

Smith, G. T. 1990. Potential lifetime fecundity and the factors affecting annual fecundity in *Urodacus armatus* (Scorpiones, Scorpionidae). J. Arachnol., 18:271-280.

**POTENTIAL LIFETIME FECUNDITY
AND THE FACTORS AFFECTING ANNUAL FECUNDITY
IN *URODACUS ARMATUS* (SCORPIONES, SCORPIONIDAE)**

G. T. Smith

CSIRO Division of Wildlife and Ecology
LMB 4 PO Midland
Western Australia 6056 Australia

ABSTRACT

The ovariuterus of *Urodacus armatus* had three types of diverticula, Rudimentary (RD), Embryonic (ED) and Post Partum (PPD). The data suggested that all the ova were developed and enclosed in RDs by the time a female reached maturity and that the sum of the diverticula gave a measure of the potential lifetime fecundity. Samples from two populations in two consecutive years were not significantly different and the combined mean for all diverticula was 56.7 ± 8.22 .

Annual fecundity (number of EDs) did not differ between populations or years and the combined mean was 8.3 (range 4-12). Fecundity was not significantly influenced by female condition ($\sqrt[3]{\text{Mass}/\text{carapace length}}$), length of ovariuterus or the total number of diverticula. However, size and age had significant effects. The simplest adequate model explaining the variation was given by the equation $\log \text{ED} = 0.9656 - 0.07003 \text{ Age} + 0.01839 \text{ Carapace length}$. Data on age-related fecundity and total diverticula suggested that females may have from 5 to 12 litters in a lifetime.

INTRODUCTION

Studies on a variety of invertebrates have shown that fecundity can be influenced by a number of variables: size, (Juliano 1985; King 1987; Banks and Thompson 1987; Haack et al. 1987); population density, (Wise 1975; Banks and Thompson 1987); food, (Wise 1975; Riechert and Tracey 1975; Haack et al. 1987); age, (Ribi and Gebhardt 1986); temperature, (Baird et al. 1987); geographic location, (Hines 1982; Davies 1987; Atkinson and Begon 1987; Ribi and Gebhardt 1986); size of egg or offspring, (Ribi and Gebhardt 1986); size of male ejaculate, (Svärd and Wiklund 1988); number of previous matings by male, (Rutowski et al. 1987), and clutch interval, (Banks and Thompson 1987). The variables that affect fecundity in individual species differ as do the direction of the effect and the degree of interaction with one another. Size, for most species, is the dominant variable either directly or indirectly via its effect on other variables affecting fecundity. Lifetime fecundity or reproductive success has been studied in only a few species (Banks and Thompson 1987; Fincke 1987; Koenig and Albano 1987; Svärd and Wiklund 1988). In addition to the variables that affect individual breeding events, lifetime fecundity will be affected by the length of reproductive life, number of clutches and variables associated with the male. The majority of the above studies are on short-lived, oviparous species; there have been no studies on long-lived viviparous invertebrates.

Most data on reproductive rates in scorpions are measures of fertility (number of live births) obtained from specimens in captivity or animals in the field (Polis and Farley 1979), and both methods may give values less than the true reproductive rate. Captive specimens, depending on the time spent in captivity may have more abortions, suffer from maternal cannibalism or displacement of young from the mother's back and may fail to shed the birth membrane (Polis and Farley 1979). Similar mortality factors also operate on litters in the field but have not been directly observed (Smith 1966; Polis and Farley 1979).

In viviparous animals, such as scorpions, no methods have been developed to attain data on fecundity (number of fertilized ova) without sacrificing the animal. However, in detailed studies on population dynamics and life history strategies, it is important to have a measure of maternal investment in reproduction and the extent of pre-parturition mortality. Given that fertility (litter size) will be dependent on the fecundity, it is important to have an understanding of the factors affecting fecundity, so that these can be applied to data from a given population.

