

Reproduction of *Rhabdomys pumilio* in the Namib Desert: pattern and possible control

Cornelia B. Krug

Department of Conservation Ecology and Entomology, Faculty of Agricultural and Forestry Sciences,
University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa
ckrug@sun.ac.za

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Abstract

Arid environments are characterised by irregular rainfall and temperature extremes, resulting in highly variable resource availability. Small mammals inhabiting such environments are particularly vulnerable to unpredictable energy and nutrient supplies. Reproduction in these species is thus governed by environmental cues such as rainfall, photoperiod and temperature as well as food availability.

The aims of this study were to document the timing of reproduction in a desert dwelling small mammal and to identify the environmental cues that may be responsible for the control of reproduction. Specimens of *Rhabdomys pumilio* were live trapped and observed on a monthly basis near the Gobabeb Training and Research Centre. Occurrence of a perforate vagina or pregnancy in females and scrotal testes in males were recorded, and related to climate and food availability. Males were reproductively active throughout the year, while females stopped reproducing for a short period in winter. Reproduction of both male and female *R. pumilio* in the Namib can be described as opportunistic, with environmental factors (food availability and climate) being less of a constraint in males compared to females.

Keywords: resource use, environmental controls

Zusammenfassung

Aride Gebiete sind durch irregulären Niederschlag und Temperaturextreme gekennzeichnet, was eine hohe Variabilität in Ressourcenverfügbarkeit zur Folge hat. Kleinsäuger arider Gebiete sind von unvorhersehbarer Nährstoff- und Energieversorgung besonders betroffen. Fortpflanzung in diesen Arten ist daher durch Umweltfaktoren, wie Niederschlag, Photoperiode und Temperatur als auch Futtermittelverfügbarkeit gesteuert.

Ziel dieser Studie war es, den Fortpflanzungsperiode vom *Rhabdomys pumilio* in der Namib zu bestimmen, und festzustellen, durch welche Umweltfaktoren die Fortpflanzung

gesteuert wird. In der Nähe des Gobabeb Training und Research Centre wurden *R. pumilio* mit Lebendfallen gefangen und beobachtet. Das Auftreten einer perforierten Vagina oder Schwangerschaft in Weibchen und scrotalen Testes in Männchen wurde zu Klimavariablen und Nahrungsverfügbarkeit in Beziehung gesetzt. Männchen waren über das ganze Jahr hin fortpflanzungsfähig, während Weibchen für eine kurze Zeit im Winter nicht fortpflanzungsfähig waren. Die Fortpflanzung von *R. pumilio* in der Namib ist als opportunistisch einzustufen, wobei der Einfluss von Umweltfaktoren (Nahrungsverfügbarkeit und Klima) auf Männchen geringer ist als auf Weibchen.

Schlüsselbegriffe: Ressourcenutzung, Umweltbedingungen

Introduction

There are few studies examining the environmental cues governing reproduction in small mammals in arid environments, which are characterised by irregular rainfall, temperature extremes and associated scarcity and variability of food resources. Small desert mammals are particularly vulnerable to unpredictable dynamics of energy and nutrients, as they have low thermal inertia due to their large surface to volume ratio (Degen 1997), which increases energy apportioned to thermoregulation (Bronson 1989). With a higher metabolic rate, and therefore higher nutritional needs compared to large mammals, small mammals are more affected by resource constraints. In addition, evaporative water loss to maintain a constant body temperature is higher in small mammals than in large animals (Degen 1997). In female small mammals, energetic cost of reproduction is magnified in relation to their ability to obtain food, and to store fat (Bronson 1989). A lactating female must not only obtain energy sufficient to sustain

herself, but she must successfully allocate energy-rich milk to her offspring, and huddle with them to assist thermoregulation (Bronson 1989). Lactation may also exacerbate water loss in females. Energy and nutrient deficits thus curtail reproduction (Bronson 1989), but more severely in females than in males (Jackson & Bernard 2005), as the energetic demands for reproduction are considerably higher for females than for males. Reproduction in small desert mammals thus is expected to coincide with optimal periods of availability of water and food, and favourable climatic conditions (Bronson 1989). Many cues are utilized by small mammals to adaptively allocate reproductive effort. These environmental cues include rainfall, photoperiod, and temperature (White et al. 1997, Bronson 1989, Bronson 1985), as well as food availability (Perrin 1980b). Bronson (1985) suggested that the most useful reproductive strategy for (omnivorous) small mammals inhabiting unpredictable hot deserts and semi-arid areas is to be opportunistic, and not to use any predictors. Within this strategy, males are in breeding condition at all times, while

females dictate the time period for breeding depending on short-term energetic and nutritional considerations (Bronson 1985). The availability of sufficient water to curtail the moisture lost during lactation will also influence the timing of breeding in small desert mammals.

Reproduction in *R. pumilio* has been investigated in a number of different habitats, where it is apparently affected by a number of factors (Delany 1972). Generally, *Rhabdomys* has been shown to be a seasonal breeder (Rowe-Rowe 1986, Perrin 1980a), usually with a summer peak, and breeding cessation in winter (e.g. Wirminghaus & Perrin 1993; Rowe-Rowe 1986, David & Jarvis 1985). Nevertheless, there are also indications that they breed throughout the year (Smithers 1971). Jackson and Bernard (1999) suggested *R. pumilio* exhibits a latitudinal shift from continuous reproduction at tropical latitudes to seasonal reproduction at more temperate latitudes. Through most of its distribution range, breeding season coincides with the rainy season and reproductive activity decreases or ceases during cold, dry months (Perrin 1980a, Christian 1979a, Taylor & Green 1976). Yet in the Western Cape, the main breeding season of *R. pumilio* is the summer months, with scant reproductive activity during the cool, wet winter months (David & Jarvis 1985, Krug in prep). Summer rainfall, however, only seems to control reproduction indirectly, as the concomitant increase in plants and insects may be the primary cue (Bowland & Perrin 1993, Wirminghaus &

Perrin 1993, Perrin 1980a). The secondary plant compound 6-MBOA, which is produced in fresh green tissue, and induces reproduction in a number of rodent species from the northern hemisphere (Berger et al. 1981), has no effect on *R. pumilio* (N. Mzilikazi pers. comm.). Similarly, photoperiod as a regulating factor for reproduction was ruled out for this species in the Eastern Cape (Jackson & Bernard 1999).

