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POPULATION BIOLOGY OF A DESERT SCORPION: SURVIVORSHIP, MICROHABITAT, AND THE EVOLUTION OF LIFE HISTORY STRATEGY¹

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Abstract. The population dynamics of the vaejovid scorpion, *Paruroctonus mesaensis* were studied over a 4.5-yr period. A time-specific life table is presented. The shape of the survivorship curve is intermediate between Type I and Type II curves. The survivorship of both immature and mature males was significantly lower than that of females. Density-dependent regulation is evident for both immature and mature animals. Population size is stable and fluctuates around an equilibrium point. However, density-independent events can produce severe mortality. Both the net reproductive rate and the maximum rate of increase (r_{max}) were very low. Population and life history characteristics indicate that *P. mesaensis* possesses many attributes of an equilibrium or *K*-selected species. It is theorized that existence in a burrow predisposed the evolution of life history traits associated with equilibrium species.

Key words: burrows; demography; density-dependent regulation; desert; equilibrium species; life history; microhabitat; *r*- and *K*-selection; scorpion.

INTRODUCTION

It has been proposed that environmental stability and predictability are major parameters affecting the evolution of life history strategies (e.g., Cohen 1968, Gadgil and Bossert 1970, Schaffer and Gadgil 1975, Giesel 1976). Organisms which evolve in a physically unstable and unpredictable environment must partition a large proportion of available energy into adaptation to abiotic elements; organisms which evolve in a physically benign environment are able to shunt more energy into biotic interactions. In response to these environmental extremes, two contrasting life-history strategies have evolved: (1) opportunistic or *r*-selected in unstable and unpredictable habitats; and (2) equilibrium or *K*-selected in stable and predictable habitats. Each of these life history strategies is defined by several characteristics (see Discussion).

The role of microhabitat as a refuge in a physically harsh environment has been repeatedly analyzed (e.g., see Brown 1968, 1974). However, the significance of microhabitat on the evolution of life history traits has not been examined. Deserts are physically stressful because of great temperature extremes and low, sporadic precipitation. Subterranean existence (e.g., burrows) provides a diurnal and seasonal escape for desert animals (Hadley 1970, 1974; Edney 1974). However, burrows may also represent a stable and predictable microhabitat which can influence the evolution of life history traits.

In this research, we analyze the population dynamics of the desert scorpion *Paruroctonus mesaensis*. During this 4-yr study, we monitored density, recruitment, and survivorship. Our findings of this study combined with the results of a previous paper on life history (Polis and Farley 1979b) show that the population biology and life history of these scorpions resemble those of long-lived vertebrates and have many characteristics of an equilibrium or *K*-selected species. These scorpions live ≥ 5 yr and have a low reproductive potential, are subject to density-dependent regulation, and have a population which does not fluctuate greatly in size from year to year. We postulate that the subterranean microhabitat represents a selective regime which has favored the evolution of these life history characteristics.

METHODS

The study site was a desert sand dune 9 km northwest of Palm Springs, California (Riverside County) USA. Information on climate and vegetation are given elsewhere (Polis and Farley 1979b).

Data were collected over a 50-mo period from April 1973 through June 1977. Since these scorpions are nocturnal, all field work was done at night. Scorpions fluoresce under ultraviolet light (Stahnke 1972). Portable lights (Coleman Charger[®] 3000 and Burgess Safari-light[®]) with ultraviolet bulbs (Sylvania[®] F8T5) were used to locate and observe scorpions. We generally initiated research 1-2 h after sunset and finished between 0000 and 0200; however, on ≈ 25 nights, we collected data throughout the night. Overall, the data base on this research is composed of over 900 field hours on 225 different nights.

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A quadrat (28×50 m) was established in April 1973. This 1400-m² area was gridded by placing stakes 2 m apart in 26 rows. These stakes were also separated by 2 m in 15 columns. Each of the 390 stakes was assigned a letter and a number designating its row and column position. Over 850 scorpions observed in the grid were individually color coded. Unique markings were achieved by using fluorescent paints of different colors in various dot combinations. The paint was tested on scorpions in the laboratory and found to be nontoxic; further, it did not affect the behavior of marked individuals in any detectable way. Grid surveys were conducted on an average of once per week for the entire research period. When it was necessary to estimate the population size, surveys were conducted more frequently and the interval between successive surveys ranged from 1–4 d. Vegetation cover in the grid area was estimated by methods discussed elsewhere (Polis and Farley 1979b).

Three methods were used to estimate population density in the 1400-m² grid: (1) Jolly (1965) index utilizing multiple mark and recapture data; (2) a method modified after Moran (1951) and Zippen (1956, 1958) in which we marked individuals rather than following the usual procedure of removing individuals; and (3) a direct count of the cumulative number of individuals marked during the sampling period. We utilized a computer program to estimate the various population parameters of the Jolly index.