Fecundity has been calculated for only a few scorpions (Smith 1966; Polis and Farley 1979); individual and intraspecific variability and the factors influencing this variability have not been studied. This paper examines the potential lifetime fecundity and the factors affecting annual fecundity in the burrowing scorpion *Urodacus armatus* Pocock. *U. armatus* is a burrowing species widely distributed over arid and semi-arid Australia with no apparent habitat restrictions in terms of soil type or vegetation. Scorpion activity, as measured by the number of active burrows, is greatest in the period March to May (= Fall) with a smaller peak from September to October (= Spring). Parturition starts in February and the second instars disperse from their natal burrows in March and April. The gestation period is about 11 months.

MATERIALS AND METHODS

The study site was Durokoppin Nature Reserve (1030 ha), 150 km northeast of Perth, Western Australia. The reserve had a mosaic of heath, shrub and woodland communities. *U. armatus*, a medium sized (total length 75 mm) burrowing species was found throughout the reserve, but was most abundant in woodland patches where there were 1000-3000/ha (Smith unpublished data).

Samples of pregnant female *U. armatus* were collected from two woodland patches in September and October of 1985 and 1986 and in one patch, a further sample was collected in March 1986, giving a total of 198 females. Females were collected by placing pitfall traps (plastic drinking cups) in front of the burrows. The traps were visited at sunrise in the following days and any scorpions were removed and kept cool until they were weighed to the nearest 0.01 g that evening. They were then killed by heat shock and preserved in 70% ethanol.

In the laboratory, the length of the carapace, right chela and tail were measured to the nearest 0.01 mm and the specimen dissected to expose the ovariole. Attached to the ovariole were three types of diverticula (Fig. 1) as described for *U. manicatus* (Thorell) (as *U. abruptus*, Smith 1966). Rudimentary diverticula [(RD), small finger-like projections with the ovum at the distal end, with three distinct size classes]; Embryonic diverticula [(ED), large projections