R. pumilio has been described as an opportunistic omnivore that exploits transient nutritious food sources of which various components then account for the seasonality of breeding (Perrin 1980b). A critical level of body fat appears essential for breeding (Perrin 1980a), and fat deposits correlate positively with male and female reproductive status (Taylor & Green 1976). Experimental food supplementation (Perrin & Johnson 1999), and the provision of additional free water (Christian 1979b) lead to increased occurrence of pregnancy and lactation, and population growth. Such a rapid response to favourable conditions is a typical reaction of rodents inhabiting unpredictable arid environments (Christian 1979a, b). Reproduction of *R. pumilio* in the Namib could thus be expected to be largely opportunistic, with a combination of environmental cues to trigger the onset of reproductive activity.

The objectives of this study were to document the timing and extent of reproduction in a population of *Rhabdomys pumilio* inhabiting the Namib Desert, and to identify the environmental cues responsible for the control of reproduction in this species

in an arid environment. The considerable information available for this study species should allow this study to identify environmental cues specific to the arid region based on data compiled from live trapping and direct observation, and compared to data published for populations in other biomes. Previous studies on arid ecosystems led us to hypothesise that reproduction would be opportunistic or episodic with some times of reproductive inactivity, and reproduction would be inhibited in times with low energy and water availability.

Material and Methods

Data collection

Animals were trapped and observed at VisNara (Visitor's Nara, this is the location closest to the Gobabeb Training and Research Centre (GTRC), where visitors can encounter the Nara plant, *Acanthosicyos horridus*, 15°03'E, 23°33'S) near the GTRC in the Namib Naukluft National Park between September 1998 and February 2000. Vegetation at the study site, located at the banks of the Kuiseb river, is typical for the dune valleys of the Southern Namib, but is also influenced by its proximity to the dry riverbed and its vegetation. The dominant plant at the site was *Acanthosicyos horridus* Welw. ex Hook.f. (Cucurbitaceae), an endemic of the sand dunes of the southern Namib, which is restricted to dune valleys with access to underground water (Sandelowsky 1990). Sand accumulates under the dense *A. horridus* bushes, building hummocks up to

4m in height and up to 1000 m² in size. *A. horridus* is regarded as a keystone species (Klopatek & Stock 1994), forming microecosystems within the dunes. Fruit, seeds, growing tips (shoots) and flowers are regarded as highly nutritious, and provide food for a number of species, ranging from beetles to gemsbok and ostrich. Sand accumulates under the dense *A. horridus* bushes, forming large hummocks, while the spiky branches offer shelter for many smaller animals, among them *R. pumilio*, *Desmodillus auricularis*, and *Thallomys nigricauda* (Krug, pers. obs.).

Weather data were obtained from the first order weather station at Gobabeb. The following parameters were used for analysis in this study: mean monthly maximum and minimum air temperature, mean monthly relative humidity, and total monthly rainfall. Total monthly fog precipitation was calculated as total number fog days per month multiplied by mean fog precipitation per day (Lancaster et al. 1984), because intra-year variation in fog precipitation does not appear to be very great (Lancaster et al. 1984).

Mean monthly photoperiod was calculated from a sunrise / sun set table for the location of the study site (15°03'E, 23°33'S) obtained through the website of the Astronomical Application Department of the US Naval Observatory (2005).

To assess availability of green vegetative matter, 10 random 0.25 m² squares were laid out in each *A. horridus* hummock at the site on a monthly basis. Within each square, the number of fresh shoots (grow-

ing tips), flower buds, open flowers, and number of melons (female plants only) were counted. Although the species is dioecious, results for male and female plants were combined. Animals were live trapped between September 1998 and February 2000. Sex and standard measurements (body mass, body, ear and hind foot length) were recorded after capture, and animals were marked individually by painting numbers on both sides of the rump with permanent black hairdye (Inecto Rapid®). In males, position of testes (scrotal, moving or abdominal), and, in females, opening of the vagina (perforate or closed) and occurrence of pregnancy (visible / palpable or non detectable) were used to assess reproductive status. Pregnancy was detected by gentle palpation or, for early stages of pregnancy, by noting a body mass increase of 10g or more in adult females in subsequent trapping sessions.

Individuals lighter than 36 grams (75% of average body mass of the population) and not in breeding condition were regarded as juvenile. Sexual maturity was taken to have occurred for males when testes were first recorded to be scrotal and for females when the vagina was recorded as perforate or pregnancy was noted.

Information on diet was obtained through direct observation of the animals by eye or with binoculars from set vantage points in and around the *A. horridus* hummocks for the same time period as for the live trapping. To increase the range of view, observations were conducted from a stepladder

(8 steps) that served as an observation tower. Due to the structure of the plants, animals were not observed for a set time period, but for as long as they were visible to the observer, which was between five and 45 minutes per individual. 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 recorded. It was assumed that optimal foraging occurred hence time budgets were used as an indirect measure of relative diet composition. To obtain relative diet composition, the time spent feeding on a specific food type was summed for an individual, and divided by the total time this same individual fed during the observation period. These individual relative diet compositions were then averaged to obtain the proportion that each food type contributed to the diet.

Preference for food types was determined using the rank preference method of Johnson (1980), to rank usage and availability of the respective food item. The difference in the ranking between usage and availability is calculated, and the resulting value serves to indicate preference of a specific food item. The lower the value of this difference, the more preferred the item.

Statistical Analysis

A T-test was used to compare body mass and body mass at sexual maturity between males and females. One-way ANOVA was used to determine seasonal differences in body mass of sexually mature and immature individuals. Observed versus expected

χ² test was used to compare the proportions of food taken versus proportion of food available. Best subset multiple regression in STATISTICA 7.0 was used to determine the effect of climatic variables, food availability and diet composition on the occurrence of reproductively active males and females in the population. Proportional values were arcsine transformed. As the factors considered may have a lag time before taking effect, variables in the month of capture and one, two and three months prior to capture were included in the analysis. Separate multiple regressions for each lag phase were performed, as the monthly environmental variables appear to be correlated. Standard deviations for values (\pm SD) are given unless otherwise indicated. Graphs were constructed with R (R Development Core Team 2005).

