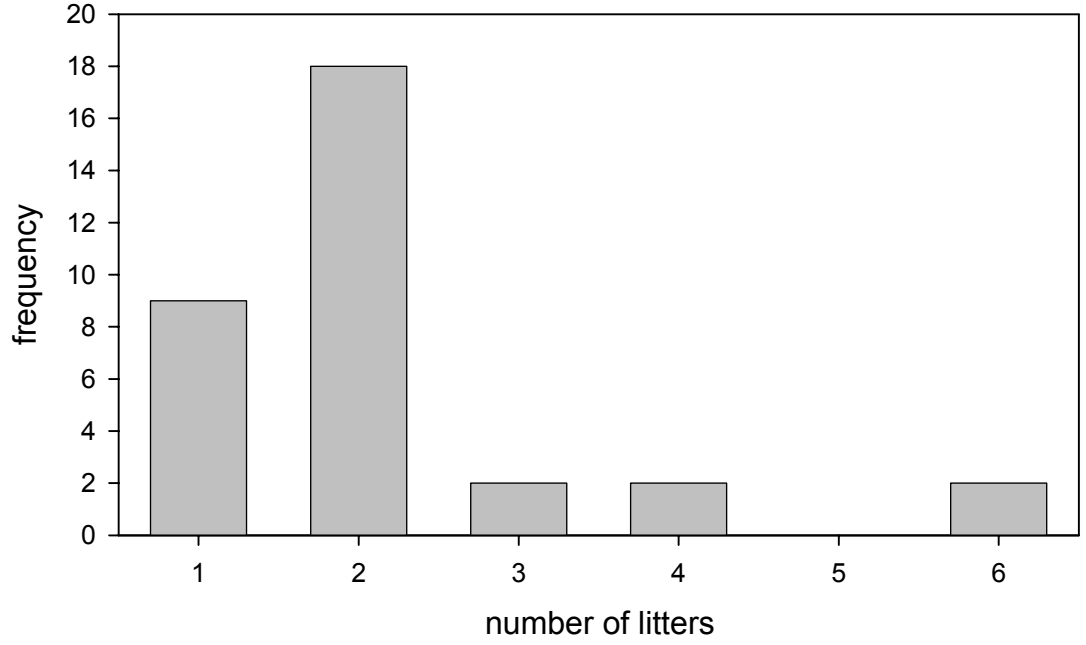


Figure IV-80: Frequency of number of litters per female in Rhabdomys in the Namib Desert. N=33 female, data for all hummocks pooled.

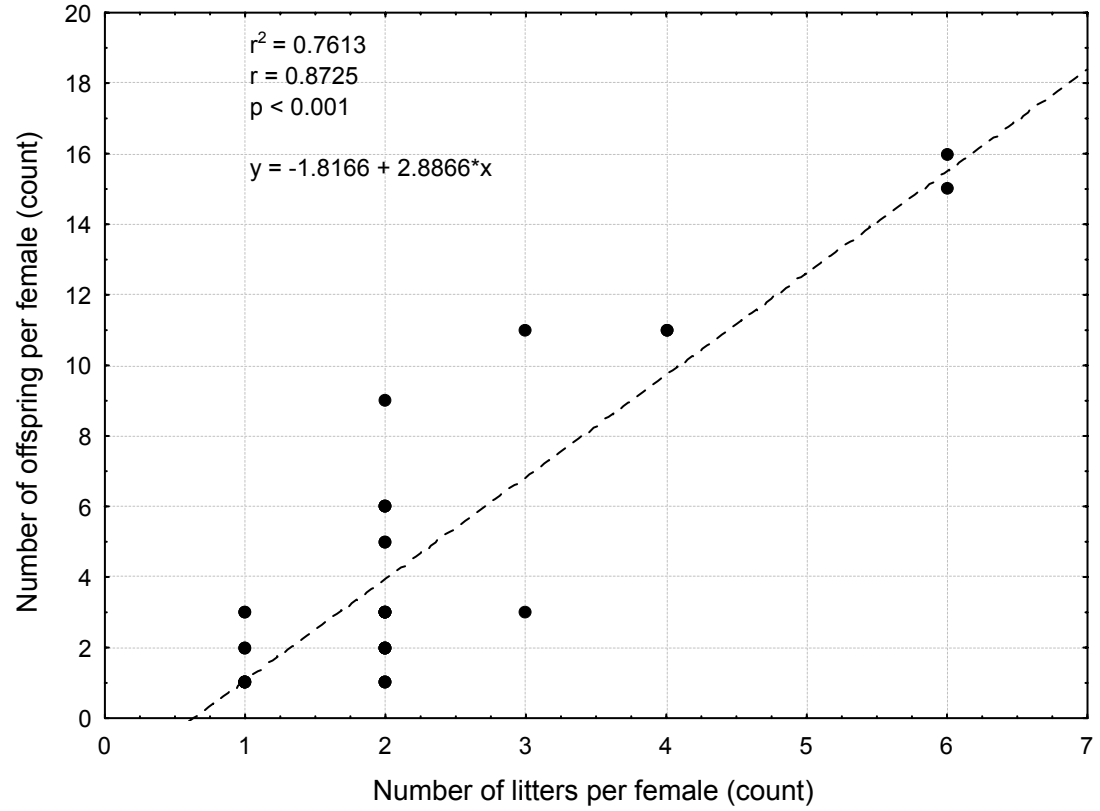


Figure IV-81: Relationship between number of litters and total number of offspring per female (N=33 females).

There was a strong relationship between number of litters per female, and the total number of offspring per female (Figure IV-81), indicating an unequal distribution of reproductive success in the population. Very few female produced a high number of

offspring; most of the females gave birth only to one or two young in their lifetime, but litter sizes were not significantly different between females (Kruskal-Wallis test: $H_{32,68}$=37.87, NS). Thirty-eight percent, i.e. 26 out of the 68 litters observed were conceived in postpartum oestrus. Females with postpartum oestrus were found in all hummocks except for V-7, and there was no significant difference in litter size between litters conceived postpartum and those not (Wilcoxon Matched Pairs Test: T=15.5, N=13, NS). Nevertheless, those females who showed postpartum oestrus generally gave birth to larger litters than those females who showed no postpartum oestrus (Mann-Whitney U-test: U=79.5, N1=20, N2=13, p<0.1).

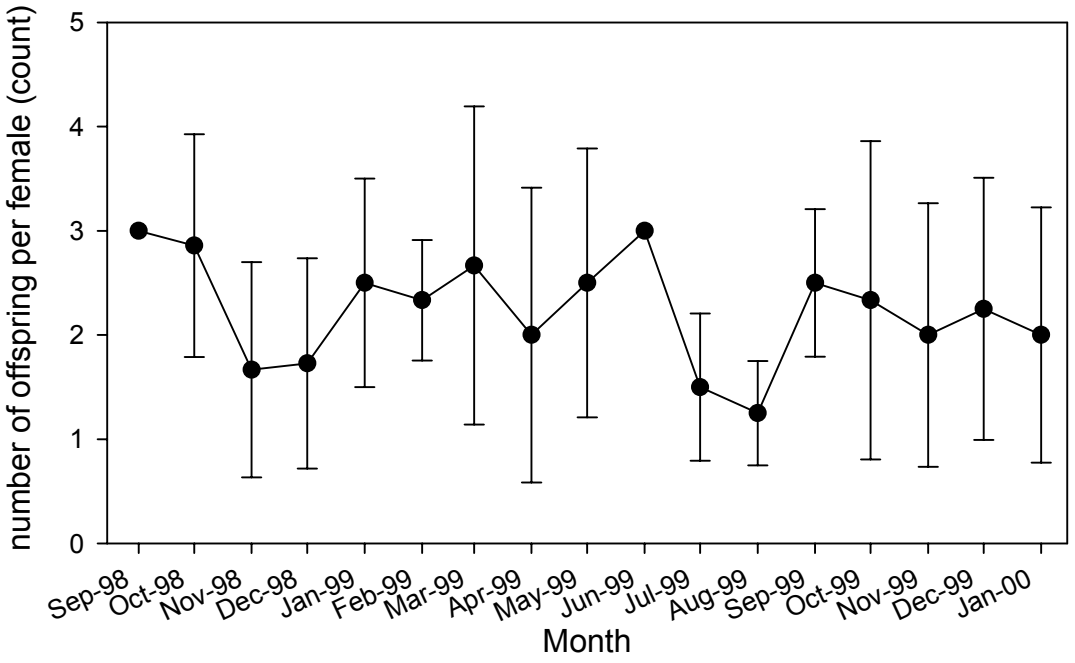


Figure IV-82: Number of offspring born per female over the study period.

Differences in the number of litters and number of offspring produced per female could not be tied to the time span adult females were present in the population. Homerange size also played no role in the size of litters produced, and did not influence the number of litters and total number of offspring per female. Differences in resource availability between the hummocks could also not explain the differences in litter size between females. Food intake seemed to have some impact on litter size; the number of offspring was negatively related to the proportion of nara flowers in the diet of adult females the month prior to the emergence of the litter (Spearman rank correlation: rs=-0.82, N=5, p<0.1). Litter size was also negatively correlated with the proportion of dry plant material in the diet of adult females the previous month (Spearman rank correlation: rs=-0.59, N=11, p<0.1). The single most important factor

influencing litter size in females was the presence or absence of a male. Litter sizes were significantly larger when an adult female shared a homerange with an adult male or both adult male and adult female than when she was alone in the homerange (Kruskal-Wallis test: $H_{3,68}$=8.25, $p<0.05$). Litter sizes were smallest when the adult female shared the homerange with another female (Figure IV-83).

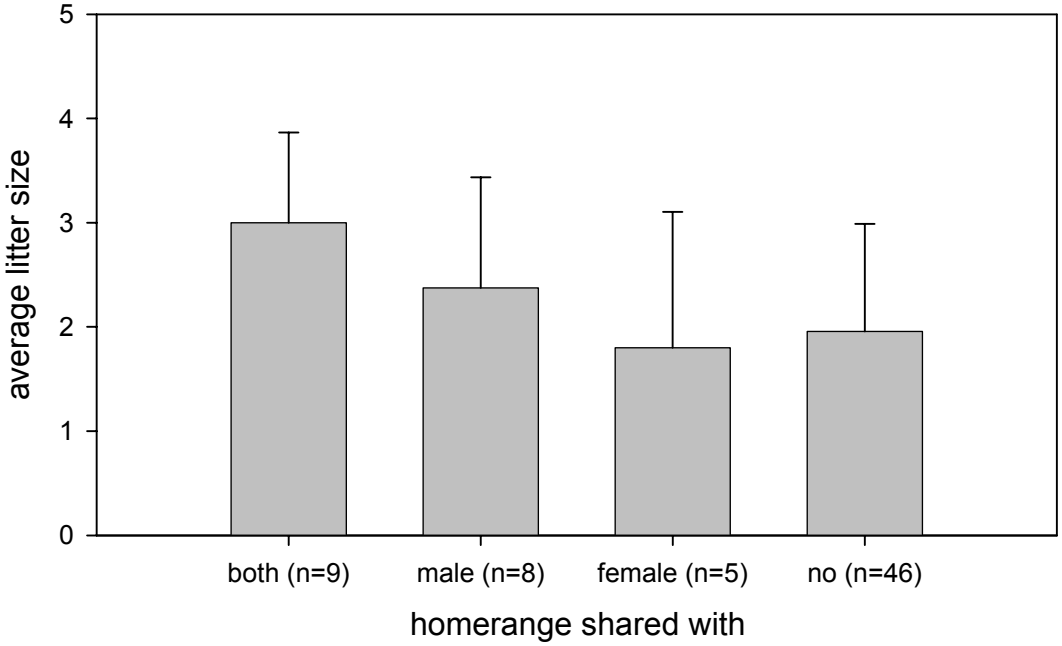


Figure IV-83: Influence of the presence of adult males and adult females in the homerange of the mother on litter size (N=68 litters).

(ii) Behaviour

Parental Behaviour

As occurrences of positive and aggressive interactions with juveniles were rather rare, data for all hummocks were combined to obtain information on parental behaviour. Adult females interacted the most with juveniles, while very few interactions between adult males and juveniles were observed (Figure IV-84). The number of interactions between juveniles was slightly lower than the number of interactions between adult females and juveniles. Adult females displayed significantly more positive than aggressive behaviour towards juveniles (Wilcoxon Matched Pairs test: T=3.0, N=10, $p<0.05$); adult males also displayed more positive than aggressive behaviour, but the difference was not significant (Wilcoxon Matched Pairs test: T=3.5, N=6, NS). Interactions between juveniles were always of a positive nature. The behaviour most often directed at the juveniles was “Sniffing”; the individuals involved touched noses and sniffed at each other.

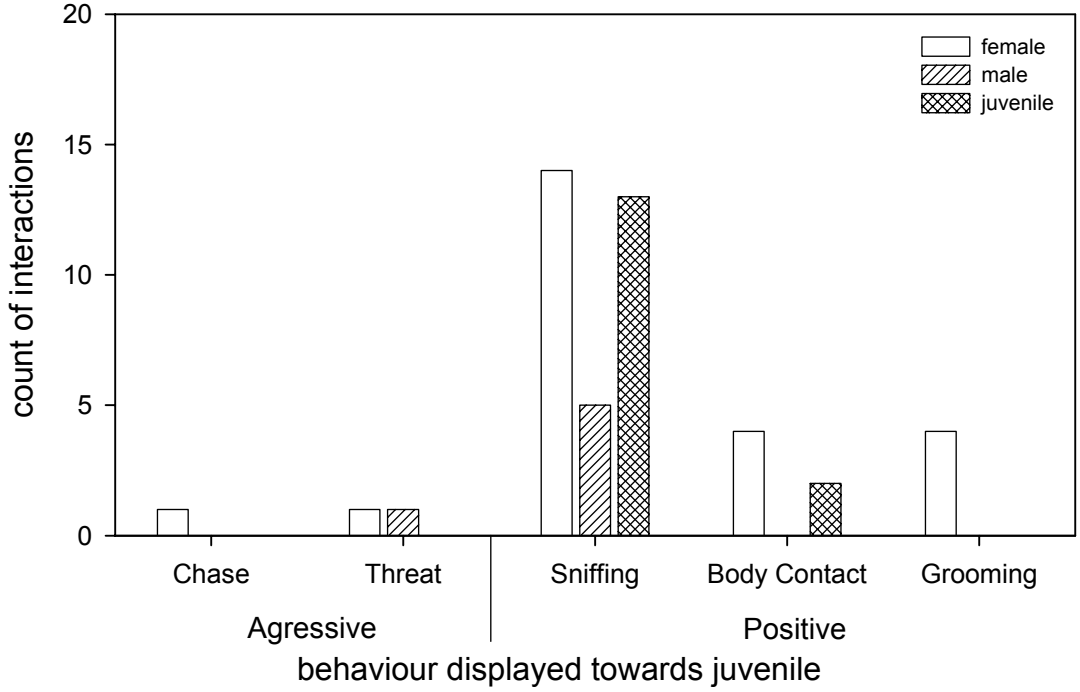


Figure IV-84: Behaviour types displayed by adult females, adult males and juveniles towards juveniles. Data for all hummocks combined.

Observations of juveniles in close proximity of focal individuals were also used as a measure of parental care. In hummock V-1, juveniles were equally often seen close to adult females and juveniles (Figure IV-85), but less often in the proximity of adult males. The differences in events observed were not significant between adult females and males (Mann-Whitney U-test: $U=7.0$, $N_1=4$, $N_2=4$, NS).