With the cumulative-count method, the total number marked always represented the minimum population size. Since most scorpions in the grid were marked, the total number of marked individuals approached the true population asymptotically. When the estimation from the Jolly and/or Zippen methods exceeded the cumulative number marked, an average of the two highest estimates was calculated and used as the estimate.

During the weeks following emergence of newborn (second instar), it was infeasible to mark each newborn scorpion with a specific color code. Therefore, for each different survey night, we marked newborn with the same color. A new color was used each night and a newborn was marked with an additional color for each night it was observed. This altered procedure did not affect the methods of population estimation.

Population estimations produced by the Jolly, Zippen, and cumulative-marked methods are valid only if basic assumptions are satisfied (Moran 1951, Zippen 1956, 1958, Jolly 1965). For the Zippen and cumulative-marked methods, populations must be closed; i.e., mortality, natality, and migration must be zero during the trapping period. This is not an important assumption for the Jolly method as it estimates these parameters. Further, each method assumes that all animals possess an equal probability of being marked.

Field estimations on immature populations of *P.*

mesanensis were designed to satisfy these assumptions. In order to assure a closed population (with minimum mortality and minimum "natality" due to reappearance of postecdysis animals), all markings were performed during short periods of time, usually between 10 and 20 d. Immature animals are basically sessile (Polis and Farley 1979a), so the variance in the population estimation contributed by migration is small. Variance due to natality is nonexistent except during the discrete recruitment period in midsummer (Polis and Farley 1979b). It is probable that almost all animals were active and therefore equally subject to marking during estimation periods. Marked 0- to 1-yr-old scorpions exhibited a yearly probability of surface occurrence (number of nights observed on surface divided by total number of possible nights on the surface) of 0.486. The probability that an average individual of this age escaped marking during an average marking schedule (six survey nights) was 0.018. Marked 1- to 2-yr-old scorpions manifested activity of 0.448. The probability that an average individual of this age group was not observed was 0.028.

During most of the year, the adult population could not be analyzed utilizing the Jolly and Zippen methods, as basic assumptions were not satisfied. The assumption that all individuals are subject to marking during the sampling period was violated due to the highly sporadic nature of adult surface activity. Average probability of adult activity ranged from 0.431 (fall) to 0.010 (winter) of all possible nights. The typical pattern of mature female activity is to appear in April, May, and/or June, again in August or September, and then not again until the next April or May. These periods of inactivity caused the Jolly and Zippen methods to underestimate the true population in all months but April through June and late August.

Therefore, adult survival rate based on successive population estimations could not be calculated in this study. Instead, data on the year-to-year presence of marked individuals were used to estimate the yearly survival rate of both males and females. Mature males and females were marked in the spring and summer of 1973, 1974, and 1975 and then censused the following year. This method assumes that adults do not molt. If adults molted, calculated survival would be an underestimate of true survival. Morphometric analysis of *P. mesaensis* did not indicate the existence of a postreproductive molt, and such molts have not been reported in the literature for scorpions (Polis and Farley 1979b).

Adult males were excluded when estimating adult populations. Mature males during the breeding season (which basically encompasses all the months of adult male surface activity) become vagrant and travel great distances nightly (Polis and Farley 1979a). This migration produces a high turnover of individuals and subsequent overestimation of the true population.

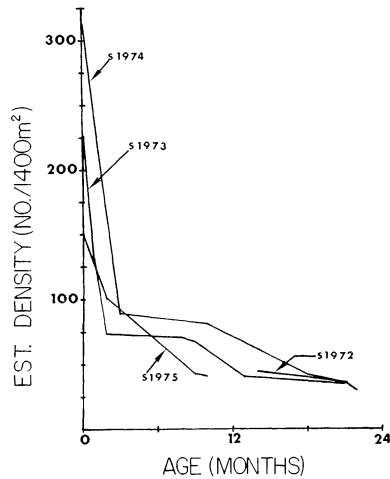


FIG. 1. Survivorship curves (arithmetic) of four cohorts. The densities of different cohorts converge at 21 mo of age. By using arithmetic instead of logarithmic scale, convergence is more apparent.

RESULTS

Survivorship

For animals 0–22 mo of age, the population per 1400 m² was estimated by the Jolly, Moran, and cumulative-count methods. The monthly age-specific survival rate (q_x) was calculated from decreases in the population size of the same cohort at different ages. The arithmetic survivorship curves for the cohorts born in the summers of 1972, 1973, 1974, and 1975 are depicted in Fig. 1. Each cohort sustained a large decrease in absolute numbers in the months immediately after birth. Losses were generally low during each winter and increased in the spring and summer.

Adult survivorship was estimated from the yearly survivorship of marked adults. Survival rate was analyzed as a function of both age and time. The overall average survival rate of marked mature females was 0.189/yr or 0.932/mo. The survival rate of adult females ($N = 169$) appears to be independent of age, as there were no significant differences among the yearly survival rates of mature females of different ages (2–3 yr of age: 0.221/yr; 3–4 yr: 0.151/yr; 4–5 yr: 0.200/yr; $P > .15$).

