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Population ecology of the Hairy-footed gerbil, *Gerbillurus paeba*, in a coastal dunefield of South Africa

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Abstract

Studied was a population of the hairy-footed gerbil, *Gerbillurus paeba*, in the Alexandria dunefield along the eastern Cape coast, South Africa, from March 1981 to July 1982. *G. paeba* is the only resident rodent species and is endemic to this dunefield. A mark multiple-recapture study showed that the gerbil density was low, averaging 1,7 gerbils/ha. Annual population turnover occurred, with highest and lowest numbers being found in late summer and late winter, respectively.

Introduction

The species *Gerbillurus paeba* Smith, 1836, contains four subspecies of "hairy-footed gerbils" typical of arid sandy habitats in southern Africa. Of these, *Gerbillurus paeba exilis* Shortridge & Carter, 1938, is unique in being recorded from only a single coastal sand dunefield. It thus warrants special conservation status for which knowledge of its population biology would be useful.

The most widely used method for obtaining data on the population dynamics of small mammal populations is mark-recapture census coupled to a population model which yields estimates of population numbers and gain and loss rates. This method was used to investigate the population ecology of the hairy-footed gerbil *G. p. exilis* in coastal dunes.

Material and methods

Study area

The Alexandria dunefield, lining the northern shores of Algoa Bay, is the largest active coastal dune system in South Africa. The major part of the dunefield lies between the mouth of the Sundays River (33° 44′ S; 25° 51′ E) and Cape Padrone, 48 km to the east. The climate is warm temperate, but variable. Rain may occur in all months of the year and averages 400–800 mm p.a. along the dunefield from W to E. Mean annual temperature for the study period (1981 and 1982) was 17.7 °C. Lowest and highest temperatures recorded were 3.9 and 40.0 °C, respectively.

The dunefield includes a series of 36 damp hollows (slacks) separated by bare dune ridges, extending in a strip 3.5 km long, parallel to the shoreline. Five slacks were covered by the live trap grid. Each slack is approximately 200 m long and 40–50 m wide. Due to the action of the predominantly west winds, the slacks migrate eastwards at a rate of 7 m per year. To the south, they are bordered by the beach, to the north, by high dunes (McLachlan et al. 1987) (Fig. 1).

Vegetation in the slacks is sparse, averaging 2–10 % cover and rarely exceeds 0.5 m in height. Most abundant plants are two hummock forming species, *Arctotheca populifolia* and *Gazania rigens*, and sandgrass, *Sporobolus virginicus*. *G. p. exilis* is the only rodent permanently resident in the slacks.

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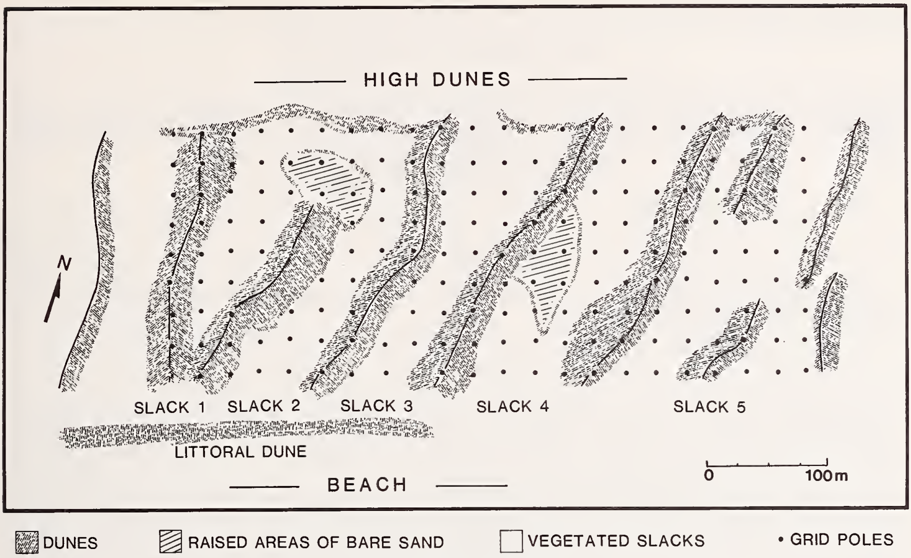

Fig. 1. The study grid

Trapping procedure

A mark multiple-recapture programme was carried out from March 1981 to July 1982 at three-weekly intervals. A fixed grid was laid out over six dunes and their five corresponding slacks, chosen as being typical of the area. The grid covered the entire length of the slacks, since a pilot study indicated that the slacks were the chief habitat of the gerbils. The grid dimensions were 525 m × 200 m (area: 10.5 ha), with the long axis lying parallel to the beach (see Fig. 1): 198 poles were placed 25 m apart in 9 rows of 22 lines. Approximately half the stations were situated on dune slopes, the remainder in slacks. Each trapping session lasted 48 h. On trap night one, all traps were moved 25 m and reset at the previously vacant stations. The two trap nights comprised one trapping session, the data from the two nights being pooled.