Results

Environmental variables

Climate at the study site followed a seasonal pattern (Figure 1). Temperatures were lowest during July / August, and highest in April, with average minimum temperatures ranging between 10.4°C and 18.7°C and average maximum temperatures between 25.8°C and 35.5°C. The

main source of precipitation at the study site (and in the Namib) was fog, with fog precipitation being highest in the second part of the year, between July and December. No fog precipitation was recorded between April and June. Rainfall events were very scarce, with some precipitation events recorded in the later half of the study period. Relative humidity is closely related to fog and rain precipitation, being highest towards the end of the year (November / December) and lowest in those months with no fog precipitation. Day length (or photoperiod) is shortest between May and July, and longest between November and January.

Flower buds of *A. horridus* were recorded throughout the year (Figure 2). The highest numbers of flower buds were documented between July and October, numbers were lowest between April and June. Only a small number of open flowers was recorded, these were most numerous between August and November. Fresh shoot tips were available to the animals throughout the year, with the highest numbers between February and June. Melons were only recorded in low numbers, and they were most numerous in form November until January.

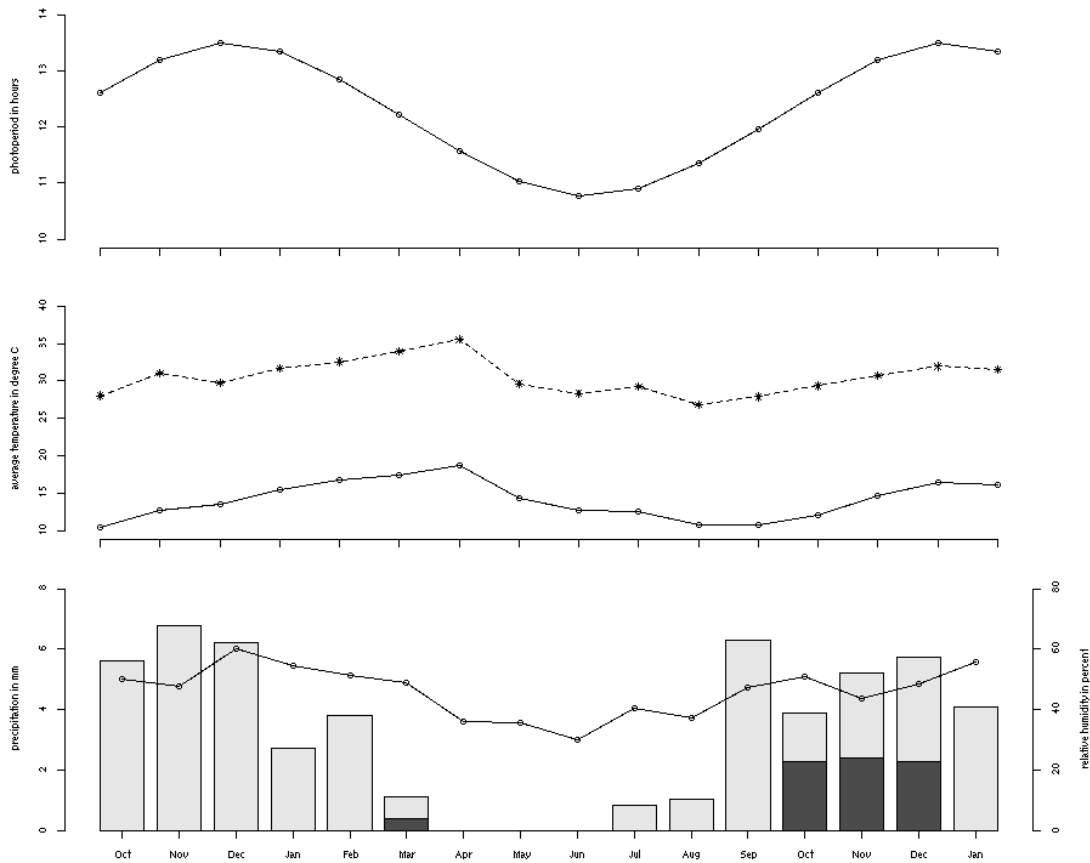


Fig. 1: Seasonal change in photoperiod (solid line, closed circles), average maximum temperature (dashed line), average minimum temperature (solid line, open circles), fog precipitation (shaded bars), rain fall (closed bars) and relative humidity (solid line).

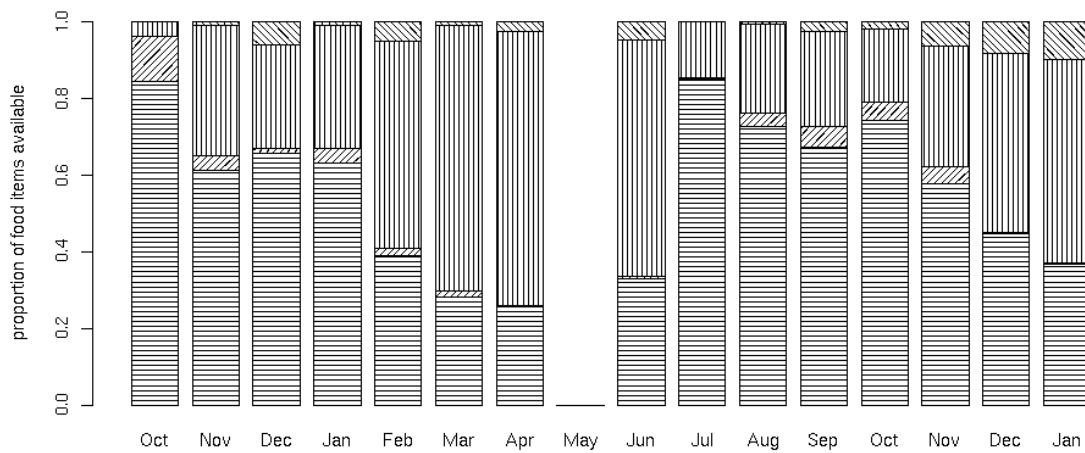


Fig. 2: Proportional availability of Nara flower buds (horizontal hatching), open flowers (upward diagonal hatching), green tips (vertical hatching) and melons (downward diagonal hatching).

