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Seasonal reproduction by small mammals of the Namib desert

by Philip C. WITHERS 1983

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Petromyscus collinus
Aethomys namaquensis
Petromus typicus
Elephantulus rupestris
Apr '77 - Feb '78
Popln size estimates

L'activité reproductrice des rongeurs du désert du Namib s'est montrée hautement saisonnière et corrélative de la présence du brouillard plutôt que la pluie. Le potentiel reproductif des rongeurs est bas du fait d'une période de reproduction courte et de portées réduites. Un taux de mortalité peu élevé permet l'établissement d'une population plus ou moins stable. Le potentiel reproductif et le taux annuel de mortalité correspondent nettement à la taxonomie et à la phylogénie des rongeurs du Namib.

INTRODUCTION

The physiological, morphological and behavioral attributes of small desert mammals which enable them to survive in their harsh environment are well documented (see Schmidt-Nielsen, 1964 ; MacMillen, 1972). The small mammals of the Namib desert are similarly adapted to tolerate water deprivation (Withers, 1979 ; Christian, 1979 ; Withers *et al.*, 1980). However, little is known concerning the possible adaptive modification in life history parameters, such as reproductive potential and annual mortality rates whiich might accompany the physiological adaptations of desert rodents. Possible adaptative variation in demographic patterns is especially of potential significance to small desert mammals, which have high metabolic and water requirements, must reproduce every one or two years, and are unable to migrate to more suitable habitats during the breeding season.

Reproduction exacerbates the problems associated with a desert existence since it incurs additional water and energy requirements for both females (fetal development, lactation) and males (testicular development). It is therefore not surprising that reproduction by desert rodents is typically associated with periods of rainfall or subsequent plant growth (Chew and Butterworth, 1964 ; Delaney and Neal, 1969 ; Bradley and Mauer, 1971 ; Beatley, 1969 ; Okia, 1976 ; Kenagy, 1980). However, at least one desert rodent, the Antelope groundsquirrel, has an endogenous reproductive cycle (Kenagy and Barthelomew, 1979).

I examine here the reproductive cycle, and life-history parameters, for three Namib desert rodents, and one elephant-shrew, to determine whether the reproductive cycles of these species are annual, and whether climatic parameters such as rainfall or fog initiate breeding. The Namib desert is a cold, coastal desert which has a very low and erratic summer rainfall, but has advective fogs which

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provide a potential and reliable source of water for many plants and animals in the Namib throughout the year (Schulze, 1969 ; Seeley and Hamilton, 1976 ; Hamilton and Seeley, 1976 ; Louw, 1972 ; Seeley, 1979). I also examine the adaptive significance of life-history parameters to small desert mammals.

MATERIALS AND METHODS

The study site in Namibia was at Tumasberg, a large granitic koppie (rocky outcrop) located at 23°10'S and 15°32'E in the gravel plains region of the Namib Desert Park about 100 km from the coast. The study site was a mixed rocky/sandy habitat with very broken terrain, and the vegetation was a *Commiphora-Anthepora* community (Robinson, 1976) with very sparse vegetation cover (Withers, 1979). Climatic data (daily temperatures, humidities, rainfall) were obtained from a weather station located at Ganab, about 2 km from the study site. The weather station was maintained by the South West Africa Nature Conservation employees located at Gobabeb.

A permantly-marked 8 × 8 station trapping-grid was live-trapped for 3-6 consecutive nights at six intervals throughout 1977-1978. The Sherman live-traps were placed about 30 m apart, so that the grid covered approximately 6 hectares. Traps were typically set at dusk and captures monitored soon after dawn, but diurnal trapping regimes and frequent monitoring of captures during the night were occasionally utilized. The study period was form late summer (April 1977) to midsummer (February, 1978) and was not a full year, but essentially covered the entire breeding cycle from immediately post-partum to prepartum. Trapped animals were weighed with Pesola spring scales, and examined to determine sex, reproductive status (males — descended or undescended testes, presence of perianal flap ; females — presence of teats, whether the vagina was perforate or imperforate, and presence of fœtuses by palpation) before being individually marked by toeclipping and released.