Every alternate trapping session the sampling was extended to last three nights. On the third night 40 traps were placed in a square outside of the grid (10 traps per side). The distance of this square from the outermost stations of the grid varied from 50 m to 200 m, averaging 100 m. The additional information obtained from these traps was used to estimate population density more accurately by quantifying immigration and emigration, and in analysis of home ranges of individuals.

Small Sherman aluminium live-traps, baited with a mixture of rolled oats and water, were set in the late afternoon and checked the following morning. Each trap was set with its entrance opposite the prevailing wind. During very windy or rainy weather each trap was covered with a plastic bag, to provide cover. Squares of loosely woven material were provided as thermal insulation. Each newly-captured gerbil was individually marked using an ear-clipping technique, identified, weighed to the nearest 0.5 g, sexed, and its reproductive condition recorded. Males were classified as having scrotal or abdominal testes, while females were classified according to nipple size [medium or large (Krebs 1966)] and pregnancy. The location of each capture was noted and the gerbils released at the point of capture.

Analysis of data : trapping success, trap efficiency and trappability of the population

Nelson and Clark (1973) have stressed the need to account for decreases in trapping efficiency resulting from traps being rendered ineffective, and suggest a correction factor. It is assumed that, on average, each sprung trap is ineffectual for half the trapping interval. The percentage trapping success has been calculated as:

$$\%\ \text{trapping success} = \frac{A \times 100}{N - S/2},\ \text{where A = no. of animals captured;}$$

N = no. traps; S = total no. of traps sprung by mice or nonfunctional.

Percentage trap efficiency is calculated as:

$$\% \text{ trap efficiency} = \frac{(N - S/2) \times 100}{N}$$

Trap efficiency was only quantified from the fourth sample onwards.
Trappability of the population (Krebs et al. 1969) was estimated as:

$$T = \frac{\text{no. caught at time t} \times 100}{\text{no. known to be alive at time t}}$$

Sex ratio

Chi-square tests, incorporating Yates' correction for continuity (Zar 1984), were used to determine whether the sex ratio deviated from parity.

Age structure

Since the only reliable age determination criteria (e.g. eye lens weights) are obtained from dead animals (Morris 1972), no absolute age classes could be established. It was felt that no animals in the dune area should be snap-trapped, since the total area of suitable habitat is small, and population numbers were low. Although body weight is not a good criterion of age, since it is influenced by, inter alia, diet and season (Pucek and Lowe 1975), it has been used as an approximate indicator of age (Krebs 1966; Tamarin 1977; Perrin 1979; Montgomery 1980) and is easily measured in the field (Ford 1981). The study population was divided into two classes, juveniles and adults, on the basis of weight (and sexual maturity). Juveniles were defined as those animals having a mass of ≤ 26 g. The males had abdominal testes and the females had very small, undeveloped nipples, characteristic of females that had never produced a litter.

Population size, recruitment, losses

Population size was estimated using the direct enumeration method of Krebs (1966).

Minimum Number Alive (MNA) at time t = actual no. caught to time t + no. of previously marked individuals caught after time t, but not at that time.

This method has been used frequently: Tamarin 1977; Perrin 1979; Christian 1979, 1980; Chidumayo 1980. Cheeseman and Delany (1979) compared the results obtained from five methods of population assessments for rodents in tropical African grassland and concluded that the direct enumeration method was the most satisfactory.

Survival rates were calculated after the method of Krebs (1966): minimum survival rate (S)

$$= \frac{\text{no. of individuals known to be alive at time t + x}}{\text{no. known to be alive at t}}$$

where t = time and x is the interval between sampling occasions. 1 − S = population loss (emigration + mortality). Student's t-test (Zar 1984) was used to test for differences between summer and winter survival rates.