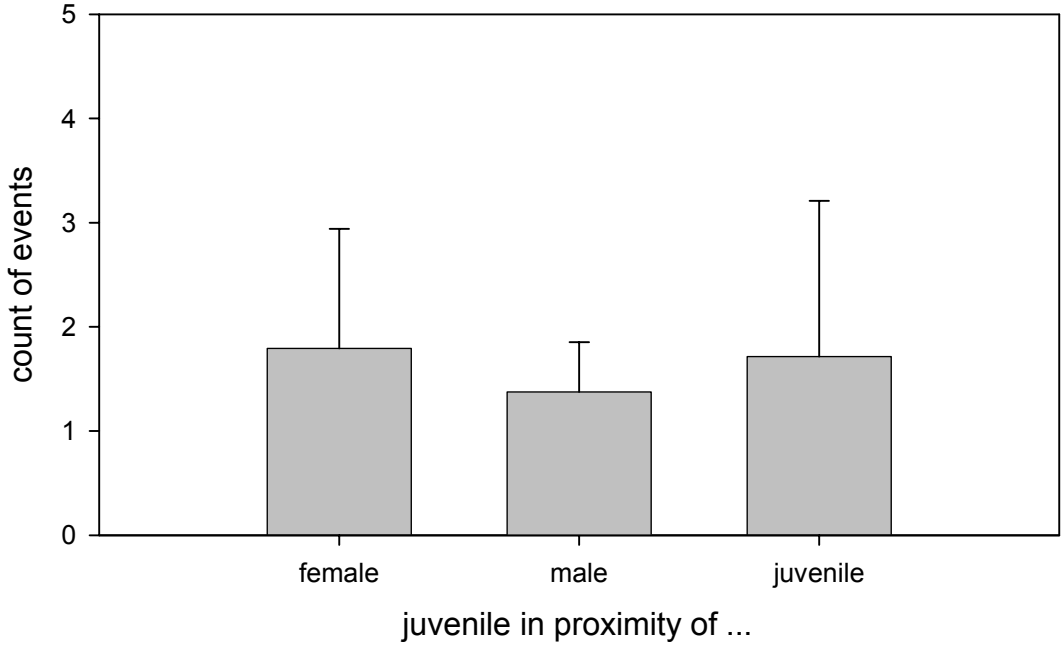


Figure IV-85: Number of times juveniles were observed in close proximity to adult females, adult males and juveniles in hummock V-1.

In hummock V-2, juveniles were most often seen in close proximity to adult females, and nearly as equally often in the proximity of other juveniles (Figure IV-86). As in hummock V-1, juveniles were least often seen in close proximity to adult males. The difference in proximity events between females and males were not significantly different (Mann-Whitney U-test: U=62.0, N_1=16. N_2=8, NS).

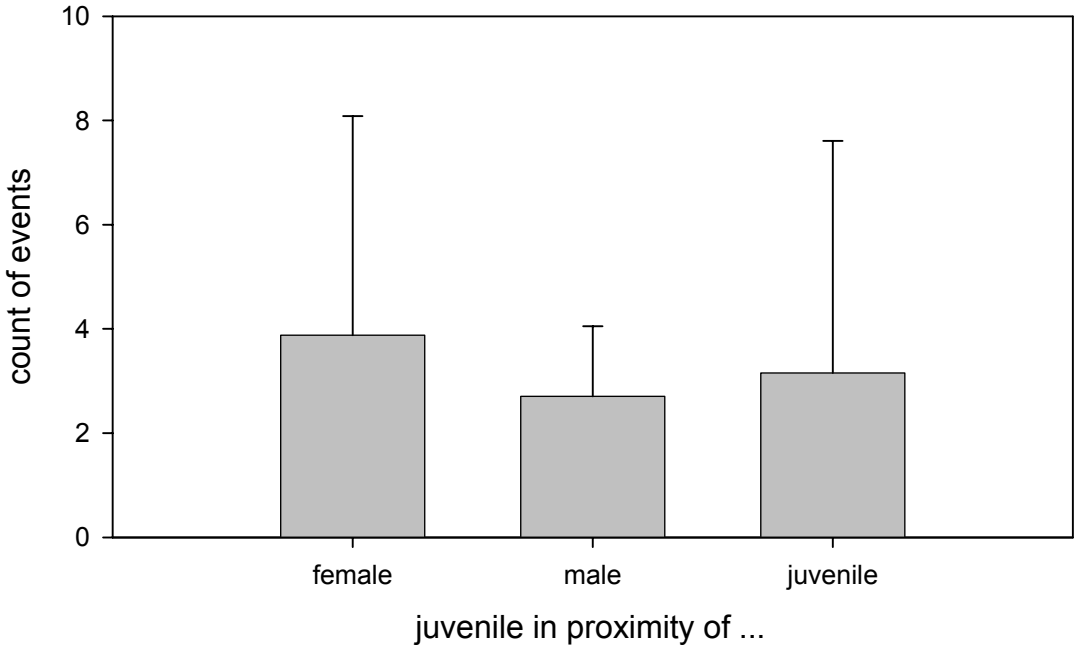


Figure IV-86: Number of times juveniles were observed in close proximity to adult females, adult males and juveniles in hummock V-2

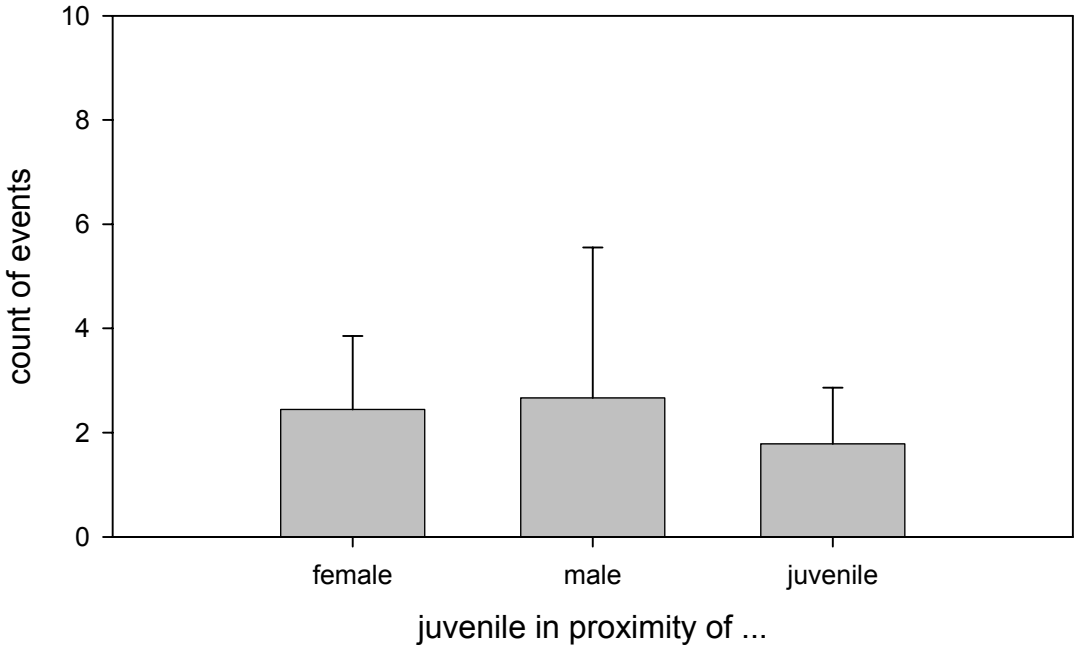


Figure IV-87: Number of times juveniles were observed in close proximity to adult females, adult males and juveniles in hummock V-3.

The picture is different for hummock V-3. Juveniles were found to be most often in the proximity of adult males, and next often close to adult females (Figure IV-87). The difference in number of events was not significantly different between males and females (Mann-Whitney U-test: U=8.0, N_1=6, N_2=3, NS). Juveniles were least often seen in the proximity of other juveniles.

As in hummock V-1, juveniles in hummock V-4 were most often observed in close proximity to other juveniles, and less often close to adult females (Figure IV-88). Juveniles were least often observed to be in the proximity of adult males, but differences in number of events between males and females was not significant (Mann-Whitney U-test: U=77.5, N_1=16, N_2=13, NS).

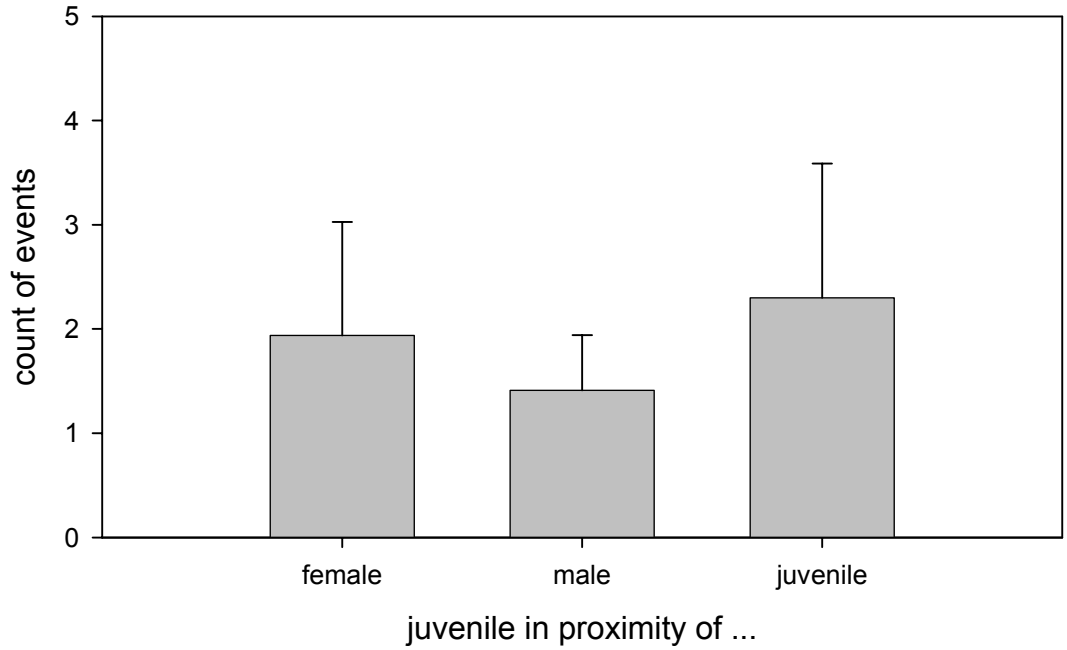


Figure IV-88: Number of times juveniles were observed in close proximity to adult females, adult males and juveniles in hummock V-4.

In hummocks V-1, V-2 and V-4, juveniles were mainly seen in the proximity of, and interacting with adult females and juveniles, presumably siblings. In hummock V-3, juveniles were most often seen in the proximity of males. As males displayed more positive than aggressive behaviour towards juveniles, and juveniles were regularly seen in proximity of males in all hummocks, paternal care can be assumed. Young juveniles were observed interacting with and being in the proximity of not only juveniles of the same age, but also of older, weaned young, which indicated that older offspring also play a role in the care for the newly born litter. In some instances, older offspring of both sexes even stayed in the family territory until they had reached sexual maturity.

Mating / Sexual Behaviour

Mating behaviour could be observed in three cases. In November 1998, male 10 was observed mating with female 4 in hummock V-2, in October 1999, male 204 displayed mating behaviour towards female 171 in hummock V-4, and in January 2000, male 64 was observed displaying mating behaviour towards female 117 in hummock V-1.

In hummock V-1, evidence for the Bruce-Effect and infanticide by a male could be found. At the end of October 1999, the group consisted of three adult females (female 113, female 117 and female 209), and one adult male (32), which, at that stage, was estimated to be 18 months old. A younger male (male 98), approximately 9 months of age, and originating from hummock V-3, joined the group in V-1 three weeks later. Both male 32 and female 209 displayed aggressive behaviour towards the young male, but a week later, the older male had moved to hummock V-3. In the trapping session in the same week, two of these females (113 and 117), were diagnosed pregnant, while the third, female 209 was found lactating. Assuming a gestation period of about 3 weeks (Brooks 1982), it was therefore concluded that female 209 had mated with the old male, male 32, while the other two females had both mated with the new male in the population, male 98.

In early December, another male (male 64), about the same age as male 98, from the neighbouring hummock V-2 moved into V-1, and displayed aggressive behaviour towards male 98. At the same time, female 117 started behaving aggressively towards female 113. Both male 98 and female 113 disappeared shortly afterwards from the hummock and were neither trapped nor observed again. No juveniles were observed in the middle of December, as was expected, as 209 was found lactating at the end of November, assuming weaning after 14 days. It was suspected that male 98 had committed infanticide after male 32 left the group. Live trapping at the end of December revealed that female 209 was highly pregnant again, but no juveniles conceived in November by this female were trapped. The juveniles should have been 4-5 weeks of age at that time. It is therefore highly likely that male 64 mated with female 209 after he drove male 98 away in early December. In the same trapping period, female 117 showed no sign of lactation (the nipples were not enlarged, as was expected, assuming again a 3 week gestation period), but was pregnant again. No juveniles of about three weeks of age were trapped in this trapping session. This was explained with female 117 reacting to the presence of male 64 with aborting her litter

(Bruce-Effect). Subsequently, male 64 mated with this female in mid-December, who was found to be lactating in mid-January 2000. Two 3-week old juveniles were trapped at the end of January, and thought be the offspring of female 117 and male 64. At that time, the group in hummock V-1 consisted of one male, two females and two juveniles. Female 130 of hummock V-2 and her offspring were also using this hummock occasionally.

ii. Social Structure

To establish the social structure of Rhabdomys pumilio in the Namib Desert, only adult focal individuals were regarded, and events of interaction and proximity of the focal individual to other animals were used to establish group sizes.

Average group size in hummock V-1 was 1.3±0.47 adult females, 1.2±0.53 adult males and 1.6±0.53 juveniles (Figure IV-89). During most of the study period, one breeding female and one reproductively active male, formed the nucleus of the group, and juveniles of different ages were the other group members. During winter and early spring, up to two adult females were found in the group. Differences in group size were not significant between months (Kruskal-Wallis-test: $H_{11,40}$=12.53, NS).

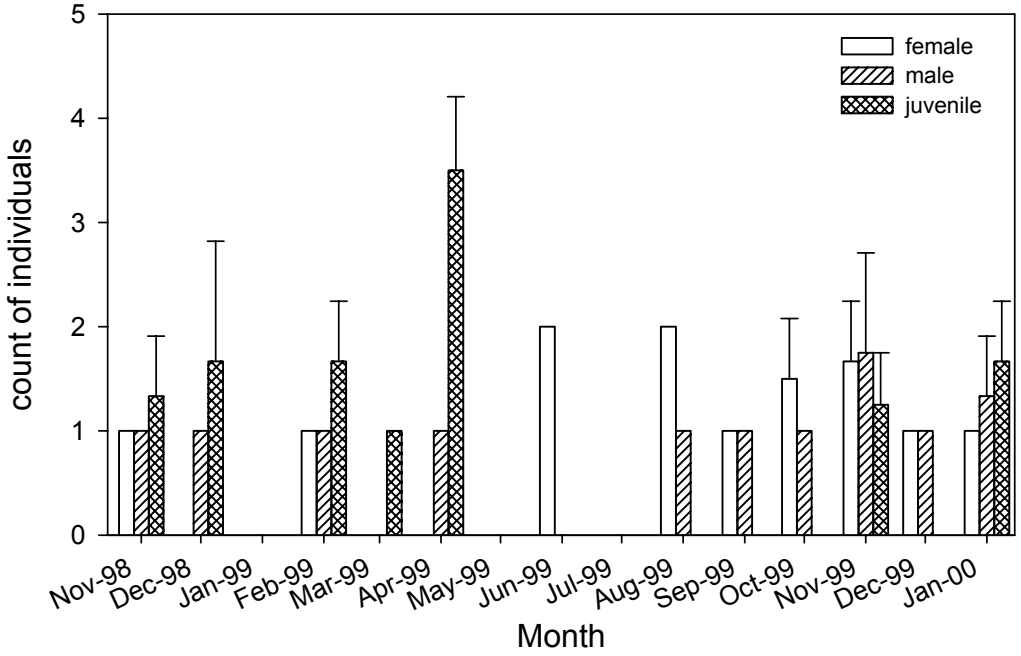


Figure IV-89: Number of adult females, adult males and juveniles per group in hummock V-1.

Adult females were most often observed in proximity to adult males, less often near other adult females, and least often close to juveniles (Figure IV-90). Differences in the number of times the focal animal was seen in proximity to other animals were not significant between classes (adult female, adult male, juvenile) (Kruskal-Wallis test: $H_{2,18}$=0.08, NS). Adult males were most often seen close to other adult males, to adult females, and less often in the proximity of juveniles. The differences in the number of times the focal individual was seen close to other animals were not significant between classes (Kruskal-Wallis test: $H_{2,12}$=2.99, NS). There were no differences in the number of times focal individuals of both sexes were seen in proximity to adult females (Mann-Whitney U test: U=11.0, N_1=6, N_2=5, NS) and adult

males (Mann-Whitney U test: U=8.0, N_1=8, N_2=3, NS). Adult female and adult male focal individuals were also equally often seen near juveniles (Mann-Whitney U test: U=7.5, N_1=4, N_2=4, NS).

