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Variation in reproductive investment among and within populations of the scorpion *Centruroides vittatus*

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Abstract Although information concerning variation among and within populations is essential to understanding an organism's life history, little is known of such variation in any species of scorpion. We show that reproductive investment by the scorpion *Centruroides vittatus* varied among three Texas populations during one reproductive season. Females from the Kickapoo population produced smaller offspring and larger litters than females from the Independence Creek or Decatur populations; this pattern remained when adjusting for among population variation in either female mass or total litter mass. Relative clutch mass (RCM) and within-litter variability in offspring mass (V^*) did not differ among populations. Among-population variation may result from genetic differences or from phenotypically plastic responses to differing environments. Within populations, the interrelationships among reproductive variables were similar for Decatur and Independence Creek: females investing more in reproduction (measured by total litter mass, TLM) produced larger litters and larger offspring, and V^* decreased with increased mean offspring mass (and with decreased litter size at Decatur). At Kickapoo, larger females produced larger litters and had larger TLM; females investing more in reproduction produced larger litters but not larger offspring. Within litter variability in offspring mass was not correlated with any reproductive variables in this latter population. These patterns may be explained by the fractional clutch hypothesis, the inability of females precisely to control investment among offspring or morphological constraints on reproduction.

Key words Reproduction · Interspecific variation · Offspring size · Scorpions · *Centruroides vittatus*

Introduction

Reproductive investment concerns both the total amount of investment (energy or resources) by an individual into reproduction and the way that investment is apportioned among offspring (Wilbur 1977). Total investment is usually thought to be limited by food availability or some important nutrient (e.g., Lack 1954) and is expected to trade off with future survival. The apportionment of reproductive investment into offspring involves the trade-off between size and number of offspring (initially reviewed in Stearns 1976); that is, given a certain level of investment, an individual can make either many small eggs (offspring) or a lesser number of large eggs (offspring).

The first models of this trade-off between size and number of offspring (Smith and Fretwell 1974; Brockelman 1975; Wilbur 1977) predicted that, within a given environment, one should find a single (optimal) egg or offspring size produced by all individuals. However, a number of studies have shown that many species exhibit a great deal of variation in egg or offspring size among populations, among individuals within a single population, and/or within clutches for individuals. Some authors (Capinera 1979; Crump 1981; Kaplan and Cooper 1984) have argued that such variation may in and of itself be adaptive for organisms living in unpredictable environments, although McGinley et al. (1987; but see Kaplan and Cooper 1988) have suggested that selection for variation in offspring size should be rare.

The causes of variation in offspring size, as well as other reproductive traits, are in general poorly understood, especially within and among populations of a particular species. Such variation may arise due to genetic differences (e.g., among populations of the wood frog *Rana sylvatica*, Berven 1982), or it may be due to differential expression of a certain phenotype in different environments (phenotypic plasticity, e.g., among populations of the Columbian ground squirrel *Spermophilus columbianus*, Dobson and Murie 1987). This latter explanation is suggested to be more important to understand intraspecific

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cific variation in life history traits (Dobson and Murie 1987). For many systems, however, the environmental factors influencing variation are unknown or incompletely understood.

Recently, there has been an increase in the use of invertebrate species to test predictions of life-history theories, particularly optimality models and natural selection of reproductive traits (see review in Godfray 1991). Calow (1983) has suggested that invertebrates which cease growth at maturity may be especially useful in testing models of reproductive investment, since energy invested in growth and reproduction are essentially decoupled. Scorpions may be excellent organisms for this type of research; they are easily captured and maintained, and for at least some species field observations and manipulations may be performed more easily than for many other invertebrates. However, although scorpions are among the oldest terrestrial invertebrates, relatively little is known about their life history traits (see Polis and Sissom 1990 for a review of the available information). For most scorpion species, life history data are anecdotal, unpublished, based on small sample sizes, or unknown. This is unfortunate, since many aspects of scorpion reproduction are unusual for a terrestrial invertebrate. Females give birth to live young and show some parental care (carrying the offspring on the female's back through their first molt); gestation times are long, ranging from 2 to 18 months; and litter sizes are relatively small compared with other arthropods, averaging 26 for the order (Polis and Sissom 1990). Three studies describe variation of and relationships among reproductive traits (e.g., offspring size, litter size, total litter mass, and relative clutch mass) within a single population (Bradley 1984; Formanowicz and Shaffer 1993) or within the family Diplocentridae (Francke 1981), but there is no available information on variation in reproductive traits among populations of a species. In this study, we examine the relationships among a set of reproductive traits (female size, mean offspring mass, litter size, total litter mass, relative clutch mass, and within litter variability in offspring mass) among three Texas populations of the scorpion *Centruroides vittatus* (Say) (Scorpionida: Buthidae) during one reproductive season.