Population density

Estimating population density, by dividing the population number by the area of the grid, usually results in an overestimate of density, since the effective sampling area (from which mice move to traps) is actually larger that the grid (Smith et al. 1975). An attempt was made to reduce this bias by adding a boundary strip to the area of the grid, the width of which represents the average distance moved between successive captures (Brant 1962). The boundary strip was added to the eastern and western sides of the grid, since only these sides were bordered by suitable habitat. Population density was estimated by dividing the MNA population estimate by: 10.5 ha (grid area) + 4.0 ha (boundary strip) = 14.5 ha.

Results and discussion

General trapping results

138 gerbils were captured 725 times during the study. There was a marked seasonal change in numbers (Fig. 2), with lowest numbers occurring in late winter and peak numbers in late summer, following the onset of the breeding season. Trapping success averaged 23 %,

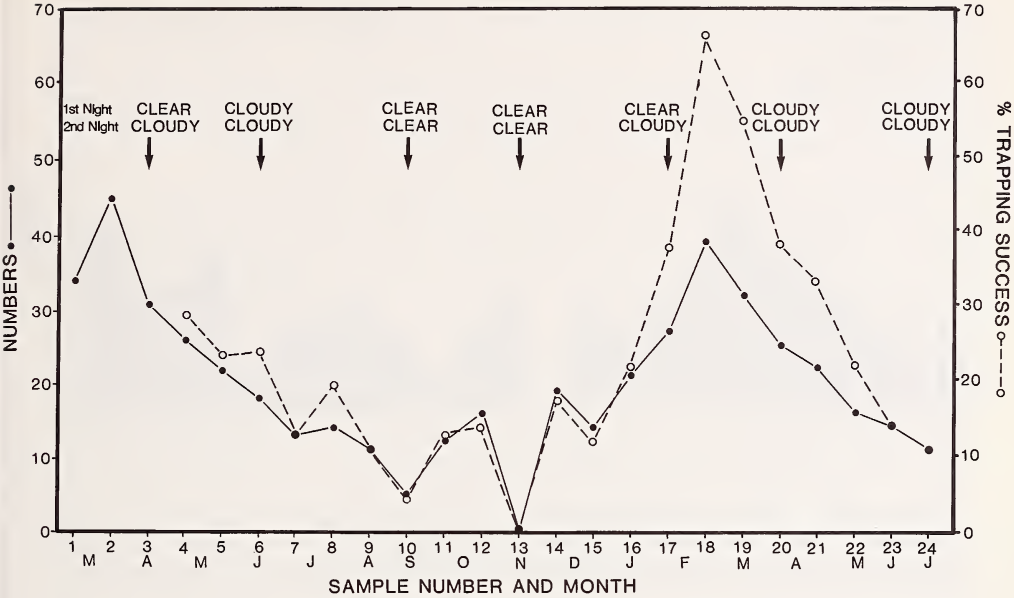

Fig. 2. Numbers of *G. p. exilis* caught from March 1981 to July 1982. Arrows and annotations indicate sample near full moon and cloud cover. Broken line indicates percent trapping success

dropping to 0 % in November and peaking at 67 % in February (Fig. 2). Numbers of gerbils captured was low, despite the use of a large grid. The low capture rate is not due to a faulty trapping procedure. Smith (1968) has stated that the probability of an animal being caught in a trap is the product of: 1. the probability of the animal encountering a trap, 2. the efficiency of the trap and 3. the response of the animal to the trap. With regard to (1), the large distance moved by the gerbils reduces the probability of large trap spacing causing of small sample sizes; many gerbils were caught at several hundred meter intervals on successive nights. Southern (1973) warns that sufficient traps must be available for all potential captives: in the present study, no more that 33 % of the traps were full on any occasion.

Trap efficiency (2) was quantified regularly, each trap being checked each morning. The major causes of non-functioning traps were clogging by sand in windy conditions (24 %) and traps sprung either by the wind or by isopods *(Tylos capensis)* or earwigs *(Labidura riparia).* The unstable substrate and sparseness of vegetative cover caused sampling errors: although traps were covered with plastic bags in unfavorable weather to minimise the amount of sand entering through joints, and placed with their entrances away from the prevailing wind, the wind often changed direction (unpredictably) during the night and traps facing into strong wind filled with sand within minutes. Despite these difficulties, trap efficiency never fell below 59 %, and averaged 69 %. Trap efficiency is unlikely to have biased sampling results significantly. This leaves only the response of animals to the traps as a possible cause of small samples. Since both adults and juveniles, males and females, were captured, recapture numbers were high and the average trappability of the population was 79 %, it seems unlikely that any part of the population was permanently untrappable. A variable response by individuals, or differences between animals of different social rank might be implicated.