However, survival rates were not constant from year to year. Survival rates of females marked in 1973 (0.255/yr) and 1974 (0.206/yr) were not significantly different ($t = 0.5$, $P = .31$), but females marked in 1975 exhibited a significantly lower survival (0.094/yr) than those marked in 1973 ($t = 2.2$, $P = .01$) and 1974 ($t = 1.8$, $P = .04$).

The overall survival rates of marked mature males ($N = 145$) was 0.058/yr or 0.921/mo. Survival rate was a function of both age ($t = 2.9$, $P = .002$) and time. Although some marked males were observed to live to 3 yr of age, no marked males lived to 4 yr of age.

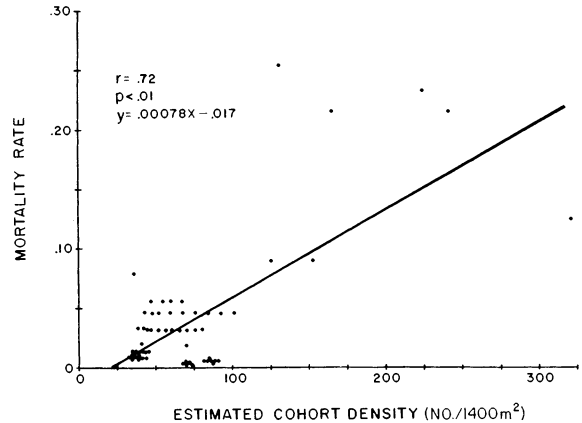


FIG. 2. Mortality rate as a function of density. Mortality rate significantly increases at higher cohort densities.

The survivorship of males marked in 1973 (0.082/yr) was significantly higher than the average survivorship of males marked in 1974 and 1975 (0.012/yr) ($t = 2.3$, $P < .01$).

Density-dependent regulation

To determine if mortality rate increased with increased density, we analyzed the monthly rate as a function of density for animals 0–22 mo of age. A non-parametric test, the Friedman two-way analysis of variance, was used. For each month from age 0 to 22 mo, the mortality rate of each cohort was ranked from highest to lowest and assigned a number (1, 2, or 3) corresponding to its rank. For each of these ages, the cohorts were placed in three columns (high, middle, or low density) corresponding to each cohort's relative density rank. The columns were then summed and the null hypothesis (sum rank of mortality is independent of density) was tested. The results ($\chi^2 = 214$, $P < .001$) indicate that mortality rate varied significantly with density. Therefore, at these ages, the population exhibits positive density-dependent mortality.

The results of a regression analysis (Fig. 2) also indicate a highly significant ($r = .72$, $P < .01$) positive correlation between mortality rate and density. However, this analysis can only be inferential as it is not statistically valid. The data points were observed from five cohorts; all observations within one cohort were correlated because the density at one age was not independent of the density of the preceding ages. Therefore observations are serially correlated, violating the assumption of independence of observations.

The population size of female adults per 1400 m² and of the cohort maturing into adults was analyzed to determine if each was constant from year to year. The population of female adults was estimated in late May through early June by the Jolly, Moran, and cumulative-count methods. The same methods were used to estimate the population of animals which were

TABLE 1. Age-specific (horizontal) life table. (Symbols are defined in Appendix.)

Date	Age (mo)	S_x	l_x	$q(x)$	$d(x)$
1 August	0	0.849	1000.0	0.152	151.5
1 September	1	0.810	848.5	0.190	161.0
1 October	2	0.907	687.5	0.093	64.2
1 November	3	0.981	623.3	0.019	11.6
1 December	4	0.981	611.7	0.019	11.4
1 January	5	0.981	600.3	0.019	11.2
1 February	6	0.981	589.1	0.019	11.0
1 March	7	0.981	578.1	0.019	10.7
1 April	8	0.981	567.4	0.019	10.6
1 May	9	0.974	556.8	0.026	14.4
1 June	10	0.964	542.4	0.036	19.7
1 July	11	0.956	522.7	0.044	22.9
1 August	12	0.956	499.8	0.044	21.9
1 September	13	0.980	477.9	0.020	9.8
1 October	14	0.982	468.1	0.018	8.4
1 November	15	0.982	459.7	0.018	8.4
1 December	16	0.982	451.3	0.018	8.1
1 January	17	0.982	443.2	0.018	8.1
1 February	18	0.982	435.1	0.018	8.0
1 March	19	0.981	427.1	0.190	8.1
1 April	20	0.981	419.0	0.190	7.9
1 May	21	0.921	411.1	0.079	32.5
1 June total	22	0.930	378.6	0.071	26.9
♀♀	22	0.932	220.0	0.068	14.9
♂♂	22	0.922	159.0	0.079	12.5
1 July total	23	0.928	351.6	0.072	25.3
♀♀	23	0.932	205.1	0.068	13.8
♂♂	23	0.922	146.5	0.079	11.5
1 August total	24	0.135	326.3	0.865	282.2
♀♀	24	0.189	191.3	0.811	155.1
♂♂	24	0.058	135.0	0.942	127.1
1 August total	36	0.157	44.1	0.844	37.2
♀♀	36	0.189	36.2	0.812	29.3
♂♂	36	0.000	7.9	1.0	7.9
1 August total	48	0.189	6.9	0.811	5.6
♀♀	48	0.189	6.9	0.811	5.6
1 August total	60	0.189	1.3	0.811	1.2
♀♀	60	0.189	1.3	0.811	1.2
1 August total	72	0.189	0.2	0.811	
♀♀	72	0.189	0.2	0.811	