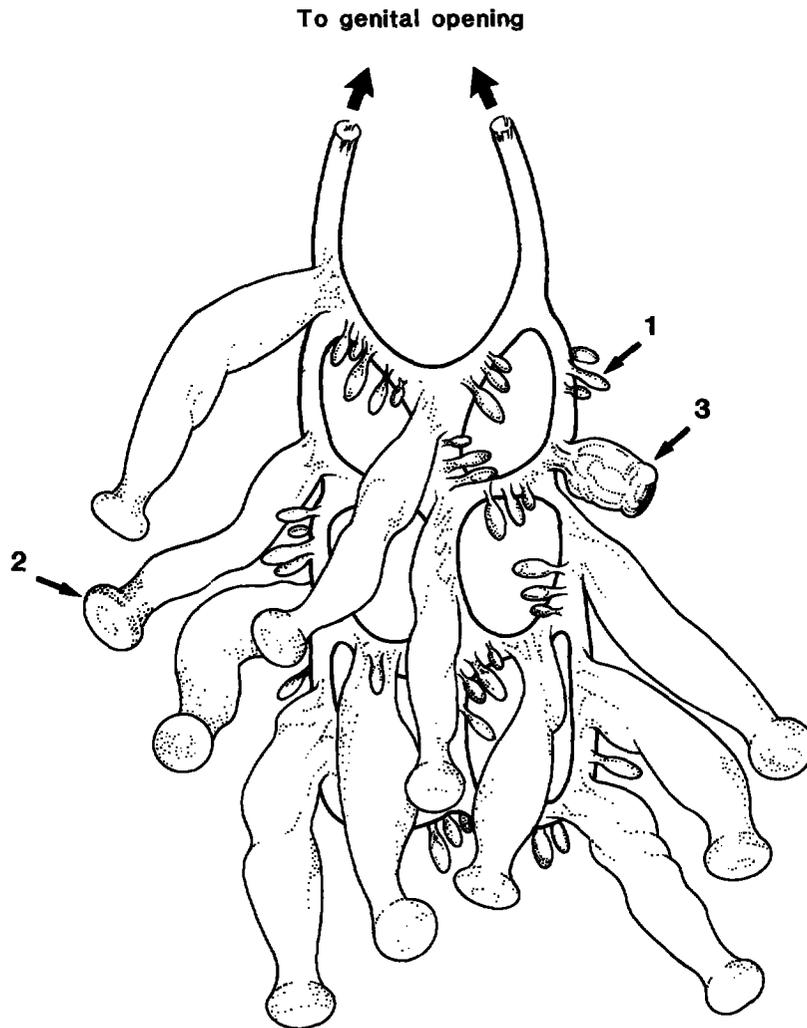


Figure 1.—Ventral view of the ovariuterus of *U. armatus* showing arrangement of Rudimentary diverticula (1) showing the three size classes, Embryonic diverticula (2) and one Post-Partum diverticulum (3) to indicate shape and size.

with a distinctive knob at the distal end and which contain the developing embryo] and Post Patrum diverticula [(PPD, small, squat infolded structures that are formed from the sheath of the EDs when the young are born]. The numbers of each type of diverticula were counted and the length of the network of the ovariuterus (OUL) was measured to the nearest 0.1 mm from the first proximal bifurcation on the lateral branches. The numbers of *in utero* deaths (= abortions) in both the current and previous pregnancies were recorded. Abortions in the current pregnancy had EDs that were shorter and thinner while abortions from previous pregnancies were distinguished by the diverticula being very short, thin and dark.

The relative age of adult females was calculated from the formula: $\text{No. PPD} / \bar{\text{XED}} + 1$. Assuming that if the numbers of PPDs were equal to or less than the

maximum number of EDs (from all samples), then they represented the first pregnancy for that individual. Knowing the mean number and range of embryos in the first and second pregnancies, the relative age of females that had had more than two pregnancies was recalculated. This procedure was repeated a number of times to produce Table 1, which was used to assign age classes to individuals. Clearly, for the individual, the method was accurate only for females in their first and, to a lesser extent, in their second pregnancy. For later pregnancies, the accuracy was unknown, but for large samples, the errors should have cancelled out each other. In this scheme, relative age was related to the number of pregnancies; its relationship to chronological age was uncertain because not all females bred every year (the number of females that did not breed is indicated by the difference in the sample sizes for ED and CL in the first four samples in Table 3) and the age at maturity was not known with certainty. Log-log plots of carapace length against length of the right chela did not give distinct clumps but suggested that adults were in their sixth instar. Using the theoretical method of Francke and Sissom (1984) to calculate the number of molts between the second instar and the adults also suggested that adults were in their sixth instar (Smith unpublished data). Second instar *U. armatus* remained in that stadium for about 12 months and assuming that later stadia were of similar duration, then females mating after their final molt were in their fifth year. For convenience, relative age or number of pregnancies will be called simply age in the following discussion.

In analyzing the data, the length of the carapace was used as a measure of size (CL) and the condition (C) of the female was calculated from the formula $C = \sqrt[3]{\text{mass}/\text{CL}}$.

Females were collected in September and October to take advantage of the increased activity at this time and to ensure that the EDs had developed to a stage where they could not be confused with RDs.

RESULTS

Potential lifetime fecundity.—Examination of the samples from September and October showed that the ovariterus in an immature female was a thin tube with no diverticula. In the fifth and possibly fourth instar, it had a number of small dense patches that may be sites of the developing ova and diverticula. By autumn, after the final molt, the ovariterus was fully developed with RDs of three distinct size classes (Fig. 1). Presumably the ovariterus of a fifth instar female finished its final development shortly before or at about the time of the final molt.

Initial inspection of the data suggested that a female's lifetime complement of ova were formed by the time she reached adult size, and that the sum of three types of diverticula were a measure of the potential lifetime fecundity, assuming that the PPDs were not resorbed.

This idea was tested with the present data in two ways. Firstly, in the March 1986 sample, the total number of diverticula in virgin females and those who were in their first pregnancy, should not differ significantly from those in their second or later pregnancies. The respective means, 51.7 and 55.5, were not significantly different ($t = 1.62$, $df = 23$, $P > 0.05$).