More mice in a population may be caught if each sampling period is extended (Smith 1968). Sampling for more than two days per sampling trip was logistically impossible in the present study. However, results obtained from 11 sampling occasions when traps were set for a third night, show that a further 6 % of marked individuals were caught on the third night that were not captured on one of the previous two nights. Unmarked gerbils caught on the third night are assumed to have been drawn from outside the study grid. Two trap nights therefore appear to be adequate for enumeration of the study grid population. Since less than half the grid area comprised suitable habitat, it might be realistic to express the effective grid as 5.25 ha, rather than as 10.5 ha, thereby doubling density.

Sampling number 13 (November 1981) was omitted from the results, because only one gerbil was caught during the entire 48 hours sample. The minimum number known to be alive was 12. The percentage of gerbils recaptured was high, averaging 80 % for the study period, excluding the first two samples, since the marking programme was just beginning, as well as sample 13. The lower number of recaptures in August and October (samples 8, 9, 11, 12) was due to the appearance on the grid of new, adult, mostly male mice, presumably to occupy gaps in the area left by gerbils that had died during the winter, and also to breed. From early December onwards (samples 14–18) the smaller number of recaptures was due to the appearance of new, juvenile mice from the spring-summer breeding period as well as new, older individuals (Ascaray 1986). The recapture rates of males and females were similar. Slightly higher recapture rates of females from March-June 1981 and males from February-May 1982 can be attributed to the higher numbers of females and males, respectively, during those periods. The high recapture rate tends to support the conclusion that the low numbers captured indicate a small population and are not a sampling artefact.

Population structure

Sex Ratio

Of the 138 gerbils marked, 67 were male and 71 were female, giving a sex ratio of 1 male : 1.06 females. This does not differ significantly from a 1 : 1 ratio (chi-squared; $p > 0.05$). Since male *G. p. exilis* move larger distances than females during the breeding season (Ascaray 1986), there may in fact be a lower proportion of males than the sex ratio suggests.

The number of females caught was consistently lower than the number of males, except for April and May 1981. Since numbers from individual samples were mostly too small to perform valid statistical tests, the data were grouped and tested for seasonal differences. There was not significant deviation from a 1 : 1 sex ratio in any one season (Chi-squared; $p > 0.05$).

Age structure

The age structure of *G. p exilis* over 17 months (Fig. 3) indicates a population of seasonal breeders, since juveniles are produced in cohorts at fixed intervals.

There were no juveniles present in the population from July 1981 to early October 1981 since all juveniles from the previous breeding season had reached maturity by July 1981. They overwintered as adults and began breeding in September. Appearance of juveniles in the population was delayed until the end of October, when those conceived at the beginning of the season had been weaned and were emerging from nests to become part of the trappable population. The number of juveniles began to decrease at the end of the breeding season as they matured. All juveniles reached adulthood by the end of June 1982.

The number of adults decreased following the end of the breeding season, despite the recruitment of maturing juveniles. This appears to have been due to the death of the adults born in the previous breeding season. Of 71 gerbils, only three individuals (4 %) were known to have survived one year. The longest-lived gerbil survived 13 months. *G. p. exilis* exhibits annual population turnover, i.e. juveniles from one breeding season do not survive beyond the next breeding season.