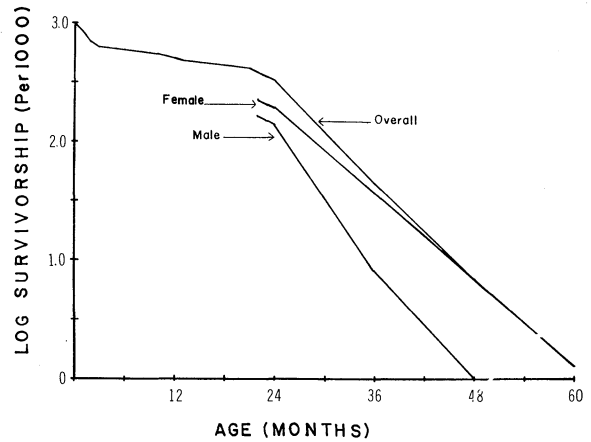


FIG. 3. Survivorship curve (logarithmic) of an average cohort. The curve is intermediate between Type I and Type II survivorship curves (Deevey 1947), and there are three general phases of mortality. The survivorship curves of males and females are first separated at maturity.

different from the average density of the 4 yr (1973—14 adults; 1974—20; 1975—20; and 1976—10; $\chi^2 = 4.5$, $P = .22$).

Life table parameters

Life table parameters of an average cohort are presented in Table 1 and the survivorship (l_x) curve is depicted in Fig. 3. The average cohort was based on the mean monthly survival rate of all cohorts and was standardized to an initial population of 1000 animals. Life table parameters are defined in the Appendix.

The monthly survival rates of animals 0–22 mo of age were calculated by taking the geometric mean of the monthly survival rates of each cohort. The survival rate of males and females younger than 22 mo were not differentiated because in the field it was difficult to distinguish males and females without severely disturbing the animals. After maturity, sex-specific survival was calculated since the sexes could be readily distinguished.

The proportion of males and of females times the estimate of survivorship at 22 mo produces an estimate of the number of surviving males and females at this age. The average sex ratio at 22 mo of age, determined from data ($N = 162$) collected in 1973, 1974, 1975, and 1976, was 0.42 males and 0.58 females. Therefore, at 22 mo of age there were $(0.58)(378.6) = 220$ females and $(0.42)(378.6) = 159$ males of the original hypothetical cohort of 1000. From 22 mo of age onward, all animals were considered to be subject to sex-specific adult survival rate.

Age-specific mortality was very high in the 1st 3 mo after birth. The monthly mortality rates were low during the first winter, rose only slightly in spring and remained at about this level until fall. The monthly mortality rate decreased in the second winter but again

21 mo old in May 1974, 1975, and 1976. The population of 21-mo animals in May 1973 was not actually estimated but was indirectly calculated. By applying the average adult survival rate (0.917/mo) to the estimated adult population of August 1973 we could extrapolate back to the May population size of adult and 21-mo animals. The adult population was separated from the total May population to produce the population estimation of the animals 21 mo of age.

The results indicate a high degree of convergence in population size for animals 21 mo old (also see Fig. 1). In 1973, the density of 21-mo-old animals in the 1400-m² grid was 39; in 1974 there were 36 animals; in 1975, 34; and in 1976, 36. These densities are not significantly different ($\chi^2 = 0.35$, $P = .95$). Although the spring density of adults varied by as much as a factor of two, none of the yearly densities were significantly

TABLE 2. Age distribution. Population density (number/1400 m²) was measured in June of each year. Analysis indicates that the age distribution is stable. p' = proportion of total population.

Age (mo)	1974		1975		1976		Total	
	Den- sity	p'	Den- sity	p'	Den- sity	p'	Den- sity	p'
10	60	0.526	81	0.609	43	0.518	184	0.558
22	34	0.298	32	0.241	30	0.361	96	0.291
34	20	0.175	20	0.150	10	0.120	50	0.152

$$\chi^2 = 4.63, P = .73.$$

rose in spring. The average monthly mortality rate of scorpions > 21 mo of age was higher than all other times except the period immediately after birth.

Stable age distribution

A stable distribution is necessary for calculation of the net reproductive rate and the finite rate of increase (Lotka 1925). The June population of each cohort was analyzed in 1974, 1975, and 1976 to determine if a stable age distribution exists (Table 2). During these 3 yr, there were no significant differences in the ratios of adults:22-mo animals:10-mo animals.