Secondly, the number of RDs should decline with age while the total number of diverticula (TD) should not differ significantly with age. The number of RDs

Table 1.—The calculated means of Embryonic diverticula (ED) and Post-Partum diverticula (PPD) with the range of PPDs for female *U. armatus* which have had 1 to 8 pregnancies.

| No. pregnancies | Mean ED | Mean PPD | Range PPD |
|-----------------|---------|----------|-----------|
| 1 | 9 | — | — |
| 2 | 8 | 9 | < 12 |
| 3 | 8 | 17 | 13-21 |
| 4 | 7 | 25 | 22-28 |
| 5 | 7 | 32 | 29-35 |
| 6 | 6 | 39 | 36-42 |
| 7 | 6 | 45 | 43-48 |
| 8 | 6 | 51 | 49-55 |

showed a steady decline from 44.5 at age one to 17.8 at age six (Table 2). One six year old had no RDs and the one seven and one eight year old had 20 and 8 RDs respectively. While the decrease from one age to another was less than expected from the number of embryos for different ages shown in Table 1, the true extent of the decline was masked by the variability in the numbers of TDs. A better indication of the progressive use of RDs with age was the mean percentage of TD that were still RDs (Table 2). This percentage fell from 82.6% at age one to 20.0% at age six which agreed well with the expected decline when it was calculated from the mean number of TDs and the annual fecundity with age given in Table 1 (Table 2).

The mean number of TD increased from 53.8 at age one to 62.7 for the combined five to eight age group (Table 2) and there was a significant difference with age (ANOVA $F = 6.38$, df 4, 186, $P < 0.01$). The mean number of TDs in the five to eight year olds was significantly greater than the mean TDs for one and two year olds, three and four year olds also had significantly larger mean TDs than one year olds (Newman-Keuls test, $P < 0.05$). The relationship between TD and the age, size (CL) and size of ovariole (OUL) of females was analyzed using multiple regression with a log transformation of the data from 186 females. Age had no significant effect on TD, while CL and OUL has significant positive effects, the variance ratios were 24.15 ($P < 0.001$) and 29.15 ($P < 0.001$) respectively. The relationship was expressed by the equation:

$$\log TD = 2.651 + 0.01282 CL + 0.001517 OUL.$$

Table 2.—Mean and standard deviation (SD) at different ages of the number of rudimentary diverticula (RD), the mean percentage of RDs ($RD \times 100/TD$), the calculated percentage of RDs (Calc % RD) using the average number of diverticula and the age related fecundity (Table 1) and the mean and standard deviation of the total number of diverticula (TD) in female *U. armatus*. * = mean and standard deviation from combined five to eight year old females.

| Age | RD | | RD \times 100/TD | | Calc %RD | TD | | Sample size |
|-----|------|-----|--------------------|------|----------|-------|------|-------------|
| | Mean | SD | Mean | SD | | Mean | SD | |
| 1 | 44.5 | 6.9 | 82.6 | 3.2 | 84 | 53.8 | 7.4 | 68 |
| 2 | 39.0 | 6.5 | 68.8 | 5.0 | 70 | 56.2 | 9.4 | 51 |
| 3 | 34.7 | 6.8 | 57.5 | 5.4 | 56 | 59.5 | 8.0 | 40 |
| 4 | 26.5 | 4.9 | 44.4 | 4.0 | 44 | 59.1 | 5.0 | 21 |
| 5 | 20.5 | 8.9 | 57.5 | 12.3 | 32 | 62.7* | 6.7* | 7 |
| 6 | 17.8 | 9.0 | 20.0 | 15.7 | 21 | | | 5 |
| 7 | 20 | — | — | — | 11 | | | 2 |
| 8 | 8 | — | — | — | 0 | | | 1 |

These data show that the increase in TDs with age was related to the increase in CL and OUL with age (survivorship increases with size) rather than the development of new RDs.

Annual fecundity.—The mean, standard deviation and range for fecundity and five factors that may affect fecundity are given for each sample in Table 3.