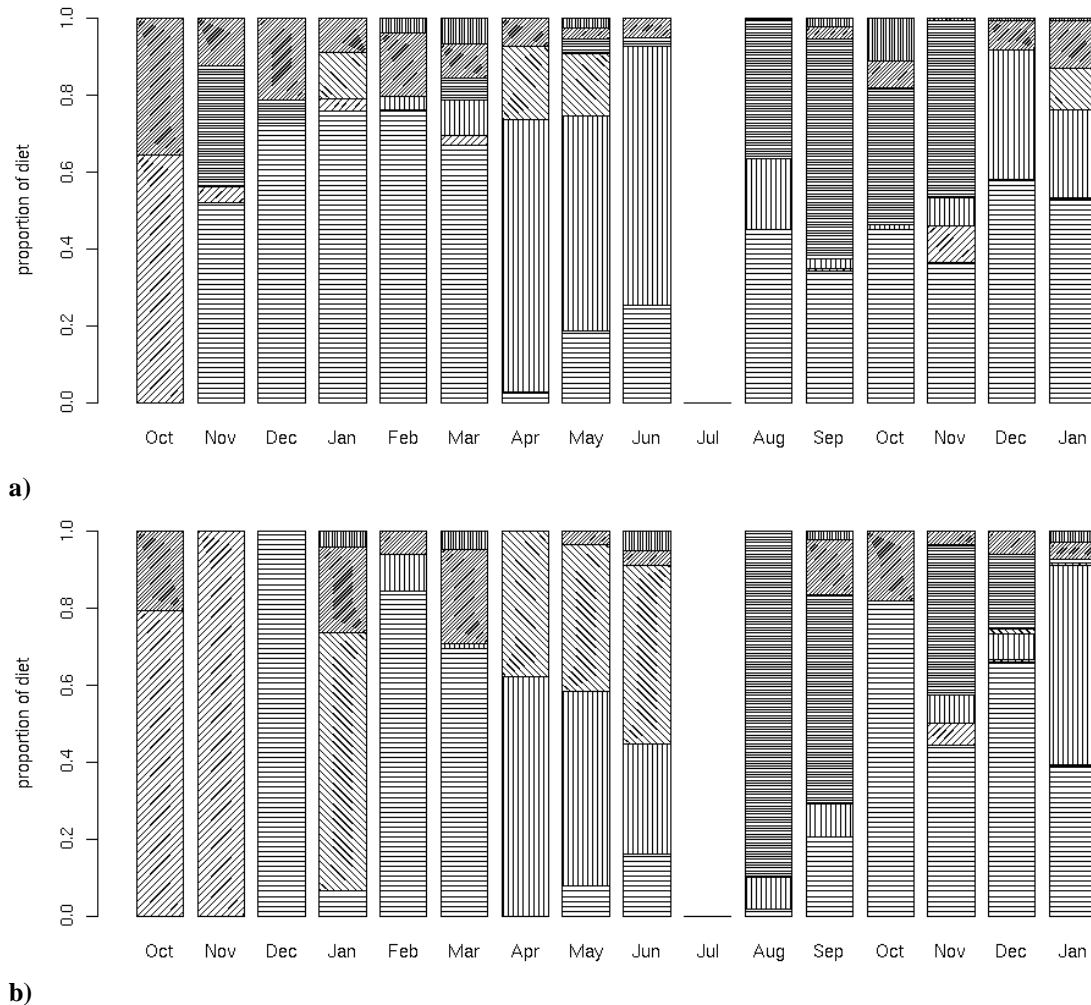


Fig. 3: Proportion of diet (a): females, b): males) consisting of Nara flower buds (wide horizontal hatching), open flowers (wide upward diagonal hatching), green tips (wide vertical hatching), melons (wide upward diagonal hatching), acacia seed pods (narrow horizontal hatching), detritus (narrow upward diagonal hatching) and other (narrow vertical hatching).

Observed animals not only fed on buds, flowers, shoots and melons of *A. horridus*, but also *A. erioloba* seed pods and dry plant matter (Figure 3). *Acacia* seed pods formed an especially important part of the diet. Both males and females showed a preference for Nara flowers and Nara melons, the items were consumed significantly more often than expected by chance (Table 1).

Patterns of reproduction

In total, 278 individuals were trapped (117 males, and 153 females). The sex of 8 individuals could not be determined. With a mean body mass of 51.0 ± 13.7 g ($n=84$) at first capture, adult males were significantly heavier than non-pregnant adult females, which weighed 45.5 ± 7.2 g ($n=87$) at first capture (T-Test, $t=-3.329$, $p<0.01$).

Table 1: Mean rank preference index (\pm SD) of *A. horridus* food items of female and male *R. pumilio*, and results of χ^2 test comparing actual availability of the food items with observed consumption. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Females	Mean	SD.	χ^2	df	significance level
Nara flower bud	0,18	0,64	1,79	13	n.s.
Nara flower	-0,52	0,60	17,29	13	n.s.
Nara melon	-0,25	1,28	71,20	10	***
Nara shoot	0,40	0,74	1,85	13	n.s.
Males					
Nara flower bud	0,20	0,82	1,64	13	n.s.
Nara flower	-0,50	0,61	98,82	13	***
Nara melon	-0,32	1,33	70,23	9	***
Nara shoot	0,46	0,85	2,23	13	n.s.