Population sizes for the different species were calculated using the methods of Schumaker and Eschmeyer (1943) and Jolly (1965) for standard mark-release-recapture studies since animals were individually marked by toeclipping. A FORTRAN computer program was developed by the author for the analysis of mark-release-recapture data after the methods of Jolly (1965). Correct operation of the program was verified by analyzing Jolly's (1965) example. The stochastic model also enables the estimation of mortality rates between trapping periods, and immigration rates. Monthly survival rates were calculated as (1 — monthly mortality rate) by assuming that the mortality rate was constant between different trapping periods. Annual survival rate was calculated as the product of all of the estimated monthly mortality rates.

More detailed accounts of other aspects of the study site, ecology and physiology of the Namib rodents are provided elsewhere (Withers, 1979 ; Withers *et al.*, 1980).

RESULTS

The climate at Tumasberg was somewhat seasonal, with higher mean monthly air temperatures, ambient humidity, and rainfall during the summer months

(January To April) (see Withers, 1979). Annual rainfall was extremely variable from 1969-1977, at 105 ± se 36 mm (n = 9 years), and the rain tended to fall in many, light showers (mean rainfall per shower was 4.6 mm). The coefficient of variation for rainfall (100 × standard deviation/mean) was about 102 %. The rainfall pattern during the study period was low, even considering the great variability in annual rainfall.

Monthly occurences of advective fog, as indicated by the frequency of days with relative humidity greater than 95 %, and by personal observations, indicate a higher frequency of fogs during December to March, but it is not possible to accurately quantify the precipitation resulting from the occurence of advective fog.

Four species of small mammal were relatively common at Tumasberg, three rodents (rock mouse, *Petromyscus collinus*; rock rat, *Aethomys namaquensis*; dassie rat, *Petromus typicus*) and one Macroscelid insectivore (rock elephant-shrew, *Elephantulus rupestris*). Over the study period, 34 individual *Petromyscus*, 8 *Aethomys*, 8 *Petromus* and 3 *Elephantulus* were captured on 226, 85, 51 and 16 occasions, respectively. Population sizes for the rodent species estimated directly

TABLE 1. — Population size for the Namib rodents, and annual survival and immigration rates, for the 6 hectare study site.

	Petromyscus	*Aethomys*	*Petromus*
Population Size[a]			
April	4,-,-	1,-	2,-
June	30,-,49	21,-	2,-
Sept.	31,37,38	9,9	5,6
Nov.	25,38,23	10,8	19,15
Jan.	27,32,31	3,3	12,-
Feb.	22,-,22	3,-	0,-
Annual Survival[b]	0.36	0.04	high
Annual Immigration[b]	0	+10	+8
Litter Size	2-3	2-5	1-2
Litter Frequency	1	2	1
Reproductive Potential[c]	2-3	4-10	2-4

a Number of individuals captured, populations size from Jolly's model, and population size from Schumacher and Eschmeyer (1943) for *Petromyscus* only

b from Jolly (1965); see text

c per female; see text

as the number of individuals captured, calculated from the frequency of recapture (Schumacher and Eschmeyer, 1943), or from the stochastic mark-release-recapture method (Jolly, 1965), were similar (Table 1), indicating the fact that most of the individual rodents of the predicted total population were actually recaptured over the 3-6 consecutive trapping nights. The smallest rodent (*Petro-*

myscus, 20 g) had the largest population size on the 6 hectare study site whereas the largest rodent (*Petromus*, 100-200 g) had the lowest population size ; *Aethomys* (50 g) was intermediate. The elephant shrew (50 g) had a very small density (2 individuals on a 6 hectare site).