Overall annual fecundity ranged from 4 to 12 with a mean of 8. Initial inspection of the above factors suggested that all exerted some effect. The data were then analyzed using an analysis of covariance with a log transformation using the GLIM program (Baker and Nelder 1977). In the sample of 198, the data from 29 females which were not pregnant were deleted for the first analysis. The analysis showed no significant difference between the samples (variance ratios from -0.3883 to 2.127) and the data from the samples were combined. The effect of four factors (Carapace length, age, condition and TD) on fecundity were then analyzed. TD, with a variance ratio of 0.8367 , was insignificant and was dropped. Condition, with a variance ratio of 2.239 , also not significant, was dropped, leaving age and size as the only significant factors with variance ratios of 6.407 and 5.455 respectively. The analysis was repeated with ovariuterus length (OUL) but excluding TD and excluding 11 females for whom data of ovariuterus length were not available. OUL was not significant (variance ratio 0.5191), leaving age and size again as the only significant factors affecting fecundity with variance ratios of 7.125 and 5.068 respectively.

The simplest adequate model explaining variation in fecundity was given by the formula:

$$\log ED = 0.9656 - 0.07003 \text{ Age} + 0.01839 \text{ CL}$$

The realized reproductive potential or the number of live births (fertility) is not necessarily the same as the fecundity because of the possibility of abortions. Of the 198 females examined, 70 had had abortions; only 4 of these were in EDs (1, 2, 2, 3). This suggested that most abortions that were recognized were in the latter half of the gestation period. Overall, the mean number of abortions per pregnancy was 0.8. In 17 age-two females, 12 had only one abortion, 3 had two abortions and one each had 5 and 6 abortions. Data from older females suggested that this was reasonable indication of the range of the numbers of abortions per pregnancy, based on the average number per pregnancy.

Number of pregnancies.—Females with the mean number of TDs and average fecundity (Table 1) could have eight pregnancies, however, females with TDs at the extremes of the range (34 to 80) could have from 5 to 12 pregnancies. Examination of the number of RDs in 4, 5 and 6 year old females showed that the potential number of pregnancies that they could have ranged from 7 to 11, 7 to 11 and 6 to 10 respectively. The two 7-year olds could have had another three pregnancies while the one 8-year old could have had one more pregnancy. Clearly, few, if any females, survive long enough to realize their full reproductive potential.

DISCUSSION

The true measure of fecundity is the number of fertilized ova; however, this is not an easy measure to obtain and is probably not important in the population dynamics of *U. armatus* given the limited provisioning required at this stage of

Table 3.—Mean (\bar{X}), standard deviation (SD), range (rg) and sample size (N) of the number of embryonic diverticula (ED), total number of diverticula (TD), carapace length (CL), condition (C), Age (A) and length of ovariterus (OUL) in female *U. armatus*. Note that sample sizes vary within a sample because some females were not pregnant or the data for some factors were not available.

| Sample | | ED | TD | CL | C | A | OUL |
|-------------------------|-----------|------|-------|---------|-------------|------|---------|
| Area 1 1985 | \bar{X} | 7.7 | 58.8 | 6.87 | 0.145 | 2.7 | 321.9 |
| | SD | 1.67 | 9.22 | 0.34 | 0.006 | 1.40 | 38.11 |
| | rg | 4-12 | 44-80 | 6.2-7.4 | 0.128-0.157 | 1-8 | 249-434 |
| | N | 50 | 53 | 53 | 53 | 53 | 50 |
| Area 1 1986 | \bar{X} | 8.8 | 54.9 | 7.05 | 0.145 | 2.2 | 306.2 |
| | SD | 1.86 | 8.20 | 0.35 | 0.008 | 1.46 | 32.46 |
| | rg | 4-12 | 34-76 | 6.4-7.7 | 0.122-0.167 | 1-7 | 248-390 |
| | N | 58 | 59 | 63 | 63 | 63 | 57 |
| Area 2 1985 | \bar{X} | 8.7 | 59.6 | 7.43 | 0.141 | 2.3 | 327.3 |
| | SD | 1.73 | 6.76 | 0.29 | 0.006 | 1.34 | 50.82 |
| | rg | 5-11 | 40-71 | 6.9-8.1 | 0.120-0.152 | 1-7 | 267-430 |
| | N | 20 | 24 | 24 | 24 | 24 | 23 |
| Area 2 1986 | \bar{X} | 8.4 | 57.2 | 7.08 | 0.142 | 2.6 | 303.7 |
| | SD | 1.25 | 7.33 | 0.38 | 0.008 | 1.41 | 32.20 |
| | rg | 6-11 | 45-72 | 6.1-7.9 | 0.111-0.157 | 1-6 | 249-364 |
| | N | 30 | 32 | 32 | 32 | 32 | 30 |
| Area 2 March 1986 | \bar{X} | 8.3 | 53.8 | 7.17 | — | 2.2 | 286.3 |
| | SD | 1.34 | 6.39 | 0.39 | — | 1.35 | 22.55 |
| | rg | 6-11 | 47-65 | 6.5-8.1 | — | 1-6 | 250-350 |
| | N | 15 | 25 | 26 | — | 26 | 262 |