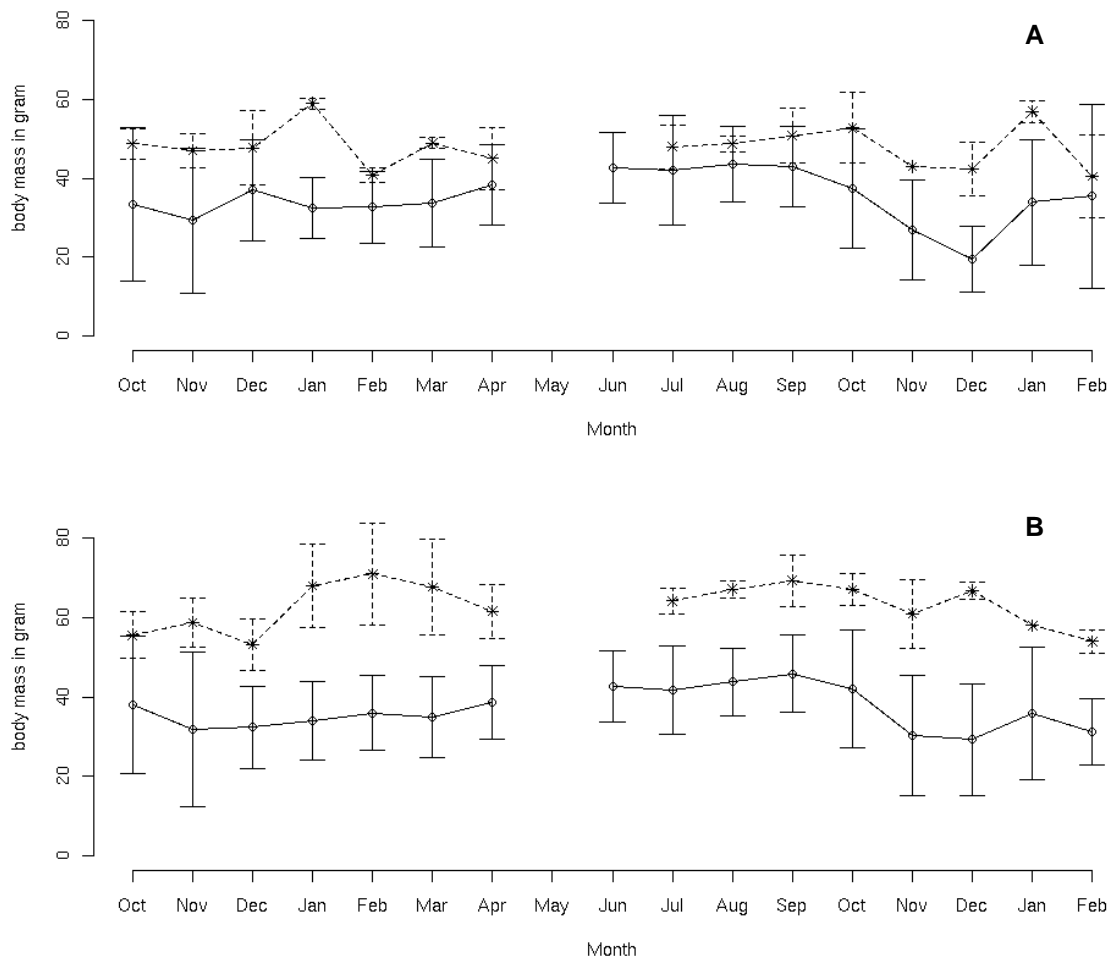


Fig. 4: Seasonal changes in mean body mass of A) females with perforate (dashed line) and imperforate (solid line) vaginas and B) pregnant (dashed line) and non-pregnant females (solid line).

Males became sexually mature (testes classified as “moving”) at a mean body mass of $40.7 \pm 10.3\text{g}$ ($n=26$). They were significantly lighter when becoming sexually mature than the females, which weighed $47.4 \pm 7.2\text{g}$ when reproductively active, i.e. the vagina was perforate for the first time (T-test, $t = -3.245$, $p = 0.002$). Body mass of non-reproductive animals changed over the study period. Males with abdominal testes were significantly heavier during months with low precipitation and low ambient temperatures (Figure 5, $F_{15,47} = 3.2288$, $p = 0.001$). This pattern was also apparent in females with closed

vaginas; individuals captured between June and September, the driest and coolest months, were significantly heavier ($F_{15,159} = 2.2619$, $p = 0.006$, Figure 4).

Reproductively active males (testes moving or scrotal) were captured throughout the study period (Figure 7) and no seasonal pattern was apparent. Reproductively active females (vagina perforate or pregnant) were also captured throughout the study period (Figure 6), although the proportion was lower than in males. No females in reproductive condition were caught during June, the month with the shortest photoperiod.

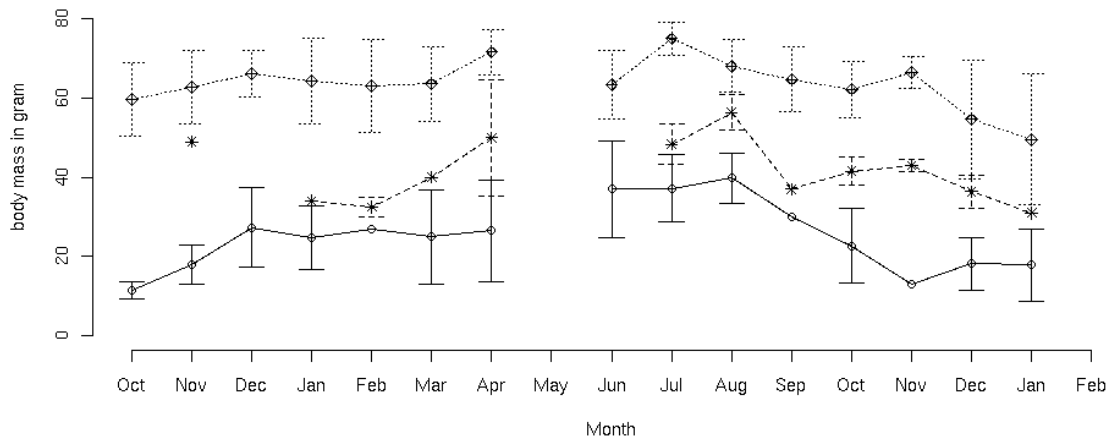


Fig. 5: Seasonal changes in mean body mass of males with scrotal (dotted line), moving (dashed line) and abdominal (solid line) testes.