Methods

A total of 73 female *C. vittatus* was collected between May and September 1992 from three populations: north-central Texas near the Lyndon B. Johnson National Grasslands, north of Decatur, Wise Co. ($n = 41$); west Texas on the Independence Creek Preserve of the Texas Nature Conservancy, south of Sheffield, Terrell Co. ($n = 15$); and south-central Texas at Kickapoo Caverns State Natural Area, on the Kinney Co.-Edwards Co. border ($n = 17$). All scorpions were collected under surface debris or while active at night on the surface (using portable flashlights with ultraviolet bulbs). When collected, females were either gravid (Decatur, $n = 39$; Independence Creek, $n = 13$; Kickapoo, $n = 9$) or carrying first instar offspring on their back (Decatur, $n = 2$; Independence Creek, $n = 2$; Kickapoo, $n = 8$).

Gravid females were individually housed in $18.5 \times 7.5 \times 9$ cm plastic containers containing a sand or gravel substrate (approx-

mately 0.5 cm) and a moist paper towel. Females with offspring were placed in $9.5 \times 9.5 \times 6.5$ cm plastic containers (also containing a moist paper towel) upon capture and kept there until dispersal of offspring (to minimize disturbance). All scorpions were maintained in the laboratory on a 14:10 h light:dark cycle at a mean temperature of 25.4°C (range $20\text{--}29^\circ\text{C}$). Each scorpion was offered one adult cricket every 3–4 weeks until parturition. Following parturition, females were not fed until the offspring dispersed. No female was kept longer than 6 weeks before giving birth, so that females were fed no more than twice during captivity (in most cases an individual was fed once). Parturition occurred during July ($n = 11$), August ($n = 16$), and September ($n = 14$) in the Decatur population; during June ($n = 1$), July ($n = 1$), August ($n = 8$), and September ($n = 5$) in the Independence Creek population; and during August ($n = 9$), September ($n = 5$), and October ($n = 3$) in the Kickapoo population.

Following parturition, neonate scorpions (scorplings) climb onto the female's back and undergo their first molt, dispersing from five to ten days following birth. Within 24 h of dispersal, each female and her offspring were weighed and their wet masses recorded (to the nearest 1 mg for the female and 0.1 mg for each offspring). Mean offspring mass and litter size were determined for each female. Total litter mass (TLM) was calculated as the sum of the individual offspring masses and relative clutch mass (RCM) was calculated as TLM divided by post-dispersal female mass. As a measure of within litter variability in offspring mass an unbiased estimate of the coefficient of variation, V^* , was used (Sokal and Rohlf 1981):

$$V^* = (1 + 1/4n) \times 100 \text{ CV}$$

where n is litter size and CV is the standard deviation divided by the mean.

Neonate scorpions do not feed while on the female's back and thus lose mass (Polis and Sissom 1990). Formanowicz and Shaffer (1993) found that neonate *C. vittatus* lost an average of 26.2% of their birth mass prior to dispersal. We used this value to calculate adjusted values for mean offspring mass, TLM and RCM. Using these adjusted values slightly changed some of the results reported below but altered no statistical results or relationships. For simplicity, only unadjusted (post-dispersal) data are reported.

Post-dispersal female mass (hereafter referred to as female mass), mean offspring mass, litter size, TLM, RCM, and V^* were compared among populations using single-classification ANOVAs. In addition, since many reproductive traits are known to scale allometrically with female body size (Blueweiss et al. 1978), differences in mean offspring mass, litter size, and within litter variability in offspring mass were examined using an analysis of covariance (ANCOVA) with female mass as a covariate. Differences in RCM were analyzed by an ANCOVA of TLM with female mass as the covariate to avoid problems with ratios (Packard and Boardman 1987). Variation in mean offspring mass among populations was also analyzed using an ANCOVA with TLM as the covariate. An *a posteriori* (conditional Tukey-Kramer) test was used to further explore significant among population differences (Day and Quinn 1989).