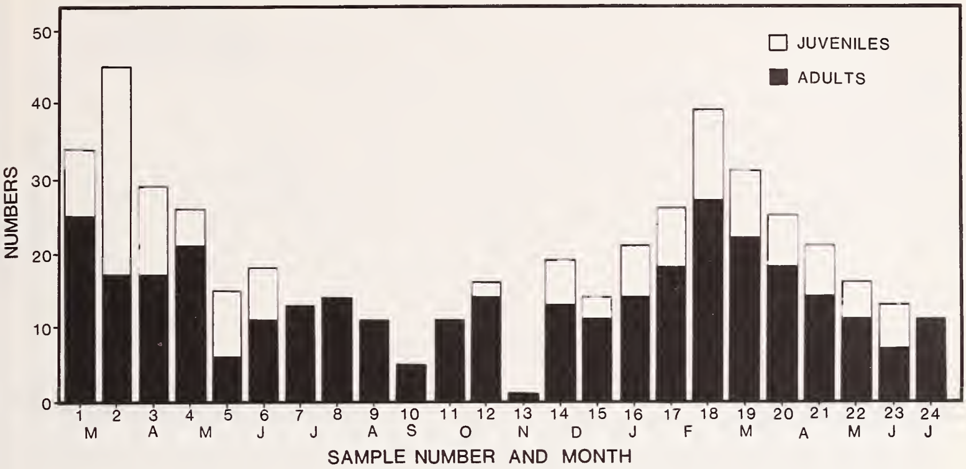

Fig. 3. Age structure of *G. p. exilis*

The unusually large number of juveniles captured directly after the flood on March 1981 may have been trapped on the grid by the water. They had died or emigrated from the area before the following trapping occasion.

Population dynamics

Population size

The MNA gave population estimates 24 % higher than the numbers trapped (Fig. 4). Bishop and Sheppard (1973) have found that the population estimate is usually reliable when 9 % or more of a population is sampled, and the survival rate is not less than 0.5; both these conditions were fulfilled. Hilborn et al. (1976) noted in simulation studies that the MNA is generally 10–20 % below population size.

Peak numbers (MNA = 48) occurred in February-April, while numbers reached their lowest just after the winter months, in later August and September (MNA = 10). This fluctuation was caused largely by the seasonal breeding pattern. The breeding period gave rise to high numbers in late summer, which, because of increased mortality during winter and very little further recruitment, declined to a low before the start of the next breeding season. Christian (1979, 1980) found that *G. p. paeba* in the Namib Desert reached peak numbers in September-October and then declined. Boyer (1987) recorded reproduction and recruitment of *G. tytonis* in summer in the Namib. This seasonal pattern is the converse of the pattern occurring in the Alexandria dunefield. In the Namib Desert, the timing of reproductive season is controlled by rainfall and there is a pronounced decline in breeding activity during the hot dry portions of the year (Christian 1980). Nel (1983) reports that *G. paeba* reaches peak numbers in July in the Kalahari Gemsbok National Park, with lowest numbers occurring in December. Similarly, this cycle appears to be adapted to the rainy season, which extends from November to April, peaking in January-March, depending on location (Nel and Rautenbach 1975). Water is not a limiting factor in the Alexandria dunefield (Ascaray 1986) and the breeding period of *G. p. exilis* appears to be controlled by plant production rather than by rainfall per se.

Marked fluctuations in density over several years are common in desert rodents. These fluctuations are caused by a variation in reproductive activity, which depends on plant production, and thus ultimately on the highly erratic rainfall such regions receive (Christ-

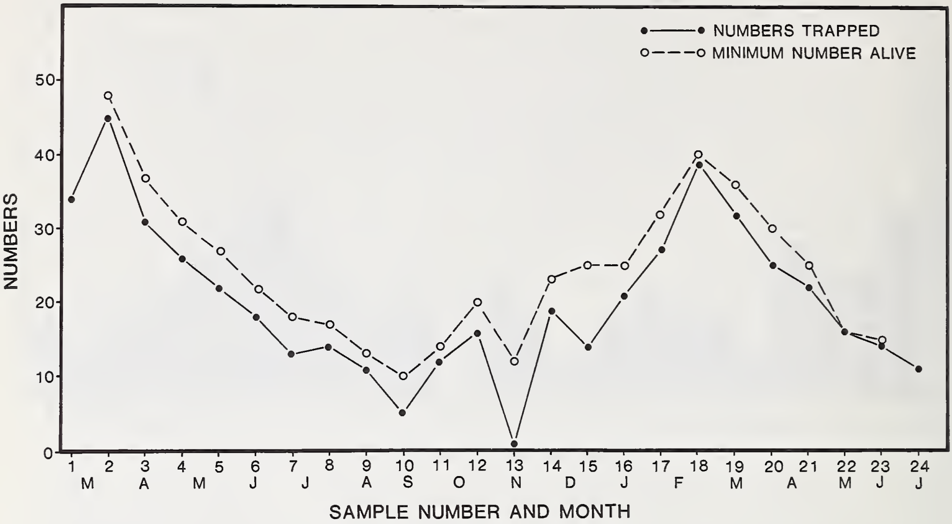

Fig. 4. Two estimates of population size of *G. p. exilis*

IAN 1980). NEL (1983) demonstrated large population fluctuations of *G. p. paeba* in two different habitats over several years in the Kalahari Gemsbok National Park. No long term data are available for *G. p. exilis*.