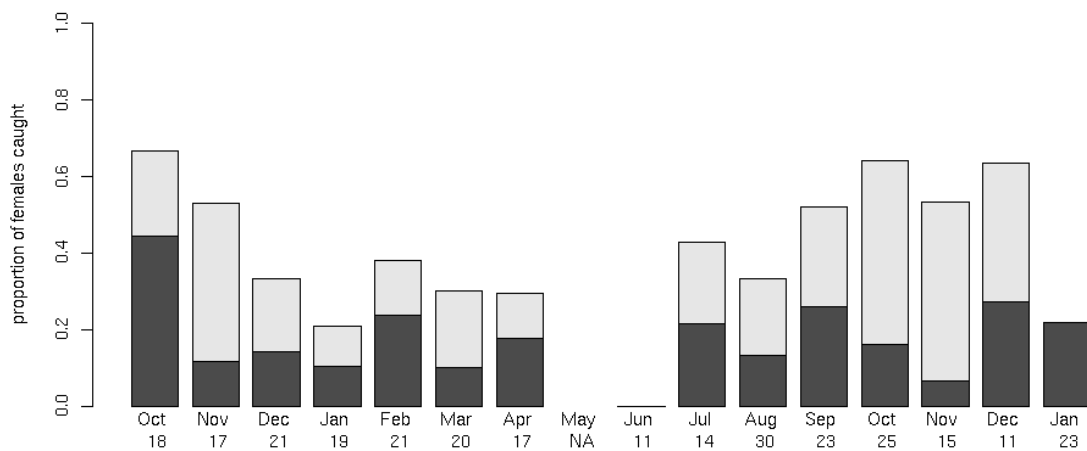


Fig. 6: Proportion of non-pregnant females with perforate vaginas (shaded bars) and pregnant females (closed bars) in the population. Numbers below columns indicate number of females captured each month.

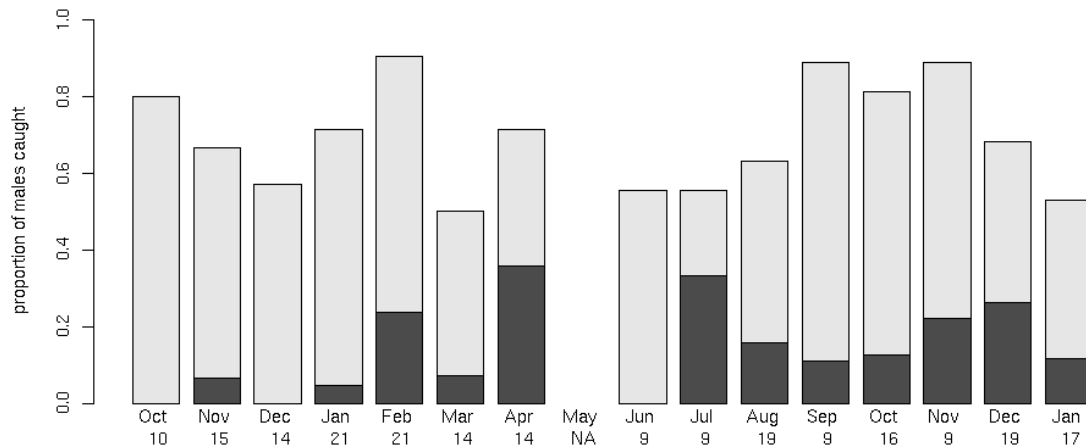


Fig. 7: Proportion of males with moving testes (closed bars) and scrotal testes (open bars) in the population. Numbers under the columns indicate total number of males captured each month.

Controls of reproduction

Reproduction in females was controlled by climatic factors and diet (resource use) (Table 2 and Table 3), although the effects were stronger on occurrence of pregnancy than on the opening up of the vagina. Vaginal perforation in females was mostly influenced by diet, as is evident by the R^2 values, with diet in the prior month being most important (Table 2). This seems to be regulated mostly by the consumption of Nara flowers. Climate was another factor in regulating the onset of reproduction, but the lower R^2 values indicate the lesser importance compared to diet. Here, climate in the months prior to observation had the greatest influence, with maximum temperature being most important. Food availability had very little influence on the occurrence of perforate vaginas in *R. pumilio* females.

Climate and diet appear equally important in determining the incidence of pregnancy, while food availability had less influence than on the opening up of the vagina (Ta-

ble 3). Occurrence of pregnancy coincided with the highest maximum temperatures and highest rainfall at the time. Diet composition three months prior to observation had the most influence on incidence of pregnancy, and pregnancy was correlated with a high intake of acacia seed pods. Reproductive activity in males was also controlled by climate and diet, although food availability had very little influence on reproduction (Table 4). In males, diet composition two months prior to observation had the greatest influence on the occurrence of scrotal testes, followed by climate three months prior. Reproductive activity coincided with long photoperiod and high minimum temperatures, as well as high fog precipitation and relative humidity.