development. Fecundity in this study was calculated at about halfway through the gestation period and was not significantly different from that obtained shortly after mating. It is therefore the best time to collect samples as it takes advantage of the increased activity and avoids any confusion in the identification of RDs and EDs. Further, the data suggest that most abortions probably occur in the second half of the gestation period.

Mean fecundity for the study was 8.3, which was considerably smaller than the mean fertility of 31.3 calculated by Polis and Farley (1979) from data on 39 species. More recently, Polis and Sissom (1990) have provided data from 77 species on litter sizes, which ranged from one to 105, with a mean of 25; only 11 species had litter sizes comparable to the fecundity of *U. armatus*. The data were not detailed enough to make statistical comparisons, however, from the data available it is clear that fecundity in *U. armatus* and its variability (CV for the 5 samples range from 14.9% to 21.8%) is among the lowest found in scorpions.

The only comparable study is that of Smith (1966), who calculated that fecundity in *U. manicatus* (a slightly smaller species, CL = 5.7 mm) to be 15.7 with 4.5% of embryos being aborted. The litter size of females in the field was 11.4, indicating a 24% mortality in immediate post-birth period.

The factors influencing variation in fecundity were examined; size had a significant positive effect while age had a significant negative effect. Other factors (condition, length of ovariterus and total number of diverticula) had positive but not significant effects. Size and age affect intraspecific fecundity in

both invertebrates (see Introduction for references) and vertebrates (Allaine et al. 1987; Sauer and Slade 1987). In invertebrates, size is commonly a positive factor, but in some species or situations, it may be neutral or negative in its effect (Haack et al. 1987). Similar effects are seen in relation to age (Davies 1987; Ribi and Gebhardt 1986). Francke (1981) showed that female size (CL) and the size of second instar young (CL) accounted for 81% of the variability in litter size in an interspecific study of diplocentrid scorpions. Bradley (1984) found that adult size (CL) in *Paruroctonus utahensis* Williams was not related to brood size (second instar) or the weight of the young. There are no data on the relationships between fecundity and size of young in *U. armatus*, however in *U. manicatus* there was no significant relationship between female size (CL) and the size (CL) of either first or second instars (Smith, unpublished data).

Female condition reflects the amount of food stored in the hepato-pancreatic gland and indirectly, the females foraging efficiency and/or success. For most females collected in spring, just after reopening their burrows, condition should reflect the foraging success in autumn at mating and it might be expected that variations in condition would be reflected in the fecundity as is found in other arachnids (Wise 1975). The lack of a significant effect is similar to Bradley's (1984) finding that feeding rates do not effect brood size nor the size of the young (second instars) in *P. utahensis*. Also, Polis (1988) found that in *P. mesaensis* Stahnke, high levels of food intake increased the rate of development but not the fecundity. On the other hand, starvation eventually led to the resorption of the embryos. Similar observations have been made on various *Urodacus* species (Smith, unpublished data). Metabolic rates in scorpions are very low (Hadley and Hill 1969; Riddle 1978) and it is likely that energy requirements for the embryonic development in the first half of the gestation period are also low. If the energy requirements of pregnant female *U. armatus* are similar to those of *P. utahensis* and *P. maesensis*, then food would not be a limiting factor for *U. armatus*, except under the most severe conditions. Under average conditions, reproductive potential is strongly influenced by the size and age of the population. Size itself may be influenced also by the individual's rate of development.