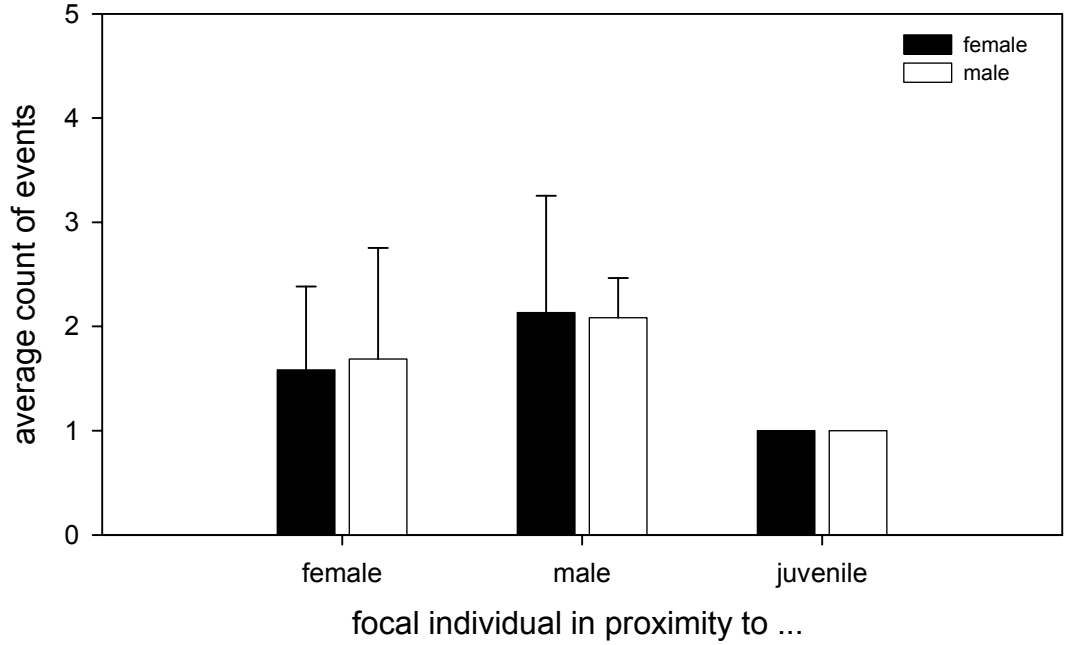


Figure IV-90: Count of events of proximity to focal individual in hummock V-1.

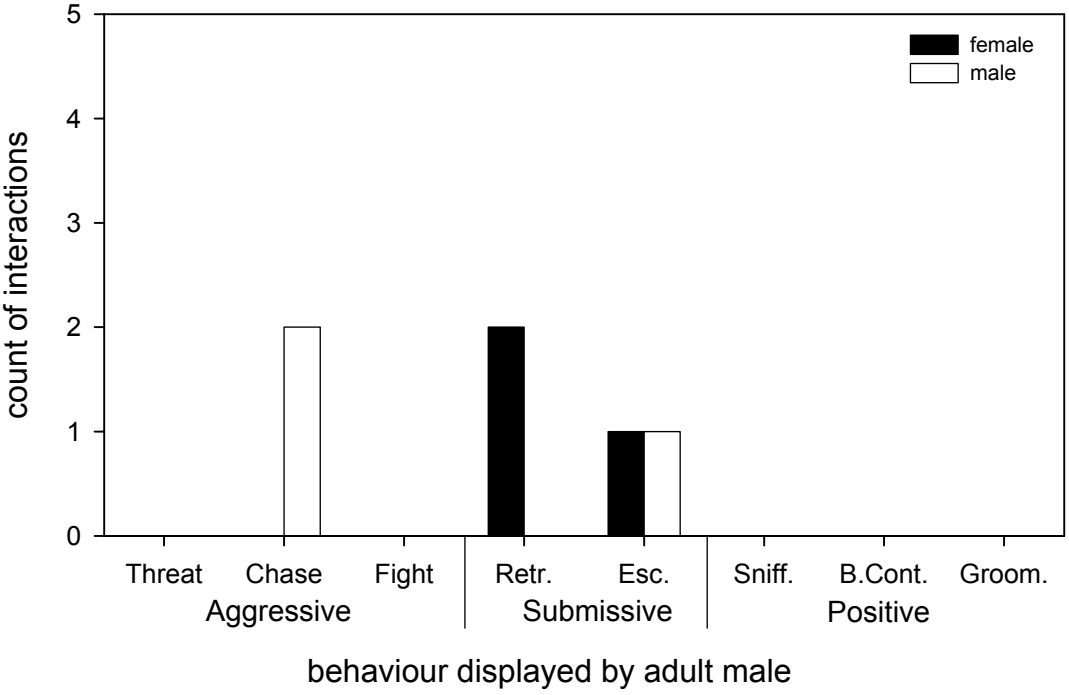


Figure IV-91: Behaviours displayed by adult males (n=2) towards adult females and males in hummock V-1. Retr.: Retreat, Esc.: Escape, Sniff.: Sniffing, B.Cont.: Body Contact, Groom.: Grooming.

Adult females in hummock V-1 displayed only aggressive and submissive behaviours to both adult males and adult females (Figure IV-92). No positive

behaviour was directed at either adult females or adult males. Adult males also were only observed displaying aggressive or submissive behaviour towards adult individuals of both sexes (Figure IV-91). It could not be determined for both males and females whether the differences in behaviour displayed towards the two sexes were significantly different from each other or not.

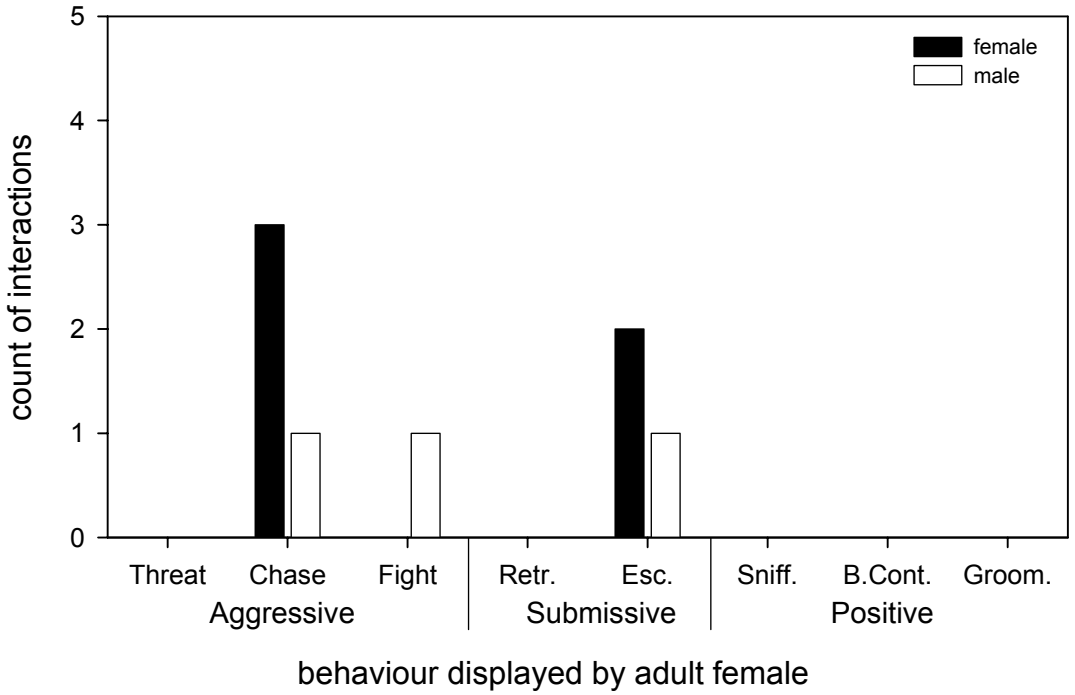


Figure IV-92: Behaviours displayed by adult females (n=3) towards adult females and males in hummock V-1. Retr.: Retreat, Esc.: Escape, Sniff.: Sniffing, B.Cont.: Body Contact, Groom.: Grooming.

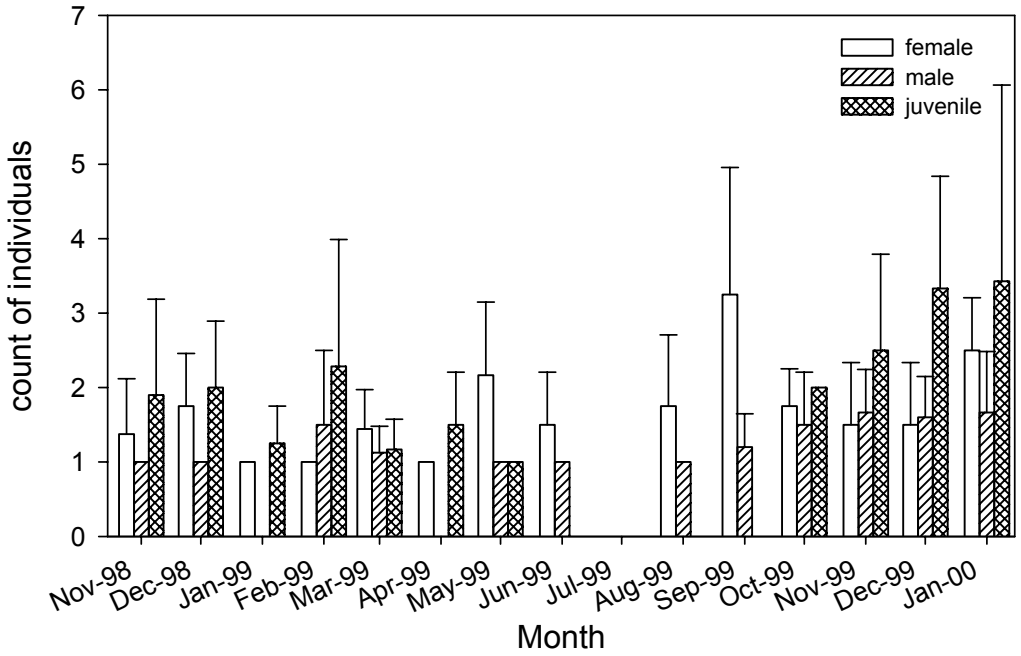


Figure IV-93: Number of adult females, adult males and juveniles per group in hummock V-2.

The average group in hummock V-2 consisted of 1.6±0.87 adult females, 1.4±0.57 adult males and 2.1±1.52 juveniles (Figure IV-93). As in hummock V-1, one reproductively active male and one to two sexually mature females formed the group nucleus, and offspring of various ages, some of them already sexually mature, were the other group members. Group size is significantly larger in the second half of the study period (Kruskal-Wallis test: $H_{14,97}$=22.82, p<0.1), mainly due to the fact that more offspring are born into the groups, and the number of adult females increased

Adult females were most often seen in the proximity of adult males, nearly as equally often close to adult females, and least often to juveniles (Figure IV-94). Differences in the number of times the focal animal was seen in proximity to other animals were not significant between classes (Kruskal-Wallis test: $H_{2,45}$=0.73, NS). Adult males were most often observed being near adult females, and less often seen in the proximity of other adult males and juveniles. The differences in the number of times adult males were seen close to other individuals were not significant between classes (Kruskal-Wallis test: $H_{2,26}$=0.68, NS). Adult female and adult male focal individuals were equally often seen in the proximity of adult females (Mann-Whitney U test: U=54.5, N_1=15, N_2=10, NS) and in the proximity of males (Mann-Whitney U test: U=52.0, N_1=14, N_2=8, NS). In contrast to this, adult female focal individuals were more often seen close to juveniles than adult male focal individuals (Mann-Whitney U test: U=34.5, N_1=16, N_2=8, p<0.1)

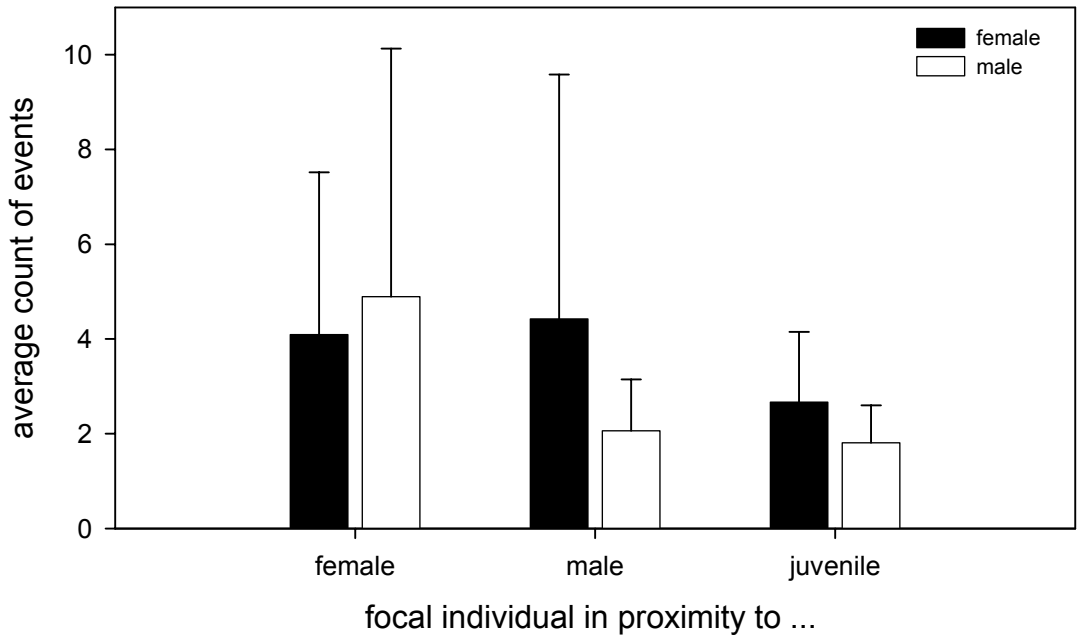


Figure IV-94: Number of times a focal animal was seen in proximity to another individual in hummock V-2.

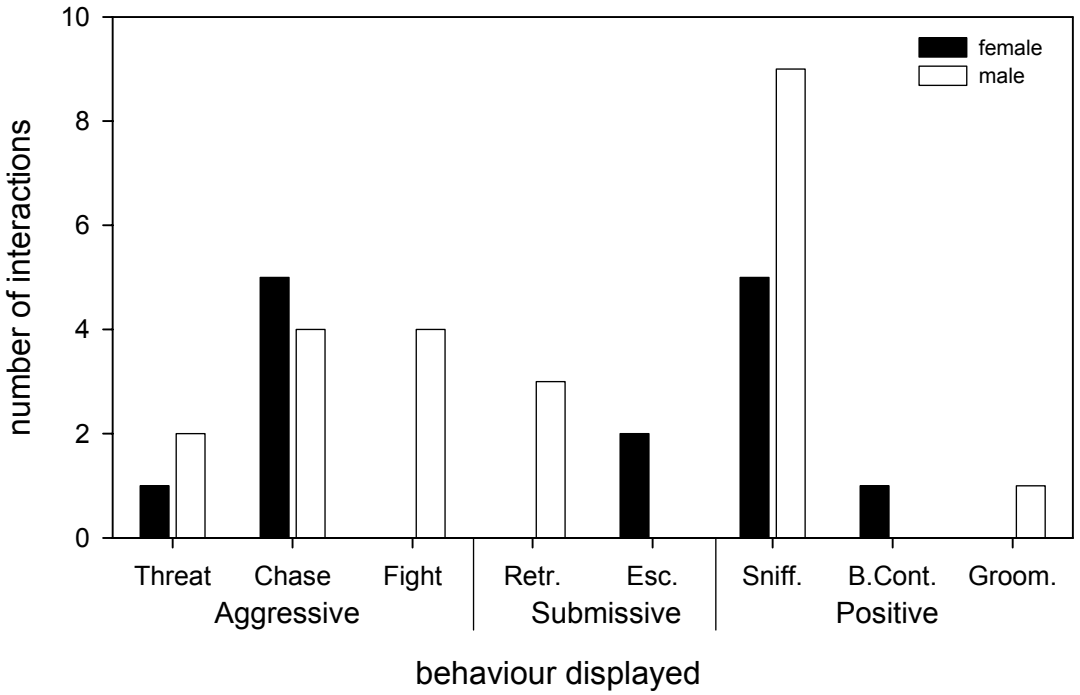


Figure IV-95: Behaviours displayed by adult females (n=7) towards adult females and males in hummock V-2. Retr.: Retreat, Esc.: Escape, Sniff.: Sniffing, B.Cont.: Body Contact, Groom.: Grooming.