Table 2: Variables best explaining variation in proportion of females with perforate vaginas as identified by best subsets multiple regression. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Factor	lag phase	Adj. R ²	p-value	Variable	lag phase	t-value	p-value	significance
Climate	at time	0,133	0,264	photoperiod	at time	-1,401	0,191	
	1 month	0,385	0,008	photoperiod	3 months	-2,486	0,029	*
	2 months	0,132	0,100	maximum temperature	1 month	-3,122	0,008	**
	3 months	0,236	0,079	maximum temperature	2 months	-1,770	0,100	
				rainfall	at time	1,603	0,140	
				fog precipitation	at time	1,717	0,117	
				fog precipitation	3 months	1,252	0,235	
				relative humidity	at time	1,180	0,265	
Food availability	at time	0,136	0,005	Nara flower bud	2 months	2,392	0,021	*
	1 month	0,044	0,071	Nara flower bud	3 months	2,747	0,009	**
	2 months	0,074	0,108	Nara flowers	1 month	1,842	0,071	
	3 months	0,106	0,069	Nara flowers	2 months	2,000	0,051	
				Nara flowers	3 months	1,998	0,052	
				Nara shoots	at time	-1,428	0,158	
				Nara shoots	2 months	2,215	0,032	*
				Nara shoots	3 months	2,523	0,016	*
				Nara melon	at time	3,181	0,002	**
				Nara melon	2 months	2,102	0,041	*
				Nara melon	3 months	2,645	0,011	*
Diet composition	at time	0,224	0,099	Nara flower buds	at time	-1,592	0,140	
	1 month	0,594	0,037	Nara flower buds	1 month	2,192	0,064	
	2 months	0,295	0,084	Nara flower buds	3 months	-1,069	0,326	
	3 months	0,320	0,189	Nara flowers	1 month	2,725	0,030	*
				Nara shoots	at time	-2,228	0,048	*
				Nara melons	1 month	-2,622	0,034	*
				Nara melons	2 months	-1,736	0,117	
				Nara melons	3 months	1,547	0,173	
				acacia seed pods	3 months	2,253	0,065	
				detritus	1 month	-3,139	0,016	*
				other	1 month	-1,313	0,231	
				other	2 months	1,739	0,116	
				other	3 months	-2,084	0,082	

Table 3: Variables best explaining variation in proportion of pregnant females with as identified by best subsets multiple regression. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Factor	lag phase	Adj. R ²	p-value	Variable	lag phase	t-value	p-value	significance	
Climate	at time	0,739	0,000	photoperiod	3 months	-2,683	0,020	*	
	1 month	0,475	0,003	minimum temperature	at time	-4,963	0,000	***	
	2 months	0,391	0,038	minimum temperature	1 month	-3,695	0,003	**	
	3 months				minimum temperature	2 months	-3,101	0,010	*
					maximum temperature	at time	4,484	0,001	***
					rainfall	at time	4,734	0,001	***
					rainfall	2 months	-1,698	0,118	
	rainfall	3 months	-2,202	0,048	*				
Food availability	at time	0,016	0,152	Nara flowers	at time	1,45	0,152		
	1 month	0,008	0,23	Nara flowers	1 month	1,214	0,23		
	2 months	-0,007	0,445	Nara shoots	2 months	-0,769	0,445		
	3 months				Nara shoots	3 months	-1,53	0,133	
					Nara melons	3 months	2,093	0,042	*
Diet composition	at time	0,296	0,058	Nara flower bud	1 month	-2,622	0,031	*	
	1 month	0,542	0,033	Nara shoot	at time	-1,073	0,306		
	2 months	0,056	0,228	Nara shoot	1 month	-3,037	0,016	*	
	3 months				Nara melon	1 month	-1,98	0,083	
					acacia seed pod	at time	2,09	0,061	
					detritus	1 month	-2,07	0,072	
					detritus	3 months	-2,978	0,018	*
					other	2 months	1,284	0,228	
other	3 months	-4,039	0,004	**					

Discussion

Climate, resource availability and use

The weather experienced during the study period followed the long-term climate pattern of the Namib Desert, although the period was drier and hotter than the long-term average. As expected for a hyper-arid area, rainfall is very low and rainfall events highly unpredictable in both space and time (Lancaster et al. 1984). Nonetheless, precipitation from advective fog occurs over the region for most parts of the year, making fog a much more reliable source of moisture in this part of the Namib. If water were a limiting factor for *R. pumilio* in the

Namib, one would reasonably expect critical processes, like reproduction, to be restricted to months with sufficient fog precipitation. Climate seems to influence food availability. The number of *A. horridus* flower buds and open flowers was lowest between February and June, the driest months, while the number of green shoots was highest during this time period. Occurrence of buds and flowers coincided with regular fog events and higher atmospheric humidity.

Food and water resources are closely linked for most rodents inhabiting arid areas (MacMillen & Christopher 1975). Desert rodents obtain water either from

food sources, e.g. succulent plants, or through metabolic water (Christian 1980). As *R. pumilio* was not observed drinking free water (available e.g. through fog or rain precipitation), it is assumed that the animals obtain water mostly through consumption of shoots and flowers of *A. horridus*, available year-round and which have a water content of more than 80% (Klo-

patek & Stock 1994). In addition to water, *A. horridus* flowers and shoots can be a source of nutrient rich food for animals feeding on it. An endomycorrhizal system that enhances nitrogen fixation in nutrient limited ecosystems, leads to a C/N ratio in the plant tissue that is higher than usual for desert environments (Klopatek & Stock 1994). Higher nutritional values of flowers

Table 4: Variables best explaining variation in proportion of males with scrotal testes as identified by best subsets multiple regression. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.00$

Factor	lag phase	Adj. R ²	p-value	Variable	lag phase	t-value	p-value	significance
Climate	at time	0,341	0,032	photoperiod	at time	2,357	0,036	*
	1 month	0,316	0,040	photoperiod	2 months	-1,372	0,198	
	2 months	0,458	0,021	minimum temperature	at time	-2,487	0,029	*
	3 months	0,545	0,008	minimum temperature	1 month	-2,162	0,052	
				maximum temperature	2 months	-1,541	0,152	
				maximum temperature	3 months	-2,098	0,060	
				fog precipitation	2 months	1,922	0,081	
				fog precipitation	3 months	1,220	0,248	
				relative humidity	1 month	1,943	0,076	
				relative humidity	3 months	-2,716	0,020	*
Food availability	at time	0,059	0,055	Nara flowers	at time	1,965	0,054	
	1 month	0,034	0,136	Nara shoots	at time	-1,275	0,207	
	2 months	0,035	0,087	Nara flower buds	1 month	1,668	0,101	
	3 months	0,161	0,024	Nara flowers	1 month	1,281	0,205	
				Nara shoots	2 months	-1,743	0,087	
				Nara flower buds	3 months	-2,297	0,027	*
				Nara flowers	3 months	-2,216	0,032	*
				Nara shoots	3 months	-2,768	0,008	**
			Nara melons	3 months	-2,032	0,049	*	
Diet composition	at time	0,270	0,071	Nara flower bud	1 month	-3,032	0,016	*
	1 month	0,526	0,037	Nara flower bud	2 months	-2,246	0,088	
	2 months	0,602	0,128	Nara flower	1 month	-2,964	0,018	*
	3 months	0,103	0,177	Nara flower	2 months	-1,784	0,149	
				Nara flower	3 months	1,467	0,177	
				Nara shoot	at time	-1,715	0,114	
				Nara shoot	1 month	-3,410	0,009	**
				Nara shoot	2 months	-2,300	0,083	
				Nara melon	2 months	-2,413	0,073	
				acacia seed pod	2 months	-1,558	0,194	
				detritus	at time	1,195	0,257	
				detritus	2 months	-3,285	0,030	*
			other	1 month	-3,115	0,014	*	
			other	2 months	2,379	0,076		