Reproductive potential

The ability of a population to grow in a particular environment is determined by its set of reproductive statistics. The average age-specific fecundity ($l_x m_x$) schedule (Table 3) was used to calculate generation time (T), net reproductive rate (R_0) and finite capacity for increase (r) (Lotka 1925). Before these statistics can be produced, the adult survivorship must be adjusted so that the 1000 individuals in the hypothetical average cohort are now all female. This was performed by doubling the female survivorship at 22 mo. The product of the average number of young born per female of age x ($=m_x$) and the surviving proportion of females from birth to age x ($=l_x$) yields age-specific fecundity ($l_x m_x$).

For empirical calculations, the estimated average production per female of second-instar scorpions, 19.1 ± 1.1 (Polis and Farley 1979b) which actually emerged to the surface was considered to be the average number of young born to each female. Using the sex ratio at birth of 0.5 males and 0.5 females (see below), we calculated a fecundity of $(19.9)(0.5) = 9.95$ female newborn per reproducing female. The calculated generation time was equal to 1176 d or 3.22 yr. The empirical net reproductive rate for the duration of the study was 0.8865; the empirical finite capacity for increase was $-0.1 \times 10^{-3}/d$. These numbers reflect the observed decrease in the population over the period of the study (see below).

Maximum potential net reproductive rate and maximum capacity for increase (r_{max}) were calculated by

TABLE 3. Fecundity ($l_x m_x$) schedule: cohort corrected to all female cohort at 22 mo of age. Net reproductive rate (a) and finite rate of increase (r) calculated from empirical data collected over period of the study. Net reproductive rate (b) and maximum rate of increase (r_{max}) calculated from theoretical maximum fecundity based on number of embryos in dissected gravid females.

Age (mo)	S_x	.001 l_x	m_x	$l_x m_x$
22	0.932	0.439		
23	0.932	0.410		
24	0.189	0.382		
36	0.189	0.072	a) 9.95 b) 24.42	a) 0.719 b) 1.766
48	0.189	0.014	a) 9.95 b) 24.42	a) 0.136 b) 0.335
60	0.189	0.003	a) 9.95 b) 24.42	a) 0.026 b) 0.064
72	0.189	0.0005	a) 9.95 b) 24.42	a) 0.005 b) 0.012
				$R_0 =$ a) 0.887 b) 2.176

Corrected for females at 22 mo of age: Sex ratio (females/total) at 22 mo = $94/162 = 0.580$; 2 (females/total) (l_x 22 mo) = $2(0.580)(378.6) = 439.3$ females; $T = \sum x l_x m_x / \sum l_x m_x = 3.22$ yr = 38.66 mo = 1175.9 d; $r = (\ln R_0)/T = (\ln 0.887)/1175.9$ d = $-1.0 \times 10^{-4}/d$; $r_{max} = (\ln R_0)/T = (\ln 2.176)/1175.9$ d = $6.61 \times 10^{-4}/d$.

using a fecundity based on the average number of embryos carried per gravid female, 48.8 ± 7.1 embryos (Polis and Farley 1979b). We calculated a fecundity of $(0.5)(48.8) = 24.4$ female newborn per reproducing female. Thus, if all embryos survived until they appeared on the surface as second instars, the maximum net reproductive rate would be 2.176 while the maximum rate of increase would be $6.6 \times 10^{-4}/d$.

Differential sexual mortality

For both immature and mature scorpions, the age-specific mortality rate of males was greater than that of females. The proportion of males to females for second instars at first surface occurrence ($\delta\delta = 0.51$, $\text{♀♀} = 0.49$) was not significantly different from 0.50 males: 0.50 females ($t = 0.30$, $P > .51$, $N = 188$). However, the proportion of males present at 22 mo of age ($\delta\delta = 0.42$) was significantly less than that at birth ($t = 1.69$, $P < .05$, $N = 163$). This difference was a product of differential sexual mortality of immatures from birth to 22 mo of age. The proportion of all adults in all seasons ($\delta\delta = 0.355$, $\text{♀♀} = 0.645$) further reflected the lower survivorship of males. This difference is also highly significant ($t = 10.14$, $P < .001$, $N = 1127$).

Differential mortality was also evident between mature males and females. The difference between yearly rate of survival of all males and all females was highly significant ($t = 3.02$, $P = .001$).

Annually, most males are newly matured virgins as

TABLE 4. Effect of the June 1975 wind- and sandstorm on survival, absolute density, surface density, and vegetation cover. All 1975 parameters are significantly lower than those in other years of study.