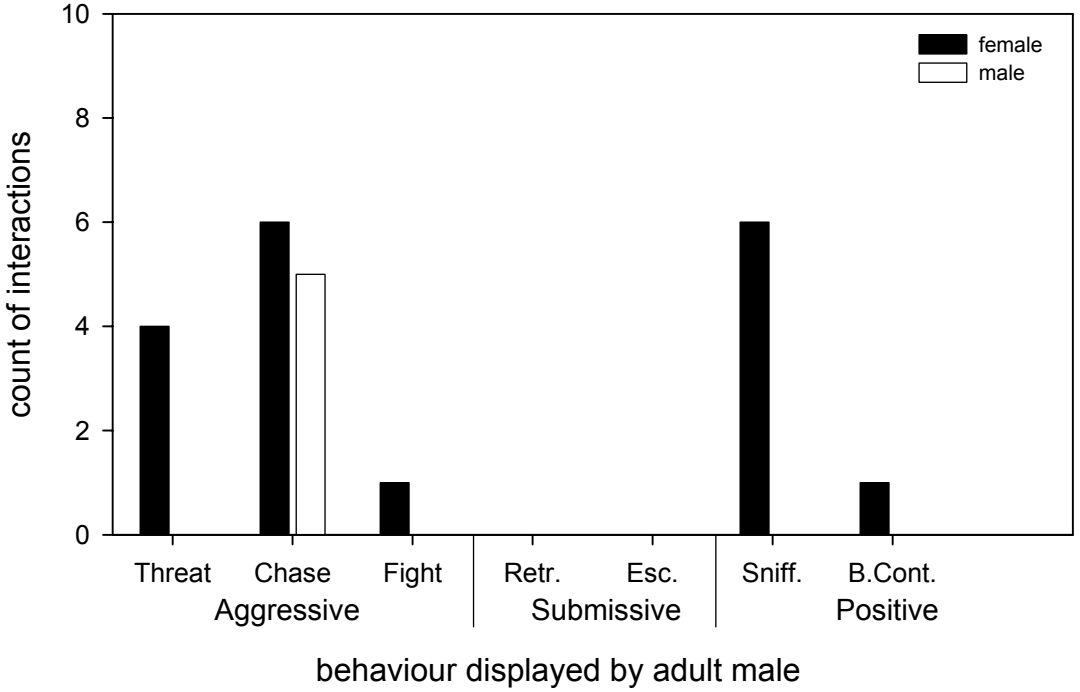


Figure IV-96: Behaviours displayed by adult males (n=6) towards adult females and males in hummock V-2. Retr.: Retreat, Esc.: Escape, Sniff.: Sniffing, B.Cont.: Body Contact, Groom.: Grooming.

Adult females were equally likely to display all three behaviour types (aggressive, submissive, positive) towards other adult females (Figure IV-95). The differences in the number of events between behaviour types were not significant (Friedman ANOVA: $\chi^2_{2,7}$=2.35, NS). Similarly, adult females also displayed all three behaviour types towards adult males, and the differences in number of events were not significant between behaviour types (Friedman ANOVA: $\chi^2_{2,7}$=4.33, NS).

In contrast to adult females, adult males did not display any submissive behaviour, neither towards other adult males, nor towards adult females (Figure IV-96). Adult males were equally likely to direct aggressive and positive behaviour at adult females; the differences in number of events between the behaviour types were not significant (Wilcoxon Matched Pairs test: T=7.5, N=6, NS). The adult males observed displayed aggressive behaviour only towards other adult males, no contact behaviour was observed between adult males in this hummock.

Average group size in hummock V-3 was similar to the groups in hummock V-2, and the group consisted of 1.8±1.03 adult females, 1.2±0.40 adult males and 1.3±0.58 juveniles (Figure IV-97). One adult male in breeding condition as well as one or two sexually mature females formed the basis of the group, other group members were offspring of various ages. The number of adult females in the group increased in winter and spring, but the change in group size was not significant between months (Kruskal-Wallis test: $H_{9,41}$=10.29, NS).

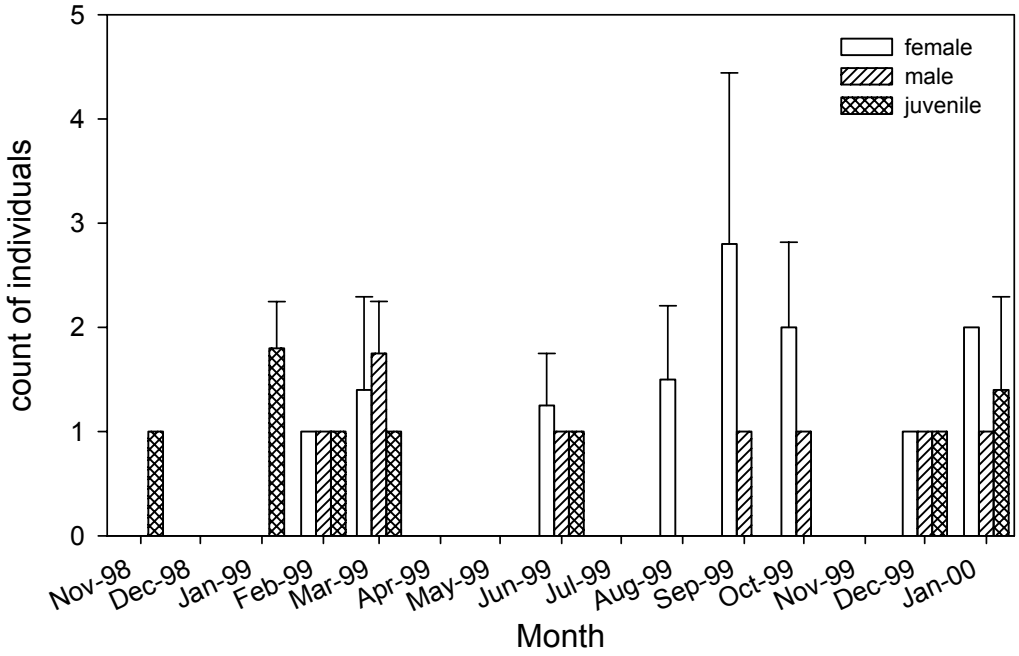


Figure IV-97: Number of adult females, adult males and juveniles per group in hummock V-3.

Adult females in hummock V-3 were most frequently observed being close to other adult females (Figure IV-98). They were equally often in proximity of adult males and near juveniles. The differences in the number of times adult females were seen close to other individuals were not significant between classes (Kruskal-Wallis test: $H_{2,18}$=0.12, NS). Adult males were also regularly observed in proximity to adult females, but were less often seen near other adult males, and rarely close to juveniles. Differences in the number of times the focal animal was seen in proximity to other animals were not significant between classes (Kruskal-Wallis test: $H_{2,11}$=0.00, NS). Both adult female and adult male focal individuals were equally often seen in proximity of either adult females (Mann-Whitney U test: U=11.0, N_1=7, N_2=4, NS), or adult males (Mann-Whitney U test: U=9.0, N_1=5, N_2=4, NS). There were also no difference in the number of times focal individuals of both sexes were observed close to juveniles (Mann-Whitney U test: U=7.0, N_1=6, N_2=3, NS).

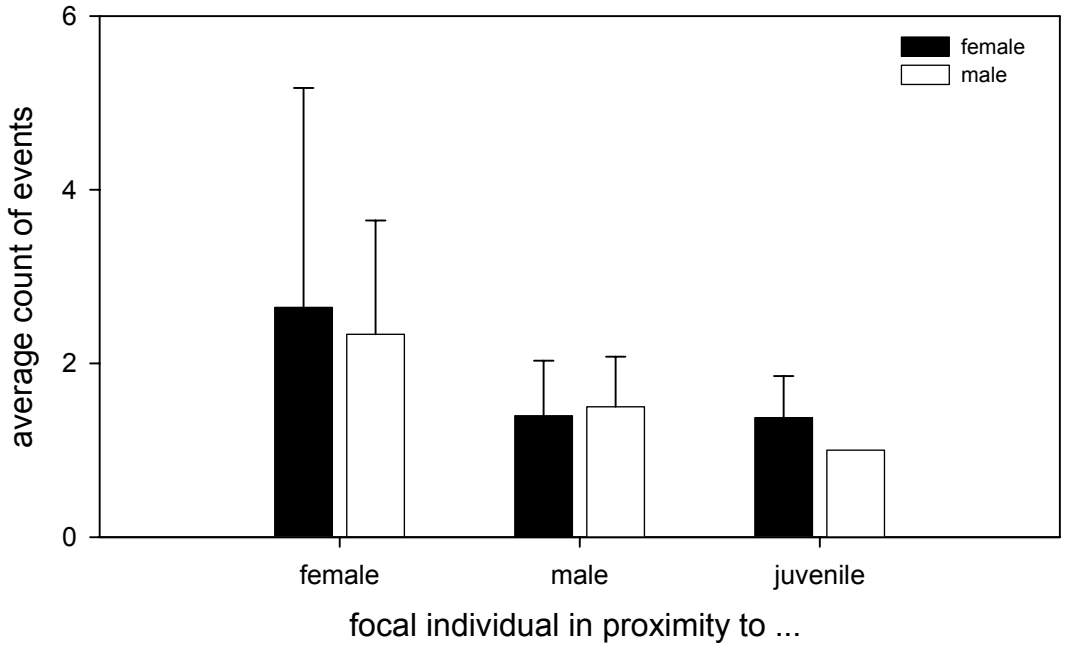


Figure IV-98: Number of times a focal animal was seen in proximity to another individual in hummock V-3.

In hummock V-3, adult females mainly displayed submissive behaviour towards other females (Figure IV-99), aggressive and positive behaviour bouts were more rare. These differences in the number of events were not significant between behaviour types (Friedman ANOVA: $\chi^2_{2,4}$=1.08, NS). Only one event of positive behaviour, sniffing, towards an adult male could be observed. No interactions between adult males and adult individuals of both sexes could be observed in this hummock.

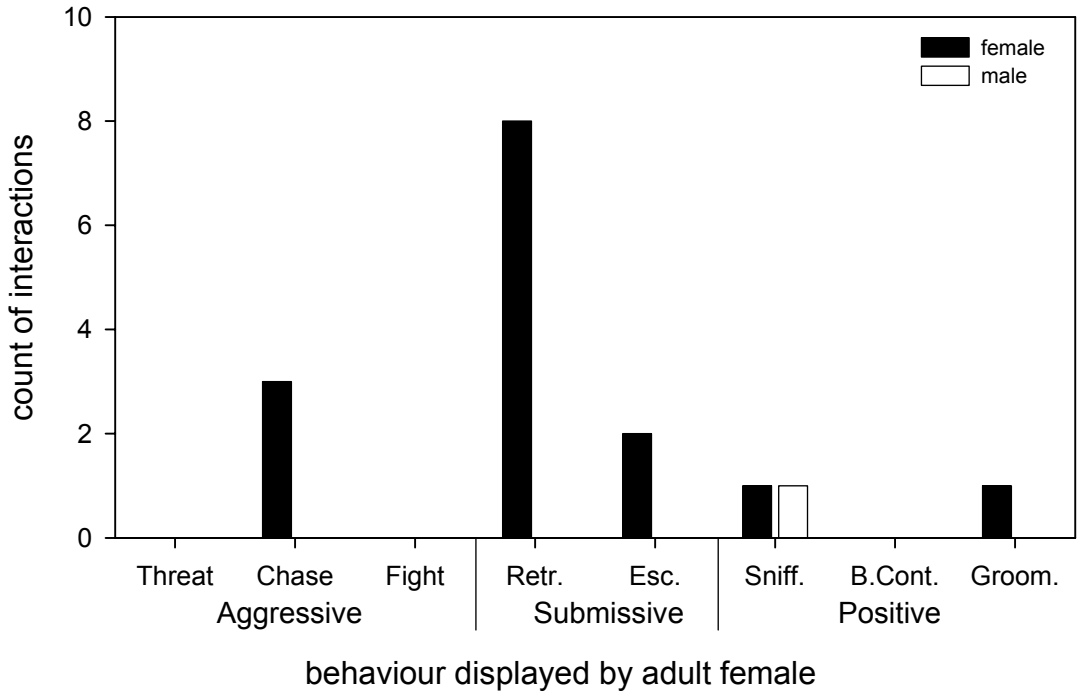


Figure IV-99: Behaviours displayed by adult females (n=4) towards adult females and males in hummock V-3. Retr.: Retreat, Esc.: Escape, Sniff.: Sniffing, B.Cont.: Body Contact, Groom.: Grooming.

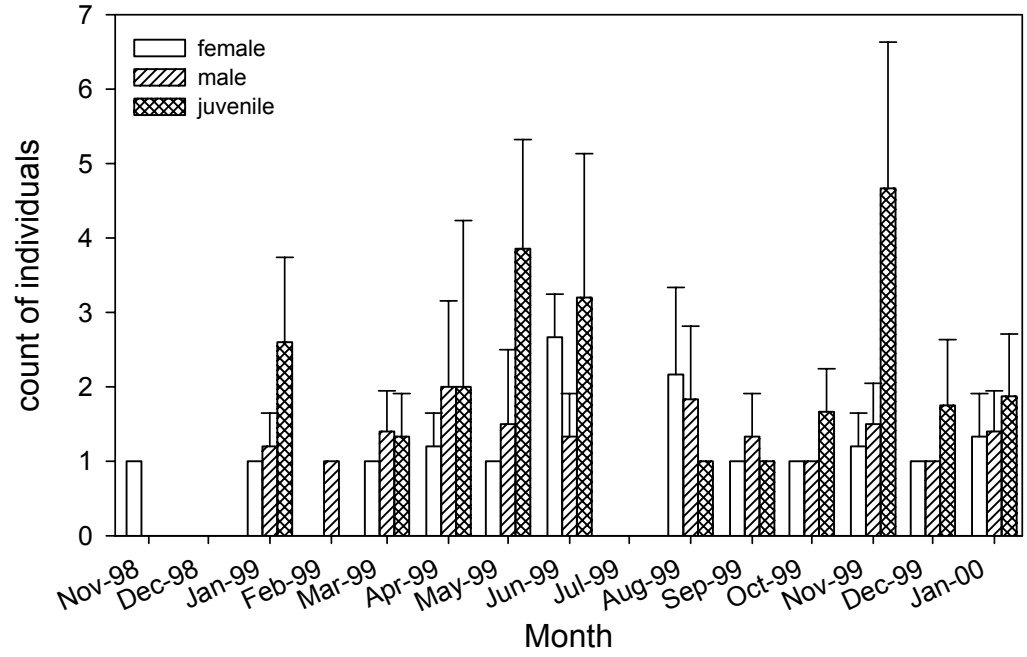


Figure IV-100: Number of adult females, adult males and juveniles per group in hummock V-4.

The average group in hummock V-4 consisted of 1.4±0.76 adult females, 1.4±0.69 adult males and 2.5±1.74 juveniles. Again, one reproductively active male and one breeding female were the nucleus of the group, with offspring of various ages being the other group members. During winter (May – August 1999), group sizes were

significantly larger, mainly due to the increase in number of juveniles and females in the groups (Kruskal-Wallis test: $H_{12,78}$=21.35, $p<0.05$).

In hummock V-4, adult females were most frequently seen in proximity of adult males, and they were less often observed close to other adult females and juveniles (Figure IV-101). The differences in the number of times adult females were seen close to other individuals were not significant between classes (Kruskal-Wallis test: $H_{2,32}$=0.85, NS). Adult males were more often seen near juveniles, and less frequently close to adult females and males. The differences in the number of times adult males were seen close to other individuals were not significant between classes (Kruskal-Wallis test: $H_{2,34}$=0.09, NS). Both adult female and adult male focal individuals were equally often seen in the proximity of adult females (Mann-Whitney U test: U=29.0, N_1=7, N_2=10, NS), and in the proximity of adult males (Mann-Whitney U test: U=46.5, N_1=9, N_2=11, NS). Both sexes were also equally often observed to be close to juveniles (Mann-Whitney U test: U=85.5, N_1=16, N_2=13, NS).