Studies on female lifetime reproductive success in invertebrates appear to be limited to a few studies on Odonata (Fincke 1987; Banks and Thompson 1987; Koenig and Albano 1987) and the monarch butterfly (Svärd and Wiklund 1988) and are not comparable with a viviparous iteroparous invertebrate, with determinate lifetime fecundity. Perhaps a better comparison is with mammals, where oogenesis and follicular formation is completed at about parturition. However, in mammals, the number of follicles far exceeds those required even under the most favorable breeding conditions (Gosden and Telfer 1987).

In this study, I have used morphological characteristics of the ovariterus and its diverticula to demonstrate that all the ova are developed and enclosed in rudimentary diverticula around the time the female molts into her last instar and that the ova are progressively used over the lifetime of the female. A study of *U. manicatus* showed a similar relationship between the numbers of the different types of diverticula with age. Further, limited histological examination of the ovariterus of females of different age showed no evidence of new ova being developed after the females had completed their final molt. Examination of a limited number (1-20) of 5 other species of *Urodacus* suggests that all *Urodacus*

may have a similar reproductive strategy and further, that this strategy may be common to all scorpions with katoikogenic development (Scorpionidae and Diplocentridae).

The reproductive strategy of *U. armatus* is one of long life, delayed maturity and low potential lifetime fecundity and annual fecundity; traits that have probably coevolved with the habit of burrowing and foraging from the burrow entrance; both will increase survivorship. The most vulnerable period for *U. armatus* is when the second instar individuals are dispersing from their natal burrows as was found for *U. manicatus* (Smith 1966). Once the second instars have dug their own burrows, survivorship is probably high and hence there is no need for a high reproductive rate. These adaptations are characteristic of equilibrium species and are typical of a number of scorpion species that create their own stable and predictable environment by constructing burrows (Polis and Farley 1980). Further these adaptations may be viewed as a refinement of those that led to the development of the extremely low metabolic rate which appear to be characteristic of all scorpions (Polis 1988).

ACKNOWLEDGMENTS

I would like to thank Jana Ross for her help in collecting the scorpions and for carrying out the dissections, Richard Litchfield for statistical advice and for running the GLIM program, and Perry de Rebeira for the drawing. Eleanor Rowley, Denis Saunders, James Ridsdill-Smith, Gary Polis, and David Sissom made valuable comments on various drafts, which Claire Taplin typed.

LITERATURE CITED

- Allaine, D., D. Pontier, J. M. Gaillard, J. D. Lebreton, J. Trouvilliez and J. Clobert. 1987. The relationship between fecundity and adult body weight in homeotherms. *Oecologia*, 73:478-480.
- Atkinson, D. and M. Begon. 1987. Reproductive variation and adult size in two co-occurring grasshopper species. *Ecol. Entomol.*, 12:119-127.
- Baird, D. J., L. R. Linton and R. W. Davies. 1987. Life history flexibility as a strategy for survival in a variable environment. *Funct. Ecol.*, 1:45-48.
- Baker, R. J. and J. A. Nelder. 1977. The GLIM system manual, release 3. Numerical Algorithms Group, Oxford.
- Banks, M. J. and D. J. Thompson. 1987. Lifetime reproductive success of females of the damselfly *Coenagrion puella*. *J. Anim. Ecol.*, 56:815-832.
- Bradley, R. A. 1984. The influence of the quantity of food on fecundity in the desert grassland scorpion (*Paruroctonus utahensis*) (Scorpionida: Vaejovidae): An experimental test. *Oecologia*, 62:53-56.
- Davies, L. 1987. Long adult life, low reproduction and competition in two sub-Antarctic carabid beetles. *Ecol. Entomol.* 12:149-162.
- Fincke, O. M. 1987. Lifetime reproductive success and the opportunity for selection in a non-territorial damselfly (Odonata: Coenagrionidae). *Evolution*, 40:791-803.
- Francke, O. F. 1981. Birth behavior and life history of *Diplocenurus spitzeri* Stahnke (Scorpiones: Diplocentridae). *Southwest. Natu.*, 25:517-523.
- Francke, O. F. and W. D. Sissom. 1984. Comparative review of the methods used to determine the number of molts to maturity in scorpions (Arachnida), with analysis of the post-birth development of *Vaejovis coahuilae* Williams (Vaejovidae). *J. Arachnol.*, 12:1-20.
- Gosden, R. G. and E. Telfer. 1987. Numbers of follicles and oocytes in mammalian ovaries and their allometric relationships. *J. Zool., Lond.*, 211:169-175.
- Haack, R. A., R. C. Wilkinson and J. L. Foltz. 1987. Plasticity in life history traits of the bark beetle *Ips calligraphus* as influenced by phloem thickness. *Oecologia*, 72:32-38.