and melons were reflected in the preference for these portions of Nara plants by both males and females. By making use of the Nara plant, which is a source of both water, protein and other nutrients, *R. pumilio* is able to meet both its water and protein needs in an extreme environment that is otherwise water and nutrient limited. It is interesting to note how the breeding period is not restricted by water availability, in contrast to other studies on *R. pumilio* and other small mammal species in the Namib (Withers 1983, Christian 1979b).

Patterns of reproduction

Both sexes must meet expenses for all other bodily functions before energy can be allocated to reproduction (Bronson 1989). However, considerable greater energetic costs in females likely explains why females attain sexual maturity at a higher body mass compared to males (Bronson 1989). Thus reaching sexual maturity at a higher body mass ensures that they gain sufficient energy resources for pregnancy and lactation (Bronson & Manning 1991). In both sexes, non-reproductive individuals are heavier during the winter months, and body mass declines from September onwards. The signal of an average decline in body mass reflects the influx of young animals into the population.

To meet higher energy demands during reproduction, female small mammals increase their food intake (Kenagy 1987). During the lactational period, however, females of species living in arid areas do

not only have increased energy demand, but they also have an increased need for water, as moisture is lost with the milk (Rogowitz & McClure 1995). The timing of female reproduction in the population studied appears to be shaped by two main factors:

- 1) availability of high-quality food to meet the increased energy demands of reproduction, especially during late pregnancy and lactation, and

- 2) availability of moisture to compensate for the water loss during lactation.

This study revealed how, males are reproductively active throughout the year. Conversely, females do not allocate resources to reproduction over a short period during winter, over a period of low ambient temperatures, low humidity and reduced availability of Nara flowers and Nara melons. So although the species exhibits potential for year-round reproduction in the Namib, the actual reproductive period is determined by females who react to specific cues. This finding in a hyper-arid region reveals how *R. pumilio*, which is widely distributed throughout Southern Africa, exhibits plasticity and high adaptability is life history variation. It has been shown to be either seasonal (David & Jarvis 1985, Brooks 1974) or an opportunistic breeder (Perrin 1980, Taylor & Green 1976). Food supplementation has been shown to increase the length of the breeding season in this species, as well as the number of breeding individuals (Perrin & Johnson 1999), and reproductive seasonality of *R. pumilio* in arid areas might be governed by

the availability of free water (Christian 1979a).

Some small mammal species of the Namib breed strictly seasonal, related to fog occurrence (Withers 1983), or free water availability (Christian 1979b), while others are capable of breeding throughout the year (Christian 1979b). The population investigated in this study seemed to rely principally on *A. horridus* for its water supply, such that this buffered its breeding period against acute constraints in water availability.

Controls of reproduction

Bronson (1985) suggested three potential strategies for the timing of reproduction in small mammals. Opportunism, where males are reproductively active at all times, and females breed depending on energetic and nutritional consideration; photoperiod (Bronson 1985, 1989) or secondary plant compounds (e.g. 6-MBOA, Berger et al. 1981) as predictors for upcoming favourable conditions. Females usually exhibit higher sensitivity to these predictors compared to males (Jackson & Bernard 2001, 2005), as energetic costs of reproduction are higher. So, they are thus more sensitive to energetic challenges than males (Bronson 1989).

Climate and diet acted as cues for reproduction in both sexes, but not food availability as such. Diet, with an intake of nutrient-rich food, was the most important factor influencing reproductive activity in both males and females. Males were capable of reproducing throughout the year (as was evident by the presence of males with

scrotal testes at all times), while reproduction of females was inhibited for a short time period in winter. Cessation of female reproductive activity coincided with low humidity, short photoperiod, and low availability of Nara buds and flowers. The employment of different reproductive strategies for males (capable of breeding throughout the year) and females (breeding inhibited under challenging conditions) indicate an opportunistic reproductive strategy (sensu Bronson 1985, Bronson 1989) for *R. pumilio* in the Namib. It seems however, that water restriction (i.e. low humidity) were more important in inhibiting reproduction than low ambient temperatures or energy per se, as pregnant females were present during the coolest months of the study period.

Reproduction in *R. pumilio*, which has a wide distribution range, has been described as seasonal (Rowe-Rowe 1986, David & Jarvis 1985, Perrin 1980a, David 1980, Brooks 1974) or as opportunistic, controlled by access to a nutrient rich food source (Bowland & Perrin 1993, Wirminghouse & Perrin 1993, Perrin 1980a, Taylor & Green 1976) or water (this study, Christian 1979b). Nonetheless, Jackson and Bernard (2001, 2005) argued that reproduction in this species throughout its range is opportunistic, with ambient temperature and food availability working together to inhibit reproduction. This view is supported by the occurrence of pregnant females in the Cape winter (David & Jarvis 1985), and an extended breeding season and higher pregnancy rates as response to

supplementary food (Perrin & Johnson 1999) or water (Christian 1979b). Bronson (1985) regarded an opportunistic reproductive strategy as the most beneficial for a small mammal living in an unpredictable habitat in a warm climate. A reproductive strategy with no apparent predictors, where males are capable of breeding continu-

ously, and females are reproductively active depending on energetic and nutritional considerations (Bronson 1985), allows a species to respond rapidly to favourable environmental conditions (e.g. increase in food availability), water availability or ambient temperature, and thus to maximise their reproductive output.

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