Population losses

A decrease in population size may be due to emigration and/or mortality: they are often quantified together as population loss. Population loss can only be estimated for the trappable population; neonatal mortality is excluded. Results may be expressed as survival rates, where survival = 1 – population loss (thereby introducing an error). Survival estimates, based on MNA are shown in Fig. 5. It is preferable to calculate survival of adults and juveniles, males and females, separately, since each class may suffer differential mortality. CHRISTIAN (1980), for example, found that male *G. p. paeba* in the Namib Desert have a significantly higher survival rate than females. The two estimates for the dune slack populations are very similar, the average being 4 %.

According to KREBS (1966), estimates of survival are accurate when recapture rates are high, as in the present study. Survival between samples, averaged 0.80 for the study period. CHRISTIAN (1979) found a similar mean rate of ≥ 0.84 for Namib Desert populations. Survival was significantly lower in winter than in summer ($p < 0.05$) in the dune slacks. Possible reasons are colder temperatures and decreased food availability. The combination of low temperatures and protracted rainy weather when burrows become completely saturated, may be particularly unfavorable to the gerbils.

The seasonal increase in population size appears to have two causes: and increase in survival rate as well as the influx of new individuals.

The March 1981 floods appeared to affect survival, since the survival rate dropped from 0.74 to 0.66 following the flood. Juveniles were most affected.

Predators which visit the dune slacks include jackals, genets and owls. Jackal tracks indicated that gerbils were taken by jackals. LAYCOCK (1975) reported that several gerbils were removed from traps by jackals in the Namib Desert. One gerbil was taken by a genet on the slip-face during the pilot study (ASCARAY 1980) and genet tracks were regularly observed in the dune slacks. *G. paeba* skulls have been found in barn owl pellets near the dunefield (ASCARAY 1980).

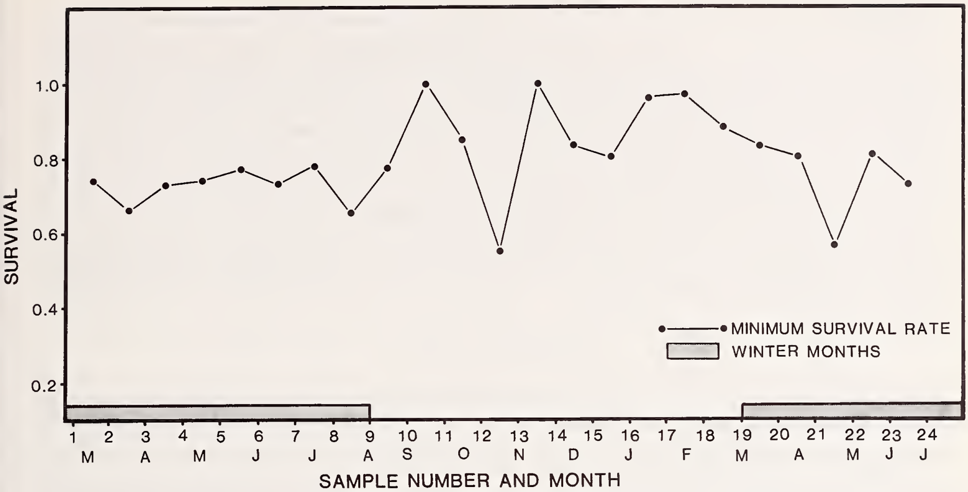

Fig. 5. Survival rate (per 3 weeks) of *G. p. exilis*

Recruitment

Recruitment is the result of two processes: immigration and birth. Minimum recruitment per trapping occasion, calculated from MNA values, is presented in Fig. 6. Actual recruitment rates might be slightly lower since 46 % of the new captures were possibly transients (gerbils captured on fewer than 3 successive sampling occasions). However, since transients are arbitrarily defined, they are not analysed separately.