	1973	1974	1975	1976
Adult female total density (August) (No. ≥ 36 months of age per 1400 m ²)	11	17	8	8
Adult female survival rate (June through August) (≥ 36 months of age)	0.79	0.85	0.40	0.80
Adult surface density (1 August–15 September) (No. ≥ 24 months of age per 1400 m ²)	14.1 \pm 8.0	15.4 \pm 4.7	3.0 \pm 1.0	5.1 \pm 2.7
	<i>t</i> value		<i>P</i>	
Survival rate (June through August): All years vs. 1975	3.32		<.001	
Surface density (number/1400 m ²): 1973 and 1974 vs. 1975	7.97		<.001	
1975 vs. 1976	2.28		<.05	
Cover: 1973 vs. 1975	14.43		<.001	
1974 vs. 1975	17.49		<.001	
1976 vs. 1975	14.27		<.001	

they generally do not live past their first breeding season. At the initiation of the breeding season in late 1975, 23.2% of the mature males that were scored ($N = 46$) were mature during the 1974 breeding season. In late spring 1976, only one-seventh of all mature males were mature during the 1975 season ($N = 75$ scored). By the end of each breeding season, individuals that reached maturity that season constituted the great majority of mature males. By comparison, almost two-thirds of the mature females were mature each of the previous seasons (1975—0.63, $N = 111$ scored; 1976—0.62, $N = 94$). For both years, these differences are highly significant (1975— $t = 5.2$, $P < .001$; 1976— $t = 7.3$, $P < .001$). The oldest marked male observed in this study was only 37 mo, while the oldest marked female was at least 58 mo.

Density-independent mortality

In the 2nd and 3rd wk of June 1975, a severe wind- and sandstorm lasted for 7–10 d. The storm greatly altered the physiognomy of the dune, buried or destroyed a large portion of the spring annual plants (and their associated insect fauna), and may have buried many scorpions below the surface. The heights of some crests and troughs were changed as much as 3–5 m. In the plot, the estimated vegetation cover (11%) after the sandstorm in 1975 was significantly less than the average cover during the same period in 1973 (22%), 1974 (24%), and 1976 (29%) (Polis and Farley 1979b).

The total density, surface density, and survival rate of adult female scorpions in 1975 were considerably lower than that which was expected based on other years (Table 4). Because of the low surface densities of the other two age groups in summer and fall 1975, we were unable to estimate their populations and therefore could not evaluate the effect of the storm on

these animals. The density of adult females ≥ 3 yr of age in August 1975 was over 40% less than their average density in August 1973 and 1974. The survival of adult females from June to August 1975 was significantly lower than the average survival rate spanning the same period in 1973, 1974, and 1976.

The average number of all adults (3 yr or older and newly matured 24-mo animals) active on the surface in August and September 1975 was significantly lower than the average number active during the same period of 1973 and 1974. Further, the density of newborn was much lower in 1975 (153 second instar/1400 m²) than either 1973 (224/1400 m²) or 1974 (321/1400 m²) (Polis and Farley 1979b).

The effects of this storm were still obvious in 1976. The density of adult females in June was lower than any other year; the August 1976 density was equal to the low August 1975 level. However, survival rate of adult females from June to August was comparable to 1973 and 1974. Further, average surface activity of all adults in August and September was low but still higher than that in 1975. Finally, newborn density was still low (170 second instar/1400 m²).

DISCUSSION

Survivorship and mortality

Analysis of the survivorship of *P. mesaensis* indicates that the rate of mortality can be divided into three general phases: (1) a period of high early mortality in the weeks directly after birth; (2) a period of constant relatively low mortality during the months of immaturity; and (3) a period of constant, relatively high mortality throughout the years of maturity. A survivorship curve of this shape (Fig. 3) represents an intermediate between Type I (rectangular: low early

mortality, then high mortality after some age) and Type II (diagonal: constant mortality at all ages) survivorship curves (Deevey 1947).

This intermediate-type curve is fairly common. For the Australian scorpion, *Urodacus abruptus*, Smith (1966) reported a survivorship curve which was similarly divided into three periods of mortality. Young suffer a high dispersal mortality of 65%. Smith attributes this mortality to predation and cannibalism. There is a relatively low mortality to intermediately aged animals of $\approx 30\%$ per year. Old adults suffer a high mortality rate of $\approx 60\%$ per year.

Analysis of the life history of another Australian scorpion, *Urodacus yaschenkoi* (Shorthouse 1971), indicates that the survivorship curve is similar to that of *U. abruptus* and *P. mesaensis*. There was relatively high early mortality (instar 2: 20.4%; instar 3: 22.0%), relatively low mortality during intermediate ages (instar 4: 13.6%; instar 5: 15.0%) with adults experiencing the highest mortality (27.3%). The survivorship of many other species also manifests three phases of mortality, e.g., Dall sheep, Herring Gull, the rotifer *Floscularia* (Deevey 1947), worker honeybees (Sakagami and Fukada 1968), and the Uganda defassa waterbuck (Springa 1970).

Several types of data indicate that the population of *P. mesaensis* responds to density-dependent regulation. For immature animals, the mortality rate significantly increases with density and cohort size converges to almost constant density at the entrance of maturity. For adults, population size is relatively uniform from spring to spring and was never observed to fluctuate by more than a factor of two.