Within populations, interrelationships among female mass, mean offspring mass, TLM, and litter size were examined using correlation analysis (Pearson's r). Following Formanowicz and Shaffer (1993), the relationships between within litter variability in offspring mass and female mass, mean offspring mass, TLM, and litter size were tested using Spearman rank-order correlation (r_s ; Daniel 1990). For all within population analyses, alpha was initially set at 0.05 and adjusted using the sequential Bonferroni procedure (Rice 1989) in order to account for multiple comparisons. For the analyses using Pearson's r ($n = 6$ correlations for each population), this gave adjusted α values of 0.0083, 0.01, 0.0125, 0.0167, 0.025, and 0.05, respectively, for each step of the Bonferroni procedure; for the analyses using Spearman rank-order correlation ($n = 4$ correlations per population), the adjusted alpha values were 0.0125, 0.0167, 0.025, and 0.05. Because several of the correlations were found to be nonsignificant despite p-values less than 0.05, we conducted a power analysis (using Table 3.3.4 of Cohen 1977; values not listed were found by linear interpola-

tion) to determine with what confidence we could make statements about these marginal results.

To correct for heteroscedasticity, raw values for female mass, mean offspring mass, litter size, and TLM were log-transformed (Sokal and Rohlf 1981) for all analyses. In all cases where an ANCOVA was performed the assumption of parallelism of regression lines was met. All data analyses were performed using the STATISTICA computer package (StatSoft 1991).

Results

Variation among populations

Since parturition occurred across several months, a MANOVA among months was performed for Decatur to determine if the timing of parturition had an effect on any reproductive variable. A MANOVA was not possible for the Independence Creek or Kickapoo populations because the variance-covariance matrix was noninvertible; thus, ANOVAs among months were performed for these

Table 1 Results of ANOVAs among months for the reproductive variables within each population of *Centruroides vittatus*. F-values are given on top, with p-values below. V^* is the within litter variability in offspring mass

	Decatur (n=41)	Independence Creek (n=15)	Kickapoo (n=17)
Post-dispersal female mass	1.47	2.67	0.13
	0.24	0.11	0.88
Mean offspring mass	0.32	0.69	0.13
	0.73	0.52	0.88
Litter size	1.77	0.45	0.26
	0.18	0.65	0.78
Total litter mass	0.74	1.74	0.48
	0.49	0.22	0.63
Relative clutch mass	0.04	1.17	1.49
	0.96	0.35	0.26
V^*	2.10	0.34	1.12
	0.14	0.72	0.35

Table 2 Means (SDs) and ranges for the reproductive variables of *C. vittatus*. V^* is the coefficient of variation of offspring mass within a litter. Post-dispersal female mass, mean offspring mass, and total litter mass are in mg. Time on back is in days. Sample sizes are indicated for each population

	Decatur (n=41)	Independence Creek (n=15)	Kickapoo (n=17)
Post-dispersal female mass	334 (51.3) 235–457	527.8 (156.3) 324–970	616.7 (109.1) 409–799
Mean offspring mass	7.63 (1.18) 4.12–10.04	8.85 (2.04) 4.82–13.26	7.35 (1.02) 5.67–8.44
Litter size	21.9 (5.0) 13–34	28.6 (6.4) 17–41	39.4 (8.8) 24–55
Total litter mass	165.1 (36.8) 70–247.1	247.9 (64.0) 158.9–376.2	287.2 (66.4) 150.6–393.6
Relative clutch mass	0.500 (0.112) 0.230–0.732	0.482 (0.101) 0.302–0.651	0.466 (0.076) 0.292–0.595
V^*	7.87 (2.65) 2.92–15.46	7.63 (2.00) 4.01–11.74	8.20 (2.81) 4.72–14.86
Time on back	6.74 (1.04) 5–9	9.09 (0.70) 8–10	8.11 (1.36) 6–10

populations. There was no among month variation at Decatur (Wilks' $\lambda = 0.65$, $P = 0.23$), Independence Creek, or Kickapoo for any reproductive variable (Table 1). All data within a population were therefore pooled across months to conduct the rest of the analyses. Means, standard deviations, and ranges are given in Table 2.