Estimated mean monthly mortality rates of *Petromyscus* for between trapping periods were fairly constant, at 0.89 (A-J), 0.92 (J-S), 0.95 (S-N) and 0.91 (N-J) ; $\bar{x} = 0.92$. Annual survival rate is therefore about 0.36 (0.92^{12}). Corresponding values for *Aethomys* monthly mortality rates were 1, 0.72, 0.82, 0.51 ($\bar{x} = 0.76$) ; annual survival rate is *ca* 0.04. The few recapture data for *Petromus* makes the calculation of mortality rate difficult — the only estimates were 1, 1 and. 1.1 ± 0.2 ; the annual survival rate cannot be calculated but is clearly higher than for both *Petromyscus* and especially *Aethomys*.

There was a seasonal pattern of change in population size for the three rodent species, but the pattern differed for each species (Table 2). The population size of *Petromyscus* was 30-40 individuals in June, and declined slowly throughout the year (annual survival rate = 0.36). *Aethomys* had a lower population size in June (about 20 individuals) and the population size declined markedly throughout the year (annual survival rate = *ca* 0.04). The population size of *Petromus* appea-

TABLE 2. — Comparison of estimated annual mortality and reproductive potential for small mammals from the Namib desert. Values are total juvenile and adult numbers for the 6 hectare trapping site.

		Petromyscus	*Aethomys*	*Petromus*	*Elephantulus*
INITIAL POPULATION SIZE		40	18	16	2
DEATHS		15	17	4°	-
NET IMMIGRATION⁺		3	1	few	0
REPRODUCTION					
Breeding females		12	2	4	1
Litters/female, young/litter		1 2	4 4	1 2	1-2
Total births		24	16	8	1-4
ANNUAL GAIN†	(1 litter)	<u>27</u>	9	<u>8</u>	<u>2</u>
	(2 litters)	51	<u>17</u>	16	4
NET ANNUAL GAIN*		12	0	4	2

⁺ calculated as total immigration X annual survival rate

° assumed for purpose of comparison; actual death rate is low, but could not be calculated (see text)

† underlined value is most likely

* calculated at 1 litter per year except 2 litters per yeat for *Aethoyms*

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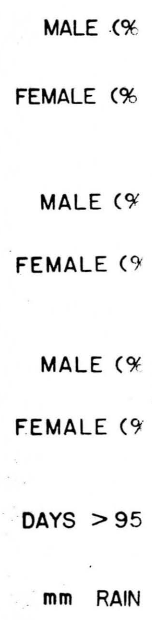

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red to increase throughout the year, according to the recapture data. However, *Petromus* could be censused visually since they are diurnally active, and there was no apparent seasonal change in population size according to visual observation. For example, no *Petromus* were captured in February, despite their being common on the study site. The apparent increase in population size of *Petromus* is inconsistent with visual observations, the timing of reproduction (see below) and estimates of immigration (Table 2), hence is likely an artifact of changes in trappability of *Petromus* throughout the year.

There were only three individual *Elephantulus* present on the trapping site (one male, one female, one juvenile) at any time, hence it is impossible to calculate any demographic parameters for this species. Nevertheless, it is clear that the density of *Elephantulus* is extremely low, their home-range area is very extensive, and they probably have a low annual mortality rate.