Density-dependent mortality and regulation generally signify the existence of strong biological factors which control the population size (Nicholson 1954). Elsewhere (Polis, *in press*) it has been noted that cannibalism increases with increased density and contributes to the maintenance of an equilibrium population.

The role of density-independent mortality factors may be important in some years. It appears that the wind- and sandstorm of June 1975 acted as an unpredictable but significant mortality factor. Andrewartha and Birch (1954) maintained that such catastrophic mortality is characteristic of arid environments and represents the major cause of mortality. At our study site, this may be true in the years of great sandstorms. However, according to long-time residents, a storm of the duration and severity of the 1975 storm occurs only once every 15–20 yr. Therefore, for the most part, the population appears to be density regulated.

Once females become adults, the risk of death is independent of age (Table 1). The probability of dying for a 5-yr-old was the same as a 2-yr-old. The survival rate of adult males may also be independent of age. The observed difference in survival between 2- and 3-yr-old males may simply be an artifact of the (unavoidably) inadequate sample size of marked 3-yr-olds.

At all ages, the mortality rate of male scorpions was significantly higher than that of females. Further, the adult sex ratio indicated differential sexual mortality. Cannibalism may be the mechanism which produced the observed disparity in survivorship between males and females (Polis, *in press*). There is a statistically significant sex bias in cannibalistic encounters. Only 23.4% of the cannibalizing scorpions were male while 63.0% of the prey scorpions were male. Although mature males are cannibalized by larger mature females in the breeding season, the high mortality rate of mature males as compared to mature females is a product of several factors: starvation, increased risk of interspecific predation, and increased risk of thermal death (Polis and Farley 1979a).

The existence of a stable age distribution indicates that the relative proportions of each age group remained constant over the duration of the study; i.e., all age groups changed in size at the same rate as the entire population. A stable age distribution has also been reported for a population of the scorpion, *U. yaschenkoi* (Shorthouse 1971).

Reproductive capacity

The finite and maximum rates of increase are not strictly valid statistics for this species. These parameters signify the daily rate increase in a continuously reproducing population and therefore are not strictly applicable to a population whose reproduction is pulsed, such as *P. mesaensis*. However, we calculated r_{\max} because it is a useful statistic in comparison with other animals. The maximum rate of increase is only $6.6 \times 10^{-4}/d$. This is one of the lowest values reported (Pianka 1970). This low r_{\max} reflects both the long generation time (3.22 yr) and the low survivorship (3.62%) of females to first age of reproduction.

In the case of species with discrete, nonoverlapping generations, the net reproductive rate is the exact amount by which populations increase each generation. The maximum R_0 indicates that the population could potentially increase 2.18 times per generation. That is, at a maximum, the population could only approximately double every 3 yr.

Using Smith's (1966) data for *U. abruptus*, we calculated the empirical and maximum net reproductive rate, generation time, finite rate of increase, and maximum rate of increase. The empirical R_0 was 1.139 per generation while the maximum R_0 was 1.50 per generation. The generation time was 5.13 yr. This indicates, at best, *U. abruptus* can only increase its population by 50% in a 5-yr period. The finite rate of increase was $6.9 \times 10^{-5}/d$ over the period of his study. The maximum rate of increase ($2.2 \times 10^{-4}/d$) was very low, even lower than that for *P. mesaensis*.

Scorpions as equilibrium species

Species can be divided into two groups according to their life history strategy: opportunistic, fugitive or

r-selected vs. equilibrium, stable or *K*-selected (Hutchinson 1951, MacArthur and Wilson 1967). Each strategy is characterized by a number of traits (MacArthur and Wilson 1967, Pianka 1970, Diamond 1976, Shapiro 1976). An equilibrium species develops slowly to a relatively large size and produces (for a series of years) relatively fewer offspring, each of which has proportionately more parental energy allocated to it; survivorship is Type I or II (Deevey 1947); mortality is predominately density-dependent and the magnitude of population fluctuation is relatively small; it inhabits a predictable environment in which species interactions are a paramount force; and it occupies a narrow, specialized niche. An opportunistic species exhibits the inverse of these characteristics.

The scorpion, *P. mesaensis*, exhibits several characteristics of an equilibrium species. The data indicate that mortality is primarily density dependent although density-independent episodes occasionally occur. The survivorship curve is intermediate between a Type I and a Type II curve. Most significantly, the population fluctuates about an equilibrium point: in the 4 yr of this study, the maximum population of scorpions 22 mo of age was only 1.15 times greater than the minimum population; the maximum adult population in June was only twice that of the minimum June population.

Development and growth are relatively slow (Polis and Farley 1979b). The period from fertilization to parturition is ≈ 1 yr. Maturity is not reached until 19–24 mo of age. The life span of these animals is at least 5 yr. Reproduction is postponed until females are ≈ 3 yr old and they exhibit iteroparity (Polis and Farley 1979b). The maximum rate of increase is one of the lowest ever reported. The mother invests a great amount of time and energy into her young. Many scorpions are viviparous and the developing embryos receive nutrients from the mother via a ‘placental’ membrane in the ovarian tubules (Savory 1964). At birth, the young remain on the dorsal surface of the female for ≈ 1 mo before they assume an independent existence (Williams 1969).