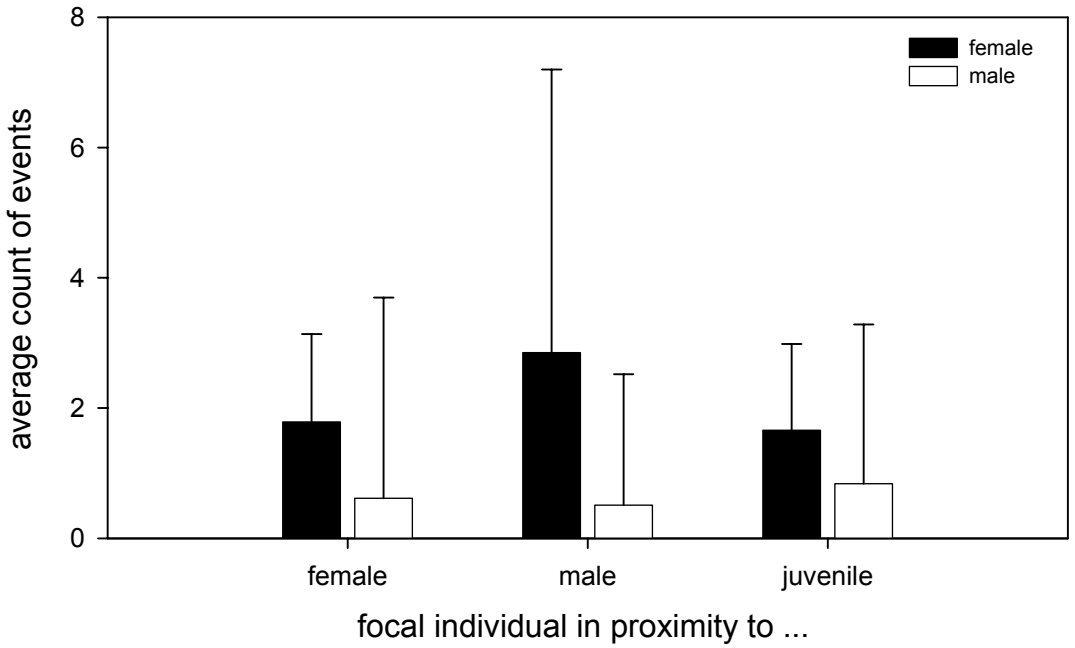


Figure IV-101: Number of times a focal animal was seen in proximity to another individual in hummock V-4.

In contrast to hummock V-3, adult females in hummock V-4 were only observed displaying aggressive behaviour towards adult individuals of both sexes (Figure IV-102). Adult males displayed mainly aggressive behaviour towards adult females, and more positive than aggressive behaviour towards adult males (Figure IV-103). These differences in the number of events were not significant between behaviour

types (towards adult females: Wilcoxon Matched Pairs test: T=0.0, N=5, NS; towards adult males: Wilcoxon Matched Pairs test: T=6.0, N=6, NS).

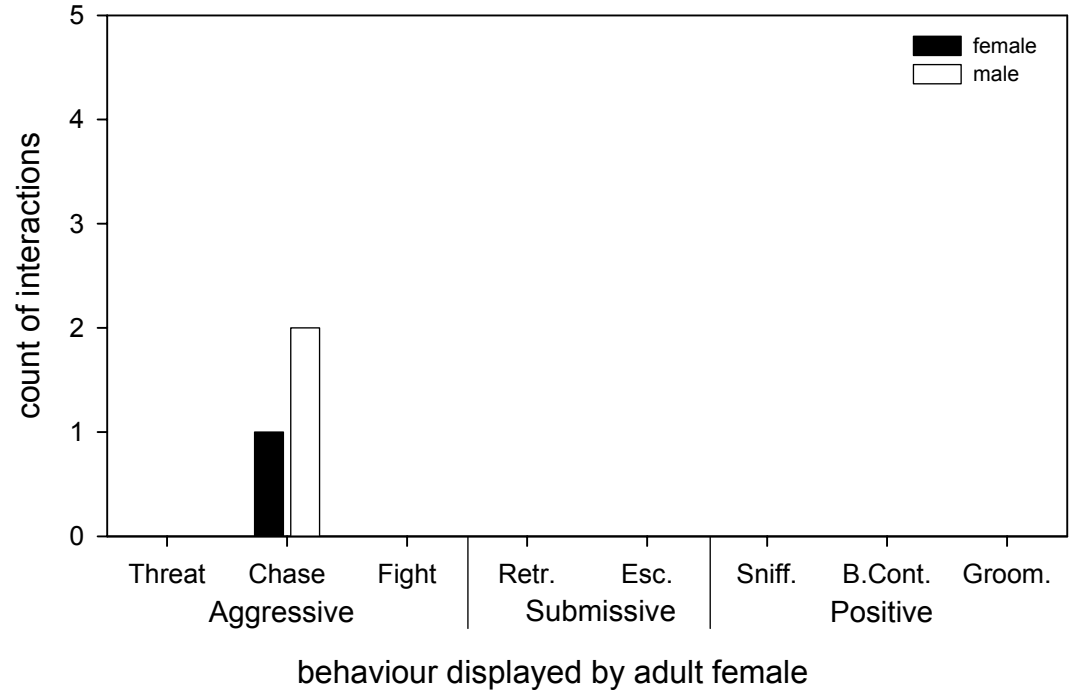


Figure IV-102: Behaviours displayed by adult females (n=2) towards adult females and males in hummock V-4. Retr.: Retreat, Esc.: Escape, Sniff.: Sniffing, B.Cont.: Body Contact, Groom.: Grooming.

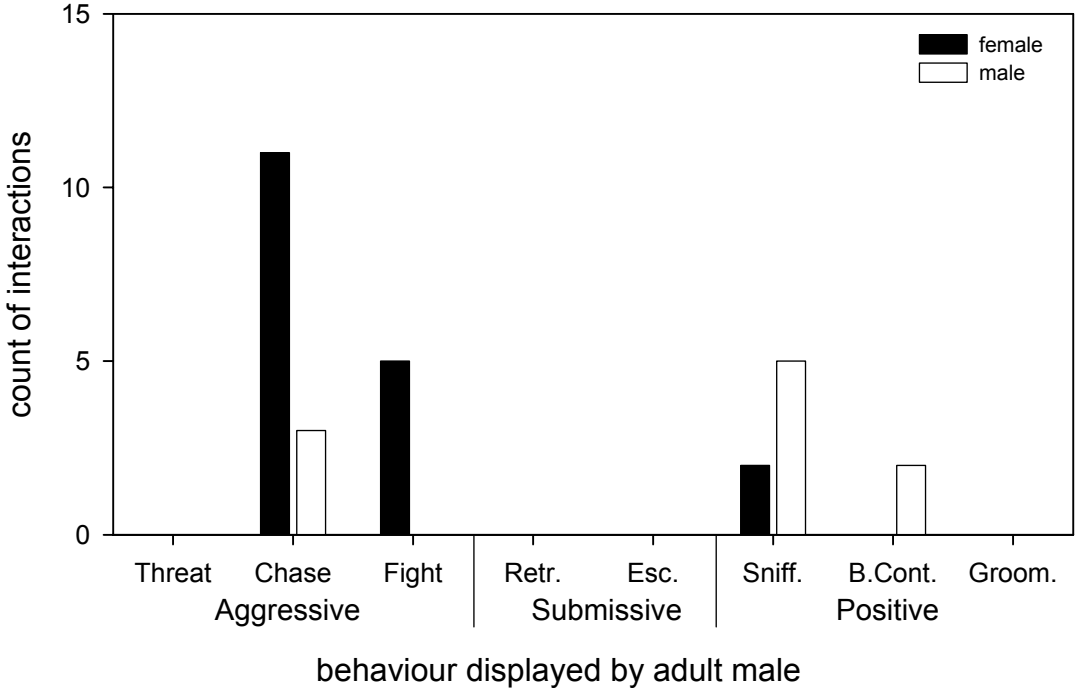


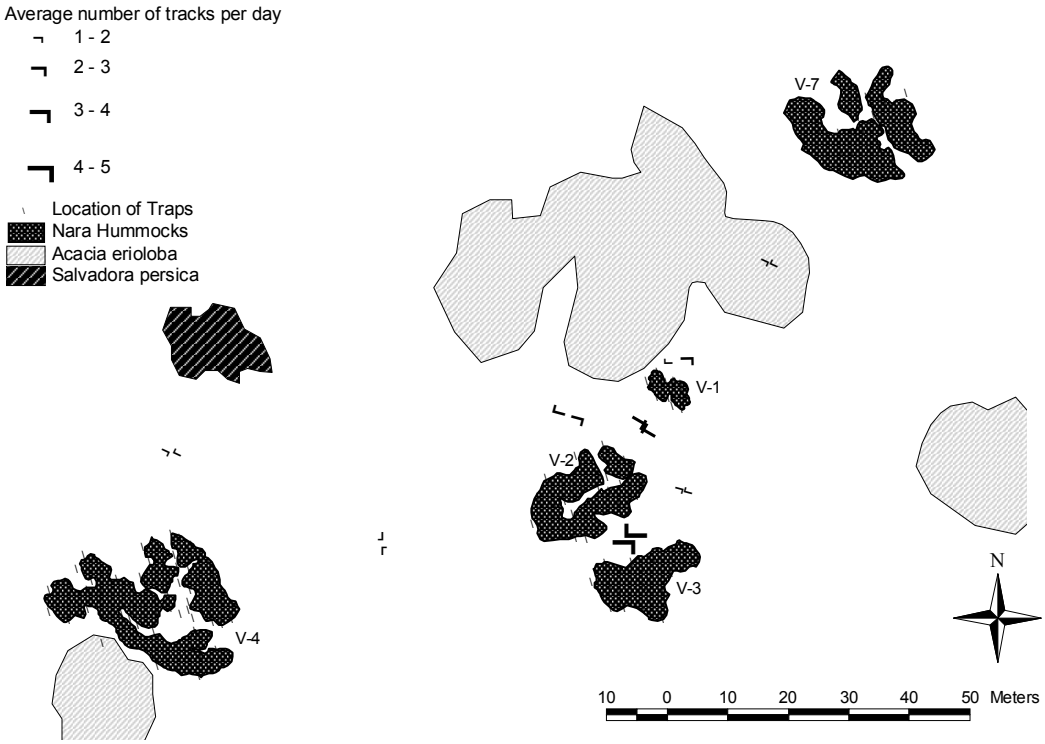
Figure IV-103: Behaviours displayed by adult males (n=10) towards adult females and males in hummock V-4. Retr.: Retreat, Esc.: Escape, Sniff.: Sniffing, B.Cont.: Body Contact, Groom.: Grooming.

Average group size in hummocks V-2 and V-4 are significantly larger than in hummocks V-1 and V-3 (Kruskal-Wallis test: $H_{3,256}$=17.77, $p<0.01$). This is mainly due to the fact that the number of juveniles per group is significantly higher in these hummocks (Kruskal-Wallis test: $H_{3,165}$=9.84, $p<0.05$), and the number of females is increased, but not significantly so (Kruskal-Wallis test: $H_{3,156}$=5.07, NS). There are no significant differences in the number of males per group between the hummocks (Kruskal-Wallis test: $H_{3,130}$=3.89, NS).

iii. Spatial Structure

Tracks

During the observations, it became apparent that individuals left the cover of the nara plants and hummocks rather seldom. If an animal had to leave the cover, it took a straight path towards its destination, either following an established track or runway, or making a new one. These tracks were very visible in the sand, especially if used often, and only disappeared after strong winds. Occurrence of tracks did vary considerably between hummocks, tracks were found most often between hummocks V-2 and V-3, a distance of about 4 metres, (on 64 observation days), and V-1 and V-2, a distance of about 6-7 metres (on 56 observation days). Tracks running between nara hummocks V-2 to V-4, which were about 100 metre apart, were only found on 5 observation days. Average number of tracks running between nara hummock V-2 and V-3 and V-2 and V-1 were significantly higher than the number of tracks found between other locations (Kruskal-Wallis test: $H_{8,157}=26.82$, $p<0.001$, Map IV-1 and Table IV-29).



Map IV-1: Occurrence of *Rhabdomys pumilio* tracks between nara hummocks. Average number of tracks encountered per day observed.

Location	Tracks
V-1 ↔ Acacia	0.15 ± 0.57
V-1 ↔ V-2	2.08 ± 2.28
V-1 ↔ V-3	0.02 ± 0.12
V-1 ↔ V-7	0.03 ± 0.14
V-2 ↔ Acacia	0.44 ± 1.29
V-2 ↔ V-3	2.54 ± 2.51
V-2 ↔ V-4	0.06 ± 0.29
V-4 ↔ Salvadora	0.01 ± 0.07

Table IV-29: Average number of tracks per observation day between selected locations at the study site. Means ± SD.

The occurrence of *Rhabdomys* tracks, and with it the movement of animals, showed only little seasonal variance (Figure IV-104).

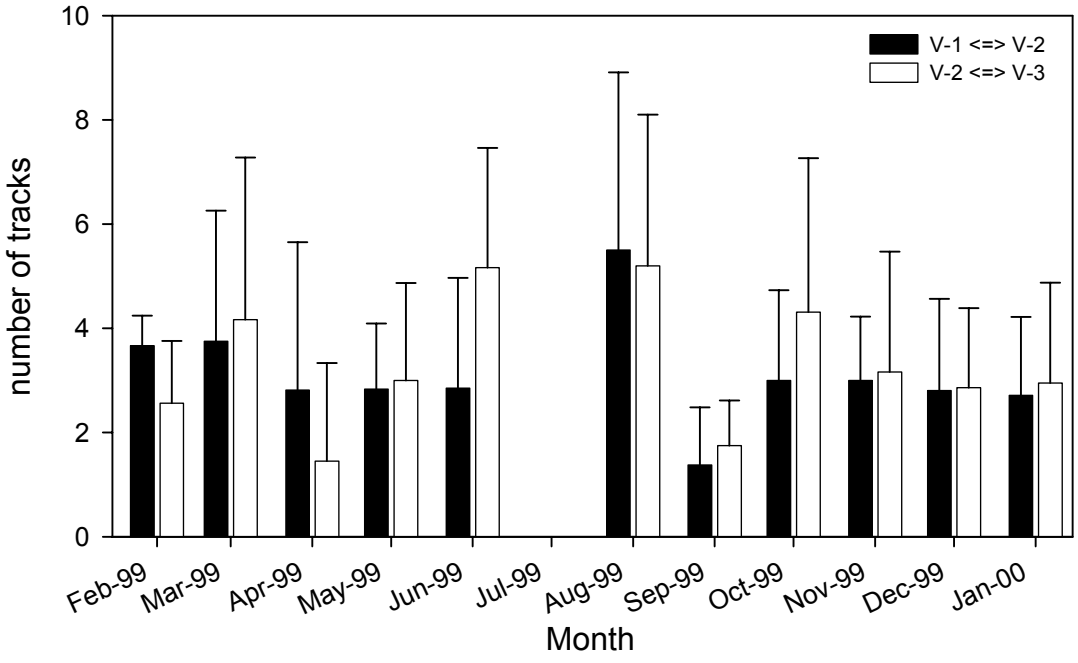


Figure IV-104: Seasonal occurrence of *Rhabdomys pumilio* tracks: Average number of tracks per observation hour between nara hummocks V-1 and V-2, and nara hummocks V-2 and V-3. Means ± SD, no data available for July 1999.

The average number of tracks between nara hummocks V-2 and V-3 was higher during the winter months (June-August) than during the remainder of the year, but not significantly so ($H_{11,64}$=14.42, NS). The individuals inhabiting hummock V-3 regularly moved into the neighbouring hummock V-2 to feed during the daily activity period. This happened mainly winter months and towards the end of the study period, when one of the females in V-3 had young. After feeding, the animals always moved back into the hummock they came from, minimising the time spent in V-2. Movement

between hummocks V-1 and V-2 showed a peak in August 1999, otherwise, regular movement between hummocks took place (Kruskal-Wallis test: $H_{11,56}$=11.15, NS). The movement between V-1 and V-2 from October 1999 is due to a shift in homerange of male 64 and female 130 and her offspring, which incorporated part of hummock V-1 into their homerange.

Homeranges

Homerange sizes of female four-striped fieldmice in hummock V-1 did vary between 18.0±7.84 m^2 and 270.9m^2 (Table IV-30), homerange sizes of adult males ranged between 7.2m^2 and 120.5m^2. There were no differences in the homerange size between sexes (Mann-Whitney U test: U=29.0, N_1=7, N_2=10, NS). Although homerange sizes of both sexes did show some seasonal variation, the differences were not significant (Kruskal-Wallis test: $H_{5,17}$=9.65, NS).

Season	female	n	male	n
Oct-Dec98	19.9 ± 10.56	2	104.86	1
Jan-Mar99	18.0 ± 7.84	3	7.2	1
Apr-Jun99			18.6 ± 16.77	2
Jul-Sep99	270.9	1	18.5	1
Oct-Nov99	32.83	1	120.5	1
Dec99-Jan00	155.7 ± 72.82	3	119.9	1

Table IV-30: Average homerange size of adult females and adult males in hummock V-1.

Homerange sizes of individuals living in hummock V-2 were larger than homerange sizes in V-1. Homeranges of adult females ranged from 86.8±94.59m^2 to 191.6±62.86m^2, adult males had homeranges between 50.5±13.52m^2 and 209.1±142.36m^2. Homerange sizes did not differ between sexes (Mann-Whitney U test: U=138.0, N_1=11, N_2=27, NS). The variation in homerange size between seasons was not significant for both adult females and adult males (females: Kruskal-Wallis test: $H_{5,27}$=8.35, NS; males: Kruskal-Wallis test: $H_{5,11}$=5.77, NS).