- Hadley, N. F. and R. D. Hill. 1969. Oxygen consumption of the scorpion *Centruroides sculpturatus*. *Comp. Biochem. Physiol.*, 29:217-226.
- Hines, A. H. 1982. Allometric constraints and variables of reproductive effort in Brachyuran crabs. *Marine Biol.*, 69:309-320.
- Juliano, S. A. 1985. The effects of body size on mating and reproduction in *Brachinus lateralis* (Coleoptera: Carabidae). *Ecol. Entomol.*, 10:271-280.
- King, G. H. 1987. Offspring sex ratios in parasitoid wasps. *Quart. Rev. Biol.*, 62:367-396.
- Koenig, W. D. and S. S. Albano. 1987. Lifetime reproductive success, selection, and the opportunity for selection in the white-tailed skimmer *Plathemis lydia* (Odonata: Libellulidae). *Evolution*, 41:22-36.
- Polis, G. A. 1988. Foraging and evolutionary responses of desert scorpions to harsh environmental periods of food stress. *J. of Arid Environ.*, 14:123-134.
- Polis, G. A. and R. D. Farley. 1979. Characteristics and environmental determinants of natality, growth and maturity in a natural population of the desert scorpion. *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *J. Zool., Lond.*, 187:517-542.
- Polis, G. A. and R. D. Farley. 1980. Population biology of a desert scorpion: survivorship, microhabitat and the evolution of life history strategy. *Ecology*, 61:620-629.
- Polis, G. A. and W. D. Sissom. 1990. Life history. Pp. 161-223. *In* *Biology of Scorpions*. (G. A. Polis, ed.) Stanford University Press. Stanford.
- Ribi, G. and M. Gebhardt. 1986. Age specific fecundity and size of offspring in the prosobranch snail *Viviparus ater*. *Oecologia (Berlin)*, 71:18-24.
- Riddle, W. A. 1978. Respiratory physiology of the desert grassland scorpion *Paruroctonus utahensis*. *J. Arid Environ.*, 1:243-251.
- Riechert, S. E. and C. R. Tracey. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. *Ecology*, 56:265-285.
- Rutowski, R. L., G. W. Gilchrist and B. Terkanian. 1987. Female butterflies mated with recently mated males show reduced reproductive output. *Behav. Ecol. Sociobiol.*, 20:319-322.
- Sauer, J. R. and N. A. Slade. 1987. Uinta ground squirrel demography: is body mass a better categorical variable than age? *Ecology*, 68:642-650.
- Smith, G. T. 1966. Observations on the life history of the scorpion *Urodacus armatus* Pocock (Scorpionidae), and an analysis of its home sites. *Aust. J. Zool.*, 14:383-398.
- Svärd, L. and C. Wiklund. 1988. Fecundity, egg weight and longevity in relation to multiple matings in females of the monarch butterfly. *Behav. Ecol. Sociobiol.*, 23:39-43.
- Wise, D. H. 1975. Food limitation of the spider *Linyphia marginata*: experimental field studies. *Ecology*, 56:637-646.

Manuscript received July 1989, revised March 1990.