There was a marked increase in recruitment rate from October. The recruitment rate for the summer months (October 1981 to February 1982) was ≥ 0.20 per three weeks, leading to a considerable increase in population numbers. Recruitment was much lower during winter, averaging 0.09. The increased summer numbers can be attributed to adult immigration, the start of the breeding period and juvenile recruitment during the season. It

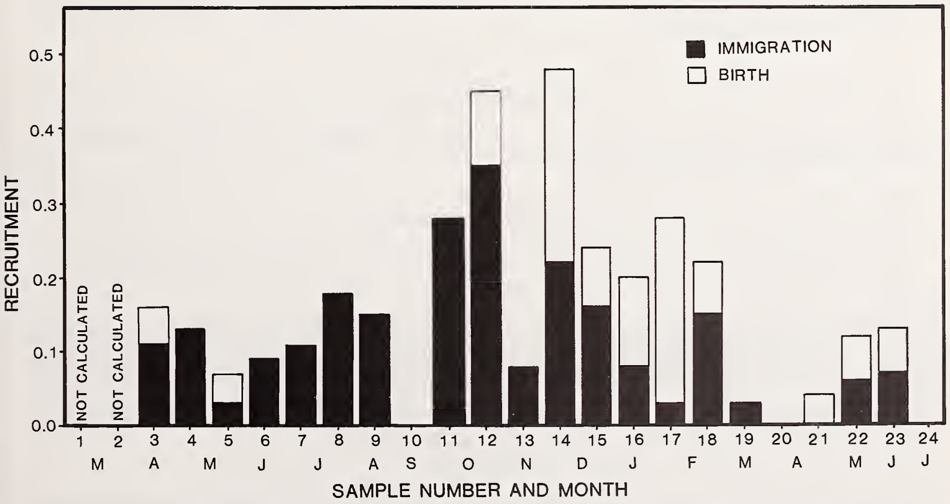

Fig. 6. Proportion of recruitment of *G. p. exilis* due to immigration and birth

is possible, to some extent, to distinguish birth and immigration, if newly-caught, young animals are regarded as juveniles and newly-caught adults are assumed to be immigrants. This division does not consider young immigrants or the fact that some individuals born in the area may not be captured until adulthood. Fig. 6 shows the likely proportions of recruitment due to immigration and birth. Juveniles first appeared at the end of October and formed a significant proportion of recruitment until the end of February. On average, however, immigration of older individuals appears to have played a greater role in recruitment than reproduction, the mean rates being 0.10 and 0.05, respectively. CHRISTIAN (1980) reported one instance of large-scale immigration of *G. paeba* onto a trapping grid, but stated that generally, rates of growth in the populations he examined were sufficiently low to be explained in terms of breeding.

Population density

Population density has been measured as MNA per hectare. Because density can only be measured for the trappable population, the actual density of the gerbil population may be higher than the estimates given here. Allowance was made for individuals whose ranges lie on or near the borders of the sampling grid by the addition of a boundary strip. Average gerbil density was 1.7 gerbils/ha, with lowest density occurring in September (0.7/ha) and highest density in March (3.3/ha). Since only 50 % of the sampled area comprised suitable habitat, the densities were recalculated using an area of 7.25 ha, which represents the vegetated parts of the grid and boundary strip, where burrows occur. This gives an average density of 3.4 gerbils/ha (range: 1.4/ha–6.6/ha), or three gerbils per slack (range 1–7). Both density estimates approximate those of other rodents inhabiting sparsely vegetated areas. Minimum and maximum densities of the beach mouse, *Peromyscus polionotus leucocephalus,* were found to be 2.2/ha and 3.4/ha, respectively (BLAIR 1951). CHEW and CHEW (1970) in DELANY (1976) give minimum and maximum densities of 0.4/ha and 3.3/ha for *Peromyscus eremicus,* a rodent inhabiting the Californian desert.

Conclusion

With 36 slacks in the Alexandria dunefield, the total population size of *G. p. exilis* is estimated at 108 (36–252) individuals, although this may be an underestimate. Since the Alexandria dunefield was declared a conservation area, the future of this small unique population seems favourable.

Acknowledgements

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Zusammenfassung

Populationsökologie des Rauhfußgerbills Gerbillurus paeba in einem Dünenfeld an der Küste von Südafrika

Untersucht wurde eine Population von Rauhfußgerbills, *Gerbillurus paeba*, von März 1981 bis Juli 1982 im Alexandria-Dünenfeld entlang der östlichen Kapküste von Südafrika. Hier ist *G. paeba* die einzig ständig vorkommende Nagetierart. Die Wiederfang-Studie einer markierten Population zeigte eine geringe Dichte von durchschnittlich 1,7 Gerbills/ha. Es findet ein jährlicher Populationswechsel statt. Die höchsten Fangzahlen wurden im Spätsommer, die geringsten im Spätwinter verzeichnet.

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