Season	female	n	male	n
Oct-Dec98	191.6 ± 62.86	5	144	1
Jan-Mar99	173.3 ± 79.55	2	206.1 ± 80.02	2
Apr-Jun99	96.55 ± 75.58	6	209.1 ± 142.36	2
Jul-Sep99	137.7 ± 85.47	5	115.9 ± 54.48	2
Oct-Nov99	86.8 ± 94.59	8	50.5 ± 13.52	2
Dec99-Jan00	230.5	1	151.4 ± 9.74	2

Table IV-31: Average homerange size of adult females and adult males in hummock V-2.

Homeranges in hummock V-3 were again larger than homerange sizes in hummock V-1 and V-2. Adult females had homeranges ranging from 172.8m^2 to 238.6m^2, homeranges of adult males varied in size between 208.1m^2 and 449.6m^2. As in the other hummocks, there were no differences in homerange size between the sexes (Mann-Whitney U test: U=43.0, N_1=7, N_2=13, NS). There was also no significant seasonal variation in homerange size (Kruskal-Wallis test: $H_{5,20}$=2.54, NS).

Season	female	n	male	n
Oct-Dec98	238.6 ± 161.84	3	305.1	1
Jan-Mar99	234.2 ± 16.87	2	208.1	1
Apr-Jun99	312.8 ± 63.09	2	244.1 ± 92.07	3
Jul-Sep99	211.8 ± 153.34	3	225.8	1
Oct-Nov99	283.6	1		
Dec99-Jan00	172.8	2	449.6	1

Table IV-32: Average homerange size of adult females and males in hummock V-3.

Homerange sizes in hummock V-4 were similar to homerange sizes in hummock V-2. Homeranges of adult females varied in size between 152.4m^2 and 261.0±294.28m^2, the homerange sizes of adult males ranged from 131.1±126.54m^2 to 350.9m^2. Again, differences in homerange size between males and females were not significant (Mann-Whitney U test: U=166.0, N_1=18, N_2=19, NS). The variation of homerange size between seasons was also not significant for both sexes (females: Kruskal-Wallis test: $H_{5,19}$=4.94, NS; males: Kruskal-Wallis test: $H_{5,18}$=7.64, NS).

Season	female	n	male	n
Oct-Dec98	261.0 ± 294.28	2	242.9 ± 47.48	3
Jan-Mar99	180.1 ± 27.20	2	152.1 ± 59.81	2
Apr-Jun99	184.7 ± 100.22	5	229.0 ± 105.88	4
Jul-Sep99	218.9 ± 146.91	8	350.9 ± 5.71	2
Oct-Nov99	152.4	1	131.1 ± 126.54	4
Dec99-Jan00	202.5	1	150.4 ± 59.16	3

Table IV-33: Average homerange size of adult females and males in hummock V-4.

Females living in hummocks V-1 and V-2 have significantly smaller homerange sizes than females living in hummocks V-3 and V-4 ($H_{3,69}$=15.34, $p<0.01$). The picture is similar for the homerange sizes of adult males. Those living in hummock V-1 and V-2 have smaller homerange sizes than males inhabiting hummocks V-3 and V-4 (Kruskal-Wallis test: $H_{3,43}$=15.12, $p<0.01$).

As the homerange sizes are rather large compared to the hummock size, homeranges of both males and females overlap to a great degree. Figure IV-105 to Figure IV-116 illustrate the distribution of the homeranges in space. Both the homeranges of adult male and female *R. pumilio* show a high degree of overlap with animals of the same sex as well as the opposite sex. Areas within the nara hummocks that are exclusively used by one individual are very rare.

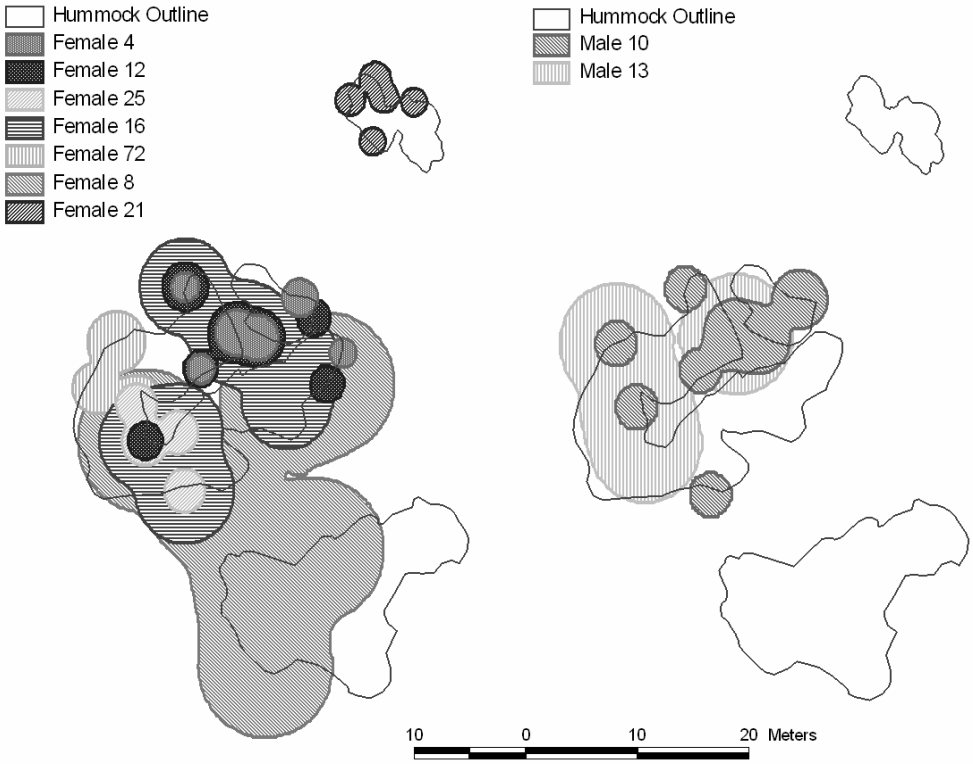


Figure IV-105: Homeranges of female (left) and male (right) *R. pumilio* in hummocks V-1, V-2 and V-3 between October 1998 and December 1998. Data from C-M-R and Observation study combined.

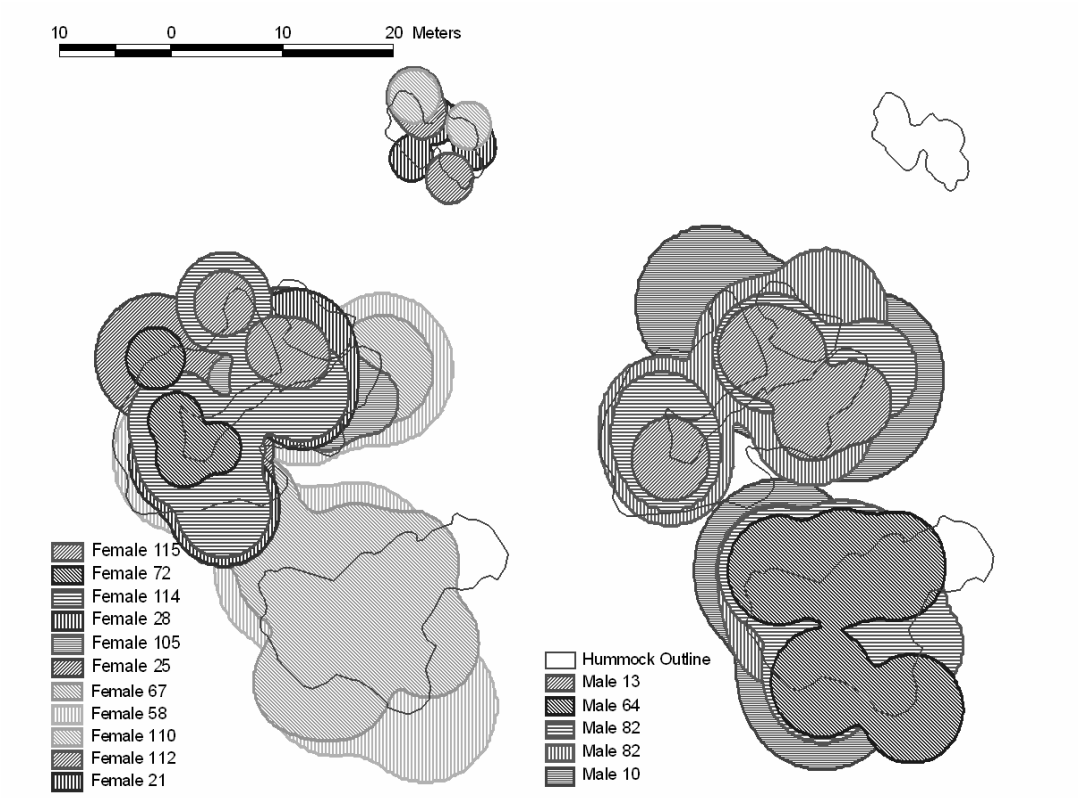


Figure IV-106: Homeranges of female (left) and male (right) *R. pumilio* in hummocks V-1, V-2 and V-3 between January 1999 and March 1999. Data from C-M-R and Observation study combined.

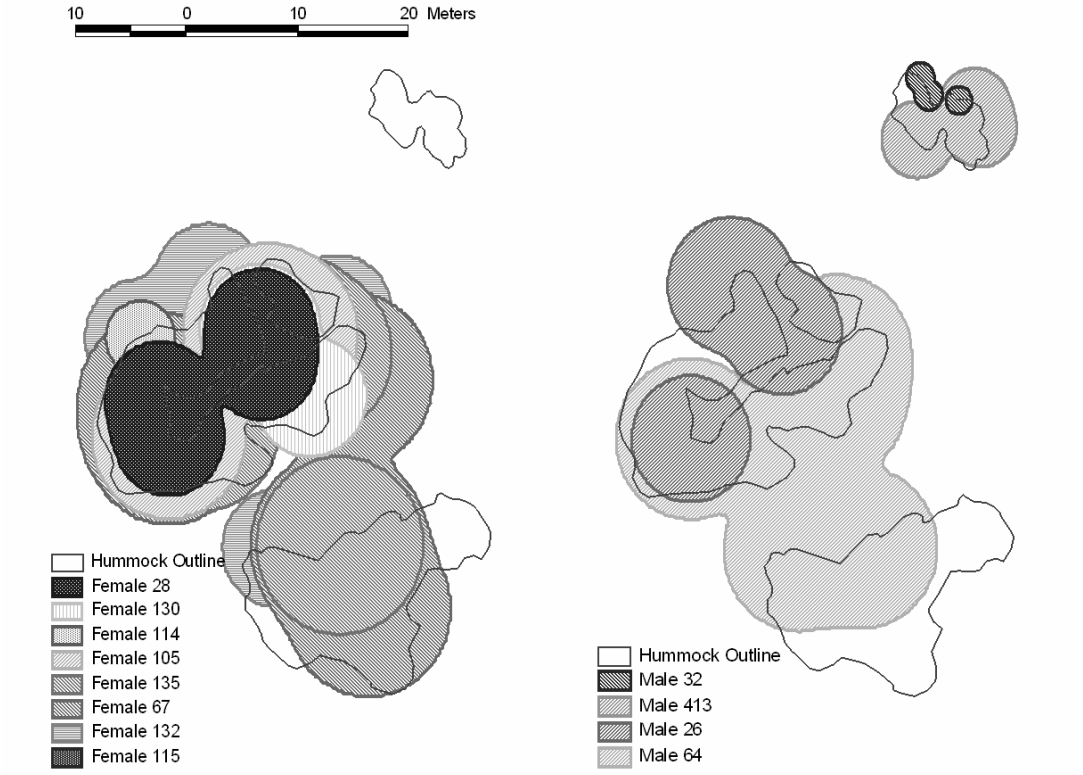


Figure IV-107: Homeranges of female (left) and male (right) *R. pumilio* in hummocks V-1, V-2 and V-3 between April 1999 and June 1999. Data from C-M-R and Observation study combined.

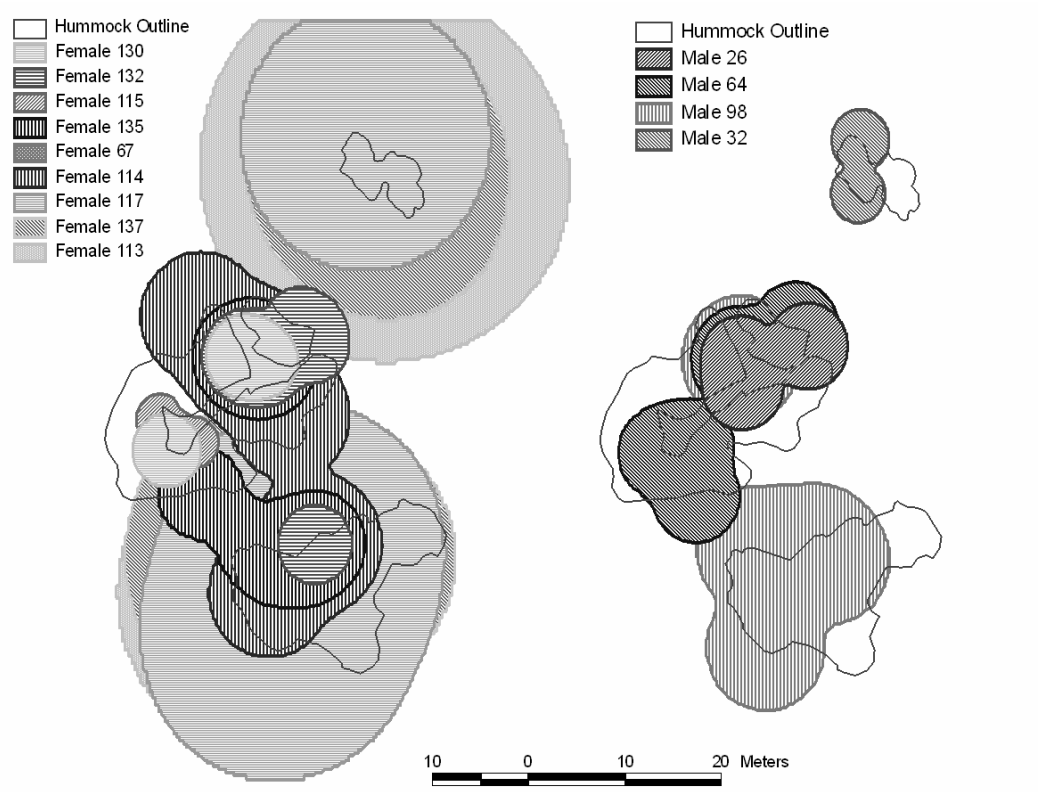


Figure IV-108: Homeranges of female (left) and male (right) *R. pumilio* in hummocks V-1, V-2 and V-3 between July 1999 and September 1999. Data from C-M-R and Observation study combined.

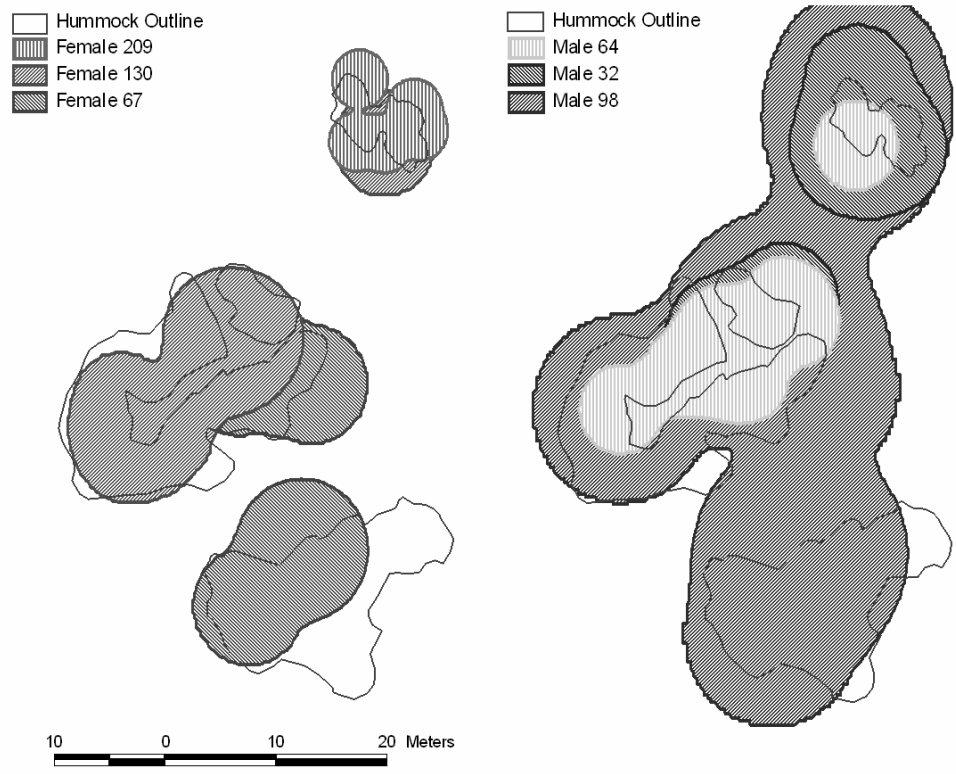


Figure IV-109: Homeranges of female (left) and male (right) *R. pumilio* in hummocks V-1, V-2 and V-3 between October 1999 and November 1999. Data from C-M-R and Observation study combined.