The size of newborn is greater than the adult size of a large proportion of North American insects (as compiled by Pianka 1970). At first surface appearance, the average net weight of newborn animals is 0.035 g and average total length is 13 mm (Polis and Farley 1979b). Adults average 2.0 g and 72 mm in length. Adults are larger than most North American scorpions (as compiled from numerous taxonomic accounts), almost all adult spiders (Kaston 1972), and most adult insects (Pianka 1970).

Although *P. mesaensis* inhabits the desert, its microclimate is actually stable and predictable. They spend from 16 to 24 h/d in their burrows and emerge to the surface an average of <40% of all possible nights. Desert scorpions are not on the surface when the environment is unfavorable, e.g., at extreme tem-

peratures or desiccating conditions of low humidity (Hadley 1970, 1974). At the depth of the burrow (25 cm) there is little daily fluctuation in sand temperature or humidity (Edney et al. 1974). Seasonal changes in burrow temperatures appear to follow predictable cyclic patterns (Polis and Farley 1979b).

A high degree of biotic interaction is characteristic of equilibrium species. For *P. mesaensis*, the magnitude of cannibalism is at very high levels and represents one of the major ecological forces in the evolution of this species (Polis, *in press*). The degree of interspecific interaction is also high (G. A. Polis, S. J. McCormick, and M. Quinlan, *personal observation*). Intraguild predation appears to be one of the major factors affecting community structure and *P. mesaensis* is the dominant in this community: in 51 cases of interspecific predation in which it was involved, *P. mesaensis* was the predator 92.2% of the time.

Equilibrium species exhibit high habitat specificity. This scorpion is quite specific in the habitat which it occupies. Restricted to sandy substrate, it occupies the narrowest habitat niche breadth of the six species in the study area (G. A. Polis, S. J. McCormick, and M. Quinlan, *personal observation*).

Another scorpion that possesses many traits of an equilibrium species is *U. abruptus* (Smith 1966): it lives to at least 10 yr, does not reproduce until its 3rd yr, and has a generation time >5 yr; it has a 16-mo gestation and the young stay with the female for over a month; its survivorship curve is intermediate between Type I and Type II curves; and it has a very low r_{max} .

Several other species of scorpions possess life history traits which are characteristic of equilibrium species. Some scorpions live at least to 25 yr of age (e.g., *Hadrurus*: Stahnke 1966) and others (*Opisthacanthus sp.*, *Pandinus gambiensis*, *Urodacus yaschenkoi*) do not reproduce for the first time until 4–7 yr. Further, species of several scorpion genera are much larger than *P. mesaensis* (e.g., *Hadrurus*, *Pandinus*, *Hadogenes*). Newlands (1972) reports that non-gravid females of *Hadogenes troglodytes* weigh as much as 32 g. As with most scorpions, these species live in a subterranean retreat (in a burrow or under a rock) and are thus sheltered from adverse climatic conditions.

The data indicate that *P. mesaensis* and possibly several other scorpion species resemble long-lived vertebrates in several aspects of their life history. Scorpions are among the exceptions of Pianka's (1970) generalization about *r*-selection of terrestrial invertebrates, probably because of the stability and predictability of their subterranean habitat. Burrowing is a major adaptation of desert scorpions to the hot, arid environment; climatic extremes are dampened and animals are sheltered from unfavorable surface conditions. Burrowing simulates some aspects of the selective regime found in stable, predictable environments:

less energy need be expended on adapting to a fluctuating abiotic environment and relatively more energy can be partitioned for other purposes. As the selective regime shifts so that the biotic environment becomes more important there is a subsequent selection for those characteristics associated with equilibrium species.

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APPENDIX

Life table definitions

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- S_x = age-specific survival = $(1 - q_x)$; fraction of cohort alive at age x not dying in interval x to $x + 1$.
- q_x = age-specific mortality = $(1 - S_x)$; fraction of cohort alive at age x dying in interval x to $x + 1$.
- l_x = age-specific survivorship = $(1000 \prod S_x)$; number living at beginning of age class x .
- d_x = age-specific death = $(l_{x+1} - l_x)$; number dying during the age interval x .
- m_x = age-specific fecundity = average number of female births per female at age x .
- $l_x m_x$ = age-specific cohort fecundity = number of females born per female in each interval.
- R_0 = net reproductive rate = total number of female offspring produced by an average female of a cohort during its existence.
- $r = r_0$ = finite capacity for increase = $(\ln R_0)/T$ = number of times a population multiplies itself per unit time. Closely approximates r_{\max} (innate capacity for increase or maximal rate of population increase) when generations are distinct, reproductive period is short and/or R_0 is low.
- T = generation time = $\sum x l_x m_x / \sum l_x m_x$.
-

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