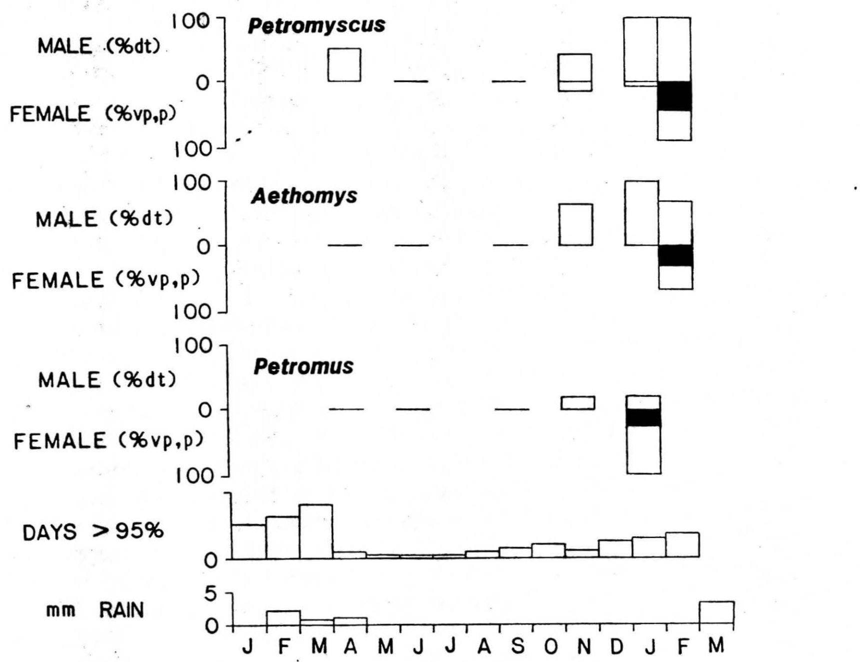

Fig. 1. — Reproductive status (males — % descended testes; females — % with perforate vagina (open) and % with fœtuses (closed) symbols) for *Petromyscus*, *Aethomys* and *Petromus*, days with relative humidity greater than 95 % (i.e. probable fog) and rain fall (mm) during this study (1977-1978).

Reproductive activity of the three rodent species was highly seasonal, with males coming into reproductive condition slightly before females, and with the peak of reproductive activity occuring during the summer (Fig. 1). The female elephant-shrew appeared to be reproductively receptive throughout the year, but it could not be determined whether the male had any seasonal reproductive cycle since the testes are internal.

DISCUSSION

The Namib desert is a coastal desert with moderate temperature extremes and low, erratic rainfall. Annual rainfall at the study site was 105 ± 36 mm, with a very high coefficient of variation, 102 %. In contrast, the deserts of North America and Australia have much lower coefficients of variation at about 20-40 % (see Morton, 1979). The physiological adaptations of desert rodents to their extreme abiotic and biotic environment are well documented, but it is not clear whether demographic parameters, such as biomass density, home range size, annual mortality rate and reproductive potential show adaptive evolution. This study documents the annual reproductive cycle for three Namib rodents, and one insectivore, and examines whether the life histories of the species indicate if certain demographic patterns confer a selective advantage to desert species.

The demographic parameters of Namib rodents, such as numerical density, biomass density, home-range area, are typical for other desert and non-desert rodents (Withers, 1979 ; French *et al.*, 1975). The rock elephant-shrew, in contrast to the rodents, had an extremely low density and very large home range area, as do bush-veld elephant-shrews (*Elephantulus intufi ;* Sauer, 1973) and golden-rumped elephant-shrews (*Rhyncocyon chrysopygus ;* Rathbun, 1973). The low density and large home-ranges of elephant-shrews most likely reflects a low density of arachnid prey items.

The reproductive patterns of the Namib desert rodents were highly seasonal, but appeared to be poorly correlated with local rainfall (Fig. 1). The male rodents, and also female *Petromus*, attained breeding condition during early summer (November), after only approx. 0.6 mm of rain. The Namib rodent species were fully reproductive, with females pregnant, in mid-January, before significantly more rain had fallen. This reproductive pattern is unlike that of other desert and non-desert rodents, which generally breed after either the main seasonal rainfall or the resulting plant bloom (e.g., Chew and Butterworth, 1964 ; Delaney and Neal, 1969 ; Beatley, 1969 ; Bradley and Mauer, 1971 ; Okia, 1976- ; Kenagy, 1979). Such conditions of seasonal onset of reproduction with rainfall is not surprising in view of the additional energy and water requirements for reproduction (e.g., Baverstock *et al.*, 1979).