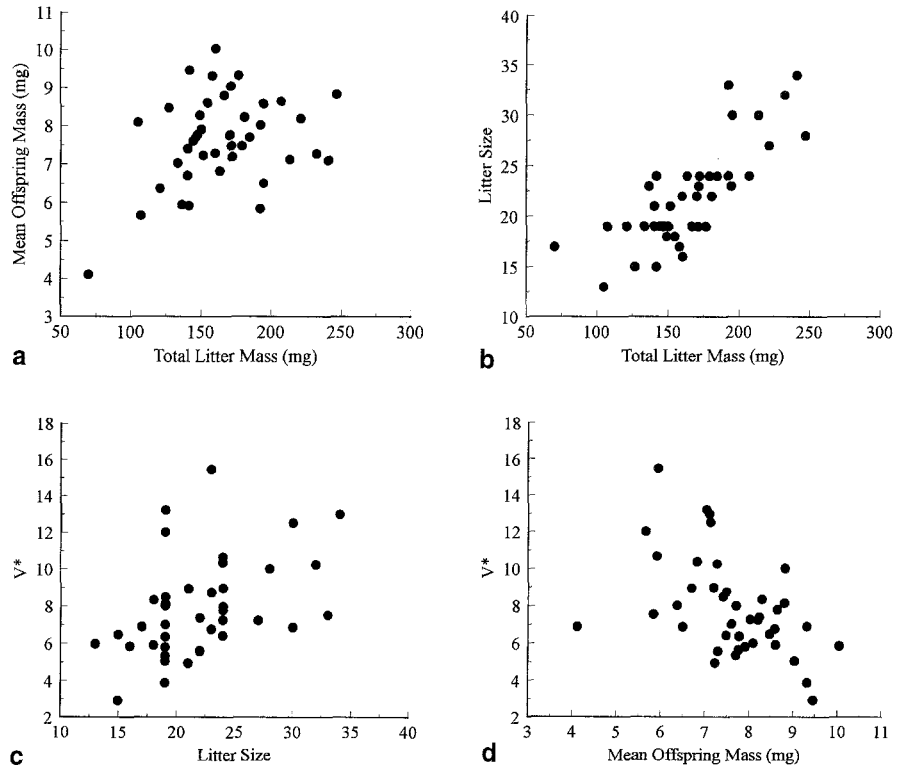
Female mass ($F_{(2,70)} = 71.8$, $P < 0.001$), mean offspring mass ($F_{(2,70)} = 3.95$, $P = 0.02$), litter size ($F_{(2,70)} = 40.9$, $P < 0.001$), TLM ($F_{(2,70)} = 35.5$, $P < 0.001$), and time between parturition and dispersal ($F_{(2,56)} = 24.1$, $P < 0.001$; field-born litters were not included) all differed significantly among populations. Female mass, TLM, and litter size all exhibited the same trend: each was largest at Kickapoo, intermediate at Independence Creek, and smallest at Decatur. Mean offspring mass was largest at Independence Creek, intermediate at Decatur, and smallest at Kickapoo. The time between parturition and dispersal of offspring was longest at Independence Creek, intermediate in duration at Kickapoo, and shortest at Decatur. Neither RCM ($F_{(2,70)} = 0.67$, $P = 0.51$) nor V^* ($F_{(2,70)} = 0.20$, $P = 0.82$) were significantly different among populations. An ANCOVA adjusting for among population variation in female mass indicated that significant differences in mean offspring mass ($F_{(2,69)} = 5.25$, $P = 0.008$) and litter size ($F_{(2,69)} = 7.55$, $P = 0.001$) remained; no among population difference was found in either V^* ($F_{(2,69)} = 0.19$, $P = 0.82$) or RCM ($F_{(2,69)} = 1.22$, $P = 0.30$) when adjusting for differences in female mass. An *a posteriori* conditional Tukey-Kramer test indicated that Kickapoo females had significantly larger litters than either Independence Creek [critical value (CV) = 0.200, $P < 0.05$] or Decatur (CV = 0.316, $P < 0.05$) females, and significantly smaller offspring than Independence Creek females (CV = 0.165, $P < 0.05$). Litter size and mean offspring mass did not differ between Independence Creek and Decatur females.

Since offspring mass may have also been affected by total litter mass, we compared mean offspring mass among populations using TLM as the covariate in an ANCOVA.

Table 3 Correlations for the reproductive variables within the three populations of *Centruroides vittatus*. Correlation coefficients