Figure IV-110: Homeranges of female (left) and male (right) *R. pumilio* in hummocks V-1, V-2 and V-3 between December 1999 and January 2000. Data from C-M-R and Observation study combined.

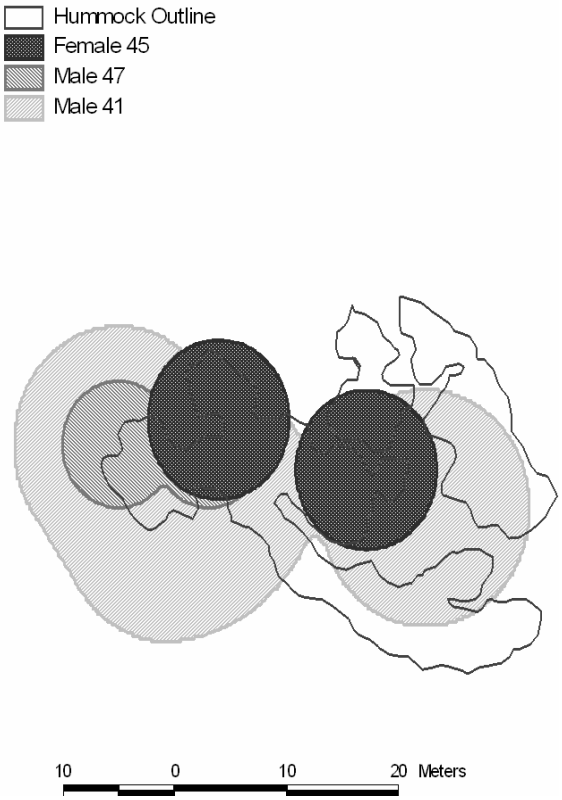


Figure IV-111: Homeranges of female and male *R. pumilio* in hummock V-4 between October 1998 and December 1998. Data from C-M-R and Observation study combined.

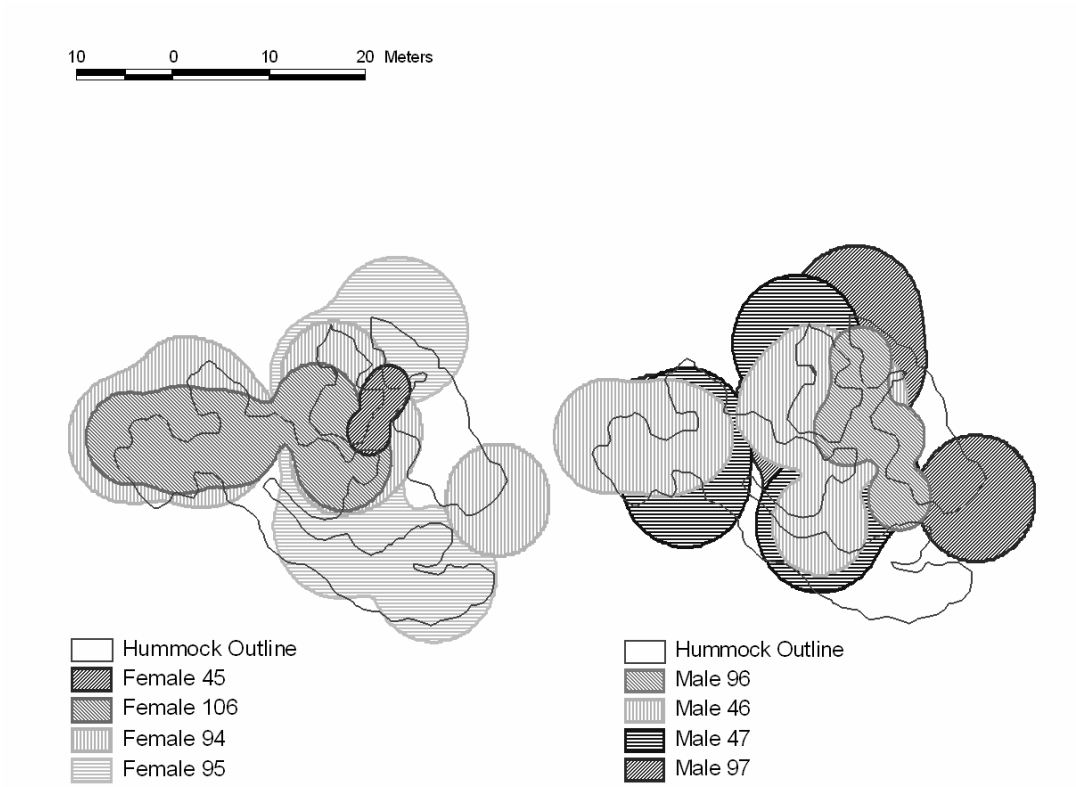


Figure IV-112: Homeranges of female (left) and male (right) *R. pumilio* in hummock V-4 between January 1999 and March 1999. Data from C-M-R and Observation study combined.

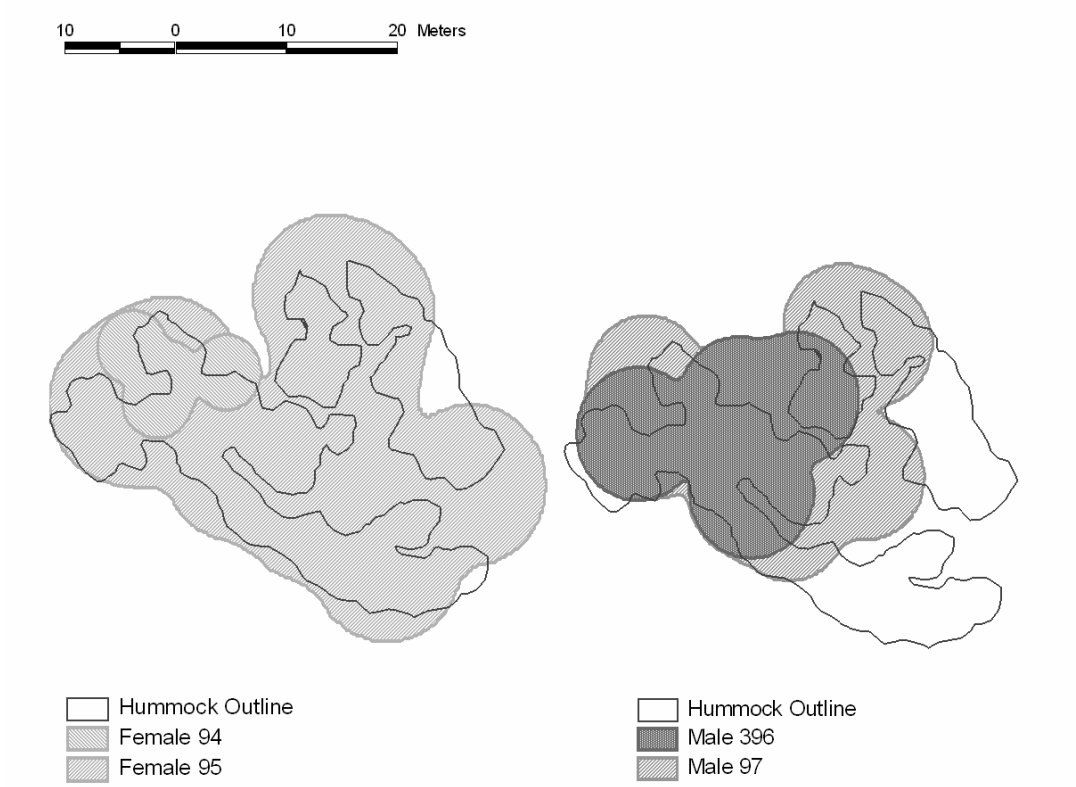


Figure IV-113: Homeranges of female (left) and male (right) *R. pumilio* in hummock V-4 between April 1999 and June 1999. Data from C-M-R and Observation study combined.

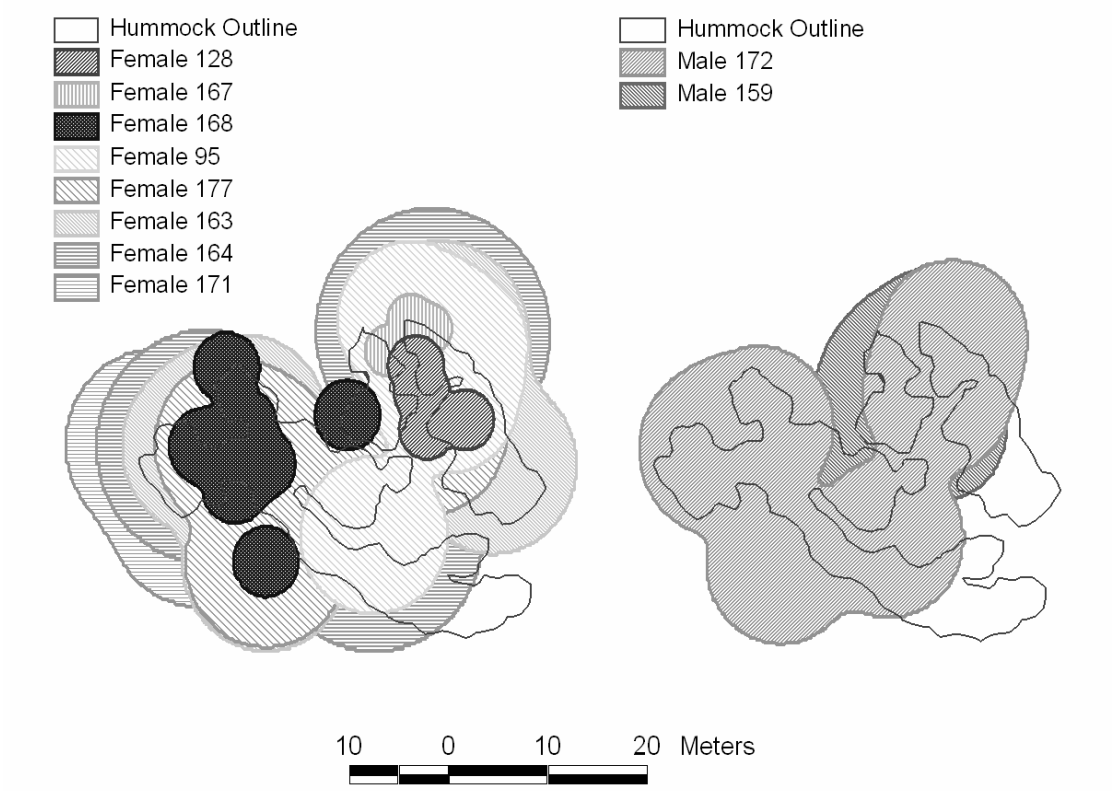


Figure IV-114: Homeranges of female (left) and male (right) *R. pumilio* in hummock V-4 between July 1999 and September 1999. Data from C-M-R and Observation study combined.

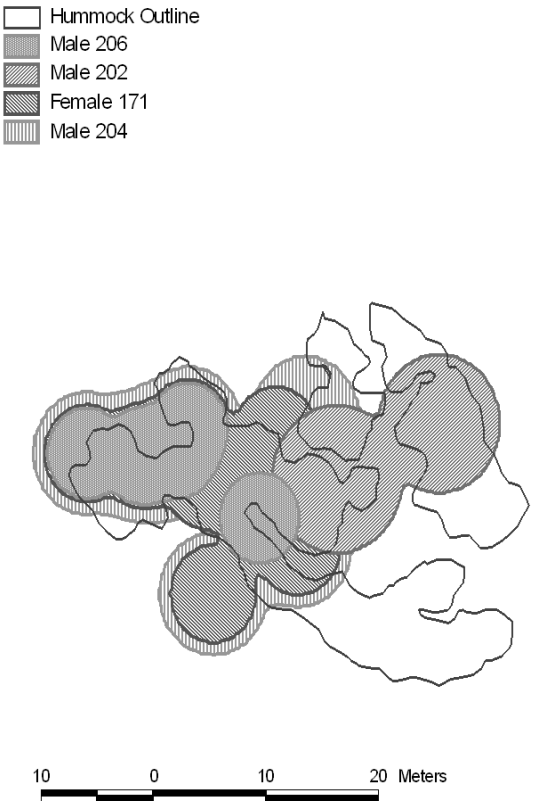


Figure IV-115: Homeranges of female and male *R. pumilio* in hummock V-4 between October 1999 and November 1999. Data from C-M-R and Observation study combined.

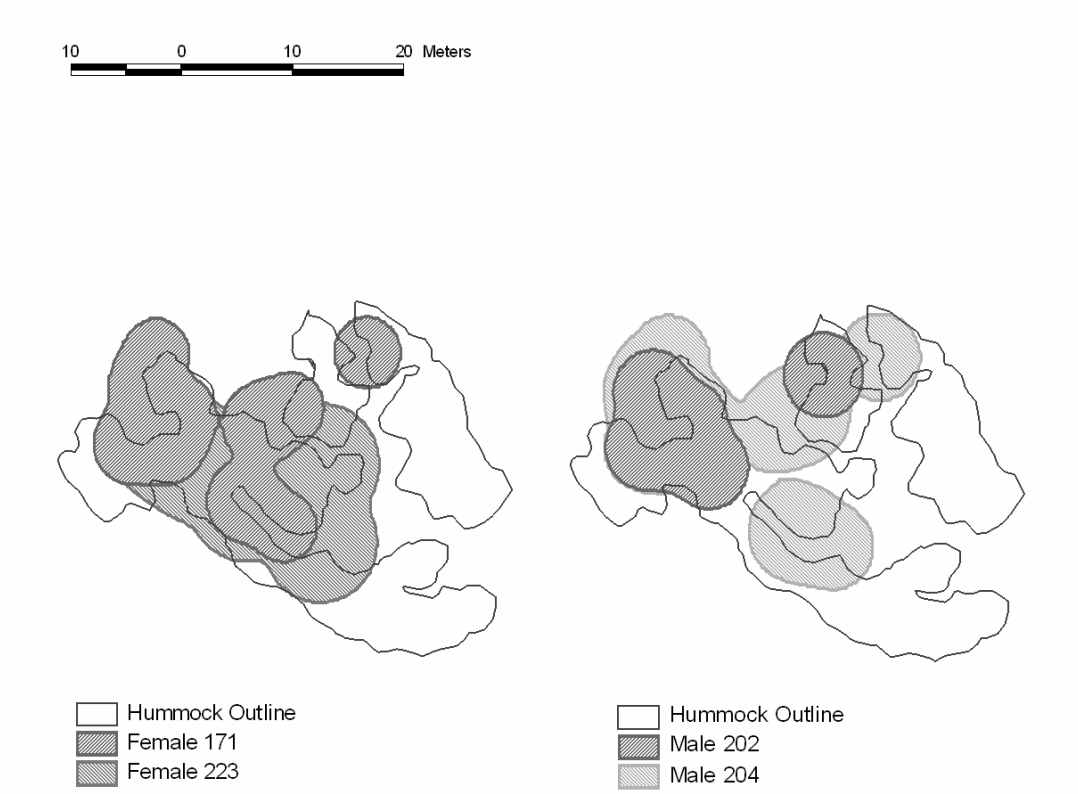


Figure IV-116: Homeranges of female (left) and male (right) *R. pumilio* in hummocks V-4 between December 1999 and January 2000. Data from C-M-R and Observation study combined

iv. Activity

In the Namib, *Rhabdomys* showed a diurnal bimodal activity pattern, with activity peaks in the early morning and the late afternoon. The number of individuals trapped and observed was significantly higher in the early morning hours and in the late afternoon than during the midday hours (Kruskal-Wallis test: $H_{12,165}$=76.54, p<0.001, Figure IV-117).