The reproductive cycle of Namib desert rodents appears to be exceptional since they breed before any significant seasonal rainfall. It is possible that the Namib rodents have an endogenous reproductive cycle, like the Antelope ground-squirrel of North American deserts (Kenagy and Bartholomew, 1979), but this is unlikely considering the low and erratic rainfall of the Namib. If rain was required for successful reproduction, then a fixed endogenous cycle would appear maladaptive for Namib species where rainfall is so ephemeral, and the breeding effort for 1980 would have failed.

Rainfall, however, is only one of the potential sources of water for the Namib rodents. Advective fogs, which form over the cold coastal ocean currents, may move up to 100 km inland, and the occurence of such advective fogs at Tumasberg (as indicated by the monthly frequency of days with relative humidity greater than 95 %) increases after September. Although rainfall is also more likely after September, the occurences of fog and rainfall are statistically-independent (association test; $X^2 = 0.85$; Pielou, 1969). This lack of assocaition between fog and rainfall is expected, since fog forms over the coast and moves towards the east, whereas the summer rains approach from the east, being remnants of subtropical anticyclones. Advective fog provides a supplemental water source for plants, invertebrates and vertebrates of the Namib (Bornmann *et al.*, 1972; Louw, 1972; Seely and Hamilton, 1976; Hamilton and Seely, 1976; Seely, 1979). It is apparent that the Namib rodents become reproductively active after an increase in frequency of fogs (Fig. 1). Withers *et al.* (1981) have shown that the rodents have an increased rate of water turnover after fogs; the water could be gained by drinking the fog condensate, by consumption of rehydrated vegetation and by consumption of hydrated insects. There was a clear alteration in the hydration state of most of the plants on the study site, although little new growth occured. Diet analysis throughout the year did not indicate any significant changes in proportion of seed, leaf, stem or insect material (Withers, 1979), but changes in plant hydration state would not necessarily be indicated by such a study. It is possible that the Namib rodents could successfully reproduce in the complete absence of rainfall by obtaining sufficient water from the advective fogs, probably via food.

Few data concerning reproductive activity were obtained for Elephant-shrews, although the female appeared to be sexually active throughout the pear. Elephant-shrew females have true polyestrous cycles. *Elephantulus* may be even less dependent upon rain and fog for reproduction than are the rodent species as their strictly insectivorous diet might provide sufficient water for reproduction throughout the year. The low density of elephant-shrews, and their extremely large home-range area, reflect, however, their reliance upon a relatively rare food resource, insects.

The seasonal reproductive cycle of the Namib rodents, despite its being potentially independent of rainfall, is clearly of short duration and markedly reduces the annual reproductive potential. Reproductive potential is equal to (number of young per litter) × (number of litters per year). The small mammal species have a variable number of young per litter; *Petromyscus*, 2-3; *Aethomys*, 2-5; *Petromus*, 2-4; *Elephantulus*, 1-2 (Shortridge, 1934 and personal observations). The number of litters per year is more difficult to estimate, but *Aethomys* might have two litters per year whereas *Petomyscus* and *Petromus* probably have only one litter per year. No data were obtained pertinent to the number of litters produced per year by *Elephantulus*. The projected annual reproductive potentials of the rodents are thus; *Petromyscus*, 2-5; *Aethomys*, 4-10; *Petromus*, 2-4; *Elephantulus*, 1-2 (Table 2). Although these data for reproductive potential of the Namib species are for one year only, they can be compared with the observed annual mortality rates to determine whether the population size of the species is stable.