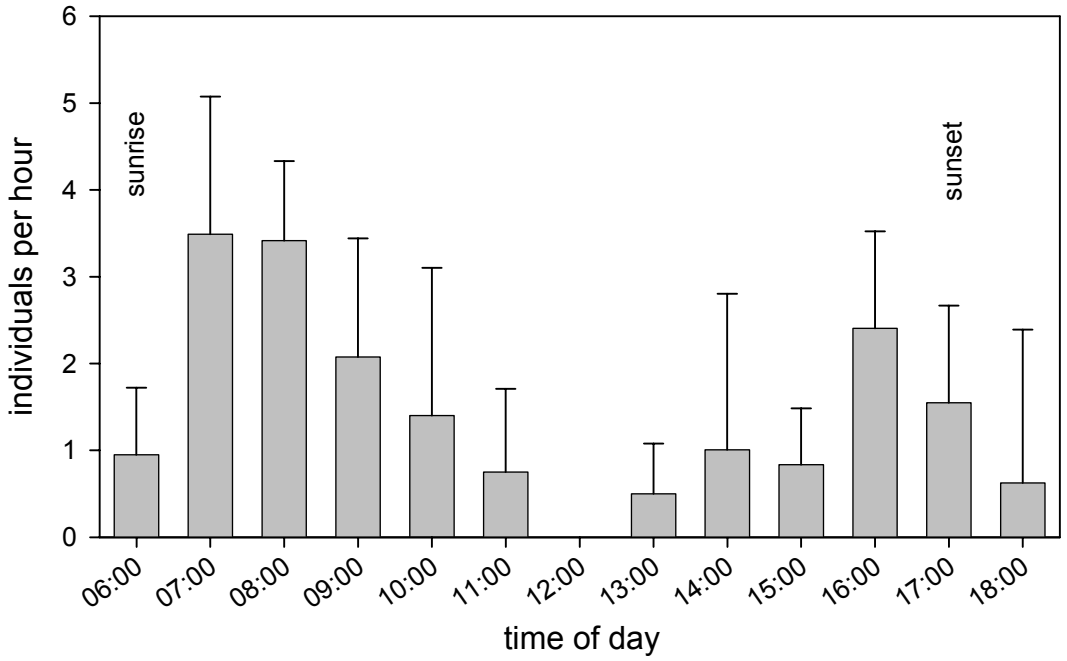


Figure IV-117: Activity pattern of *Rhabdomys*: Number of individuals encountered per hour of observation and trapping. Means ± SD; data for all observation and trapping sessions between September 1998 and January 2000 pooled; time of day relative to sunrise (6:00) and sunset (17:00).

Emergence of individuals in the morning and end of activity in the afternoon / evening did vary over the seasons (Figure IV-118). In the middle of the year (April - September), individuals emerged significantly later than at the start (January - March) or end of the year (October - December), (Kruskal-Wallis test: $H_{16,183}$=77.68, p<0.001). The opposite pattern was observed for the termination of activity in the afternoon. Individuals disappeared earlier during the middle of the year (with the exception of July and August) than during the start or end of the year (Kruskal-Wallis test: $H_{16,97}$=48.21, p<0.001). Emergence and start of activity in the morning was positively linked to sunrise (Spearman rank correlation: r_s=0.53, N=180, p<0.001); the earlier the sun rose, the earlier the mice became active. Morning soil temperature did also influence the start of activity; on cooler days, the mice emerged later (soil temperature at 30cm depth: Spearman rank correlation: r_s=-0.43, p<0.001). The

occurrence of advective fog did not influence the start of activity in the morning (Mann-Whitney U-test: U=1654, N_1=156, N_2=24, NS), although it was observed that on days with very heavy fog animals became active later. Re-emergence of individuals in the afternoon was mainly dictated by soil temperatures (5cm soil depth: Spearman rank correlation: r_s=0.50, p<0.001; 30cm soil depth: Spearman rank correlation: r_s=0.55, p<0.001). The higher soil temperatures measured at 14:00, the later the mice became active. Cessation of activity in the evening was again positively linked to ground temperature (5cm soil depth: Spearman rank correlation: r_s=0.64, p<0.001) and soil temperature at 30cm depth (Spearman rank correlation: r_s=0.59, p<0.001), but was also influenced by the time the sun set (Spearman rank correlation: r_s=0.56, p<0.001). Both sunrise and sunset times as well as soil temperatures therefore influence the activity shift of *Rhabdomys* to later hours of the day during the cooler winter months, which also have shorter day length.

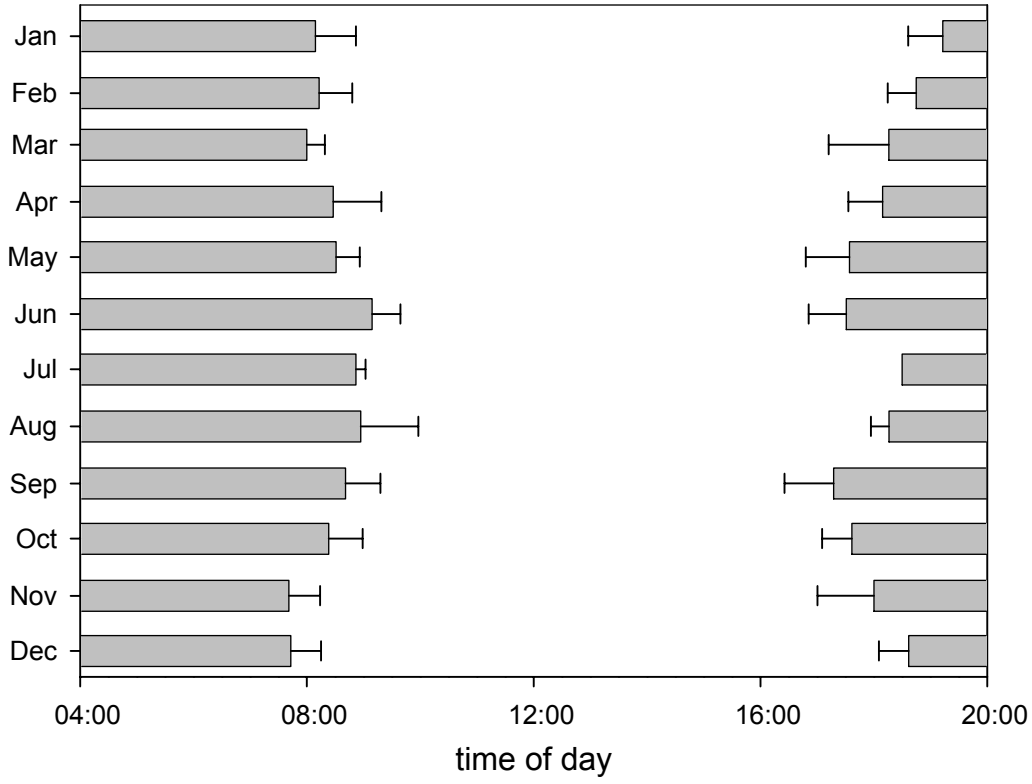


Figure IV-118: Average time of emergence in the morning (left) and disappearance in the afternoon (right). Shaded bars indicate periods of inactivity. Means ± SD; data for all observation and trapping sessions between September 1998 and January 2000 pooled.

The length of time the animals were active in the open did not differ over the study period (morning: Kruskal-Wallis test: $H_{15,182}$=22.70, NS; afternoon: Kruskal-Wallis test: $H_{15,97}$=12.61, NS). On average, four-striped fieldmice could be observed and

trapped for 1:41±0:20 hours (N=182) in the morning, and again for about an hour in the afternoon (0:53±0:16 hours, N=97), (Figure IV-119). The total time animals were active throughout the day was independent from number of daylight hours (Spearman rank correlation: r_s=0.09, NS).

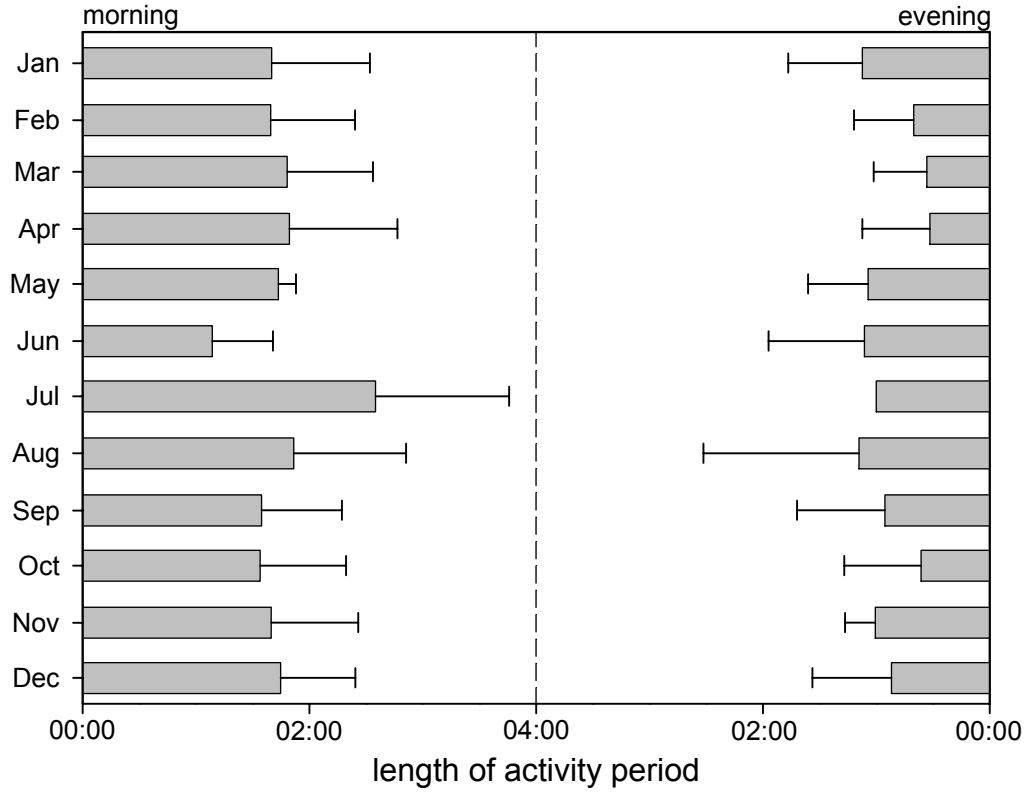


Figure IV-119: Average length of activity recorded in the mornings (left) and afternoons (right) of *Rhabdomys* over the year. Means ± SD; data for all trapping and observation sessions between September 1998 and January 2000 pooled.

Sunbasking behaviour in Rhabdomys became apparent in March 1999. On those days where individuals were observed sunbasking, soil temperatures at 5cm (Mann-Whitney U-test: U=988.0, p<0.05), 30cm (Mann-Whitney U-test: U=924.0, p<0.01), and 60cm depth (Mann-Whitney U-test: U=997.0, p<0.05) were significantly lower than the soil temperatures at these depths when animals were not sunbasking. Both ambient and minimum temperature at 08h00 on sunbasking mornings were lower than on mornings without sunbasking, but not significantly so (dry bulb temperature: Mann-Whitney U-test: U=1278.0, NS; minimum temperature: Mann-Whitney U-test: U=1341.0, NS). The average time individuals spent sunbasking was significantly higher during the cooler months (Kruskal-Wallis test: $H_{9,72}$=18.85, p<0.05, Figure IV-120). Animals spent the most time sunbasking in August and September 1999 (the coolest months of the observation period), and the least time with this activity in May

and June 1999, as well as December 1999 and January 2000 (the warmest months of the observation period). Average duration of sunbasking bouts was negatively correlated with soil temperature at 60cm depth (Spearman rank correlation: r_s=-0.36, $p<0.05$), animals were sunbasking for longer periods when soil temperatures were lower. The number of sunbasking bouts per individual did not change over the observation period (Kruskal-Wallis test: $H_{9,33}$=8.86, NS, Figure IV-121).

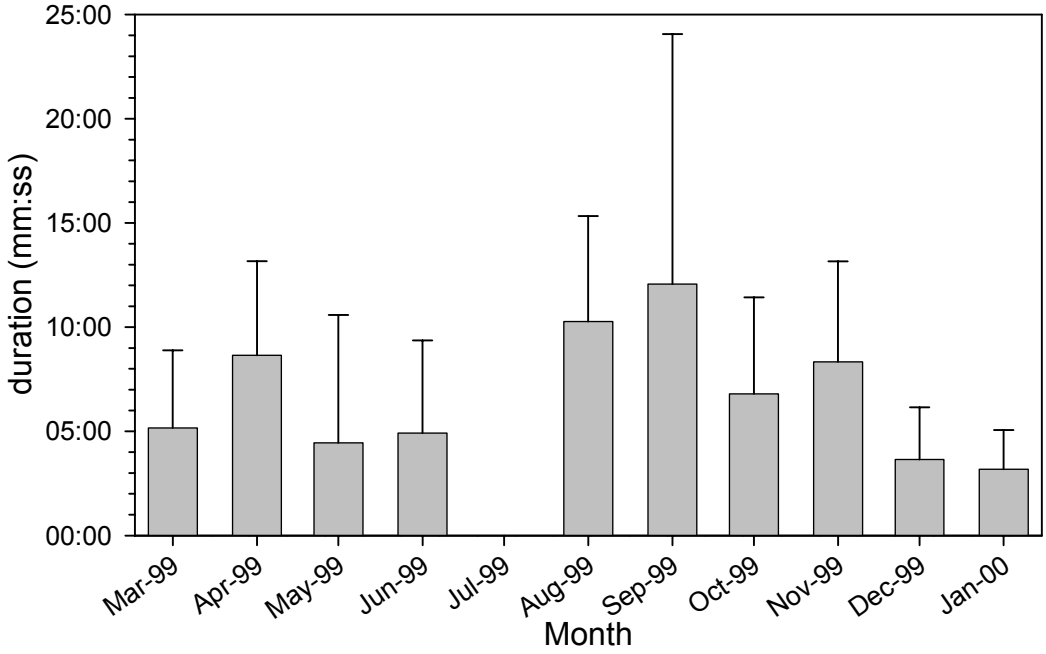


Figure IV-120: Average time individuals spent sunbasking each month. Means ± SD, no data available for July 1999.

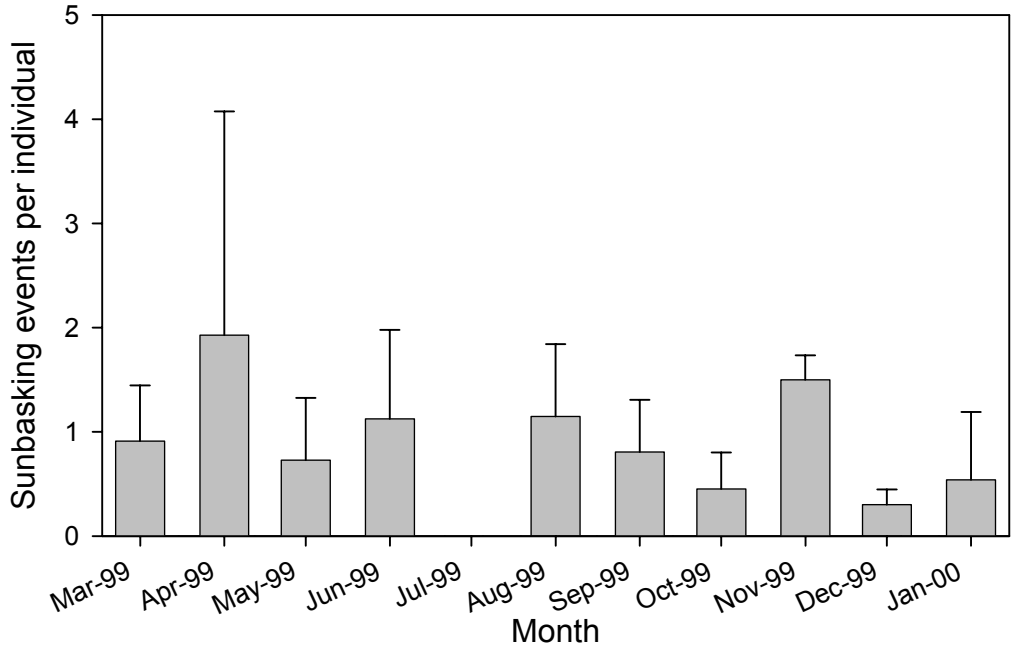


Figure IV-121: Number of sunbasking events per individual observed. Means ± SD; no data available for July 1999.

On the few occasions when rain fell during the observation period, animals that were active at the surface disappeared within minutes in the shelter of nara branches and burrows, and only emerged again well after the rain had stopped.

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
			B2 (Riboflavin)	0.2	0.0
kj / 100 g					
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.

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