The annual mortality rates of the Namib rodents, calculated from the mark-release-recapture study (Table 2), are for juvenile and adult animals only (*i.e.* animals which have left the nest and could be trapped). The annual mortality rate of *Aethomys* was much greater than that of *Petromus* and *Petromyscus* (Table 2). The observed annual mortality rates of the Namib rodents in fact are consistent with the previous estimates for annual reproductive potential (Table 2). The estimated annual reproductive potential for *Petromyscus* of 40 individuals over the six hct study site (assuming 1 litter per year) exceeds the estimated annual mortality rate of 23 individuals. Fetal and infant mortality is not included in the estimated mortality rate, and would account for part, or all, of the difference between annual production and mortality (*i.e.* 17 individuals). *Petromus* could also maintain a stable population size with one litter. In contrast, the observed annual mortality for *Aethomys* (18 individuals) is closely balanced by the reproductive potential assuming 2 litters per female per year. Cheeseman and Delany (1979) estimated in similar fashion that tropical African rodents had a considerable post-natal mortality, of about 30-60 %. I estimate that post-natal (and/or fetal) mortality for *Petromyscus* is about 50 % whereas *Aethomys* is predicted to have 0 net annual gain, i.e. no scope for post-natal mortality (Table 2). *Petromus*, given a low annual mortality, has a net annual population gain of perhaps 4 (Table 2), part or all of which could reflect post-natal mortality.

Petromus and *Petromyscus* are equilibrium species (low reproductive potential and annual mortality) whereas *Aethomys* is opportunistic with a higher reproductive potential and annual mortality. Elephant-shrews, unlike most soricid insectivores, are equilibrium species. These differences amongst the Namib rodent species are also correlated with differences in their physiological capacity and their evolutionary history in the Namib desert (Table 3). *Petromus* is the geologically-oldest inhabitant of the Namib (Meester, 1965) and is the most « K-selected » or equilibrium of the rodent species. *Aethomys* is a relatively recent invader of the Namib desert and is the most « R-selected » or opportunistic. In fact, *Aethomys*

TABLE 3. — Ranking, for comparison, of demographic parameters, physiological parameters and evolutionary history of the Namib rodents. 1 = low, 2 = intermediate, 3 = high. Data from present study, Withers (1979) and Withers *et al.* (1980) and unpublished data for kidney structure.

	Petromus	*Petromyscus*	*Aethomys*
Annual mortality	1	2	3
Reproductive potential	1	2	3
Water turnover rates	1	2	3
Energy turnover rates	1	2	2
Urine concentrating ability	3	2	1
Ability to survive on dry seed diet	?	3	1
Geologic time in Namib	3	2	1

is a marginal rodent species at Tumasberg in terms of population stability and physiological capacity ; it is not present in the more xeric parts of the Namib, although *Petromus* and *Petromyscus* are ; *Aethomys* has a very low survival rate/reproductive potential even in comparison with many other rodents. *Petromyscus* is intermediate to *Petromus* and *Aethomys* is reproductive potential, mortality rate, and a variety of physiological aspects (Table 3).

There are clear correlations between evolutionary history, population demography and physiology for these Namib rodents (present study) and other Namib rodents (Christian, 1979). It is tempting to conclude that selective pressures have operated on desert rodents to minimize the water and energy requirements of

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reproduction *i.e.* reduce reproductive potential and increase survivorship. However, reproductive potential and annual mortality rate also reflect taxonomic affinities (French *et al.*, 1975). Certain rodent taxa (e.g., cricetids, sciuro-morphs) typically have higher annual survival rates and lower reproductive potentials than other taxa (e.g., murids, microtines). The correlation between the demographic parameters of the Namib rodents reported here, and that reported by Christian (1979), with physiological parameters may be somewhat biased by the extent to which demographic parameters are determined by taxonomic affinity. Equilibrium rodents (such as sciuro-morphs and cricetids) may be preadapted to desert niches relative to opportunitic species, by virtue of their low reproductive potential and high annual survival rate.

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SUMMARY

The reproductive pattern of Namib desert rodents is highly seasonal, and of short duration. Reproductive activity appears to be correlated with the occurence of advective fog rather than rainfall. The short reproductive season is reflected by low reproductive potential, and is associated with low annual mortality. Other demographic parameters, such as numerical density, biomass density and home-range area, are similar for the Namib rodent species and other desert and non-desert species. It appears that a low reproductive potential and high annual survival are adaptations, or preadaptations, for the successful exploitation of desert niches by small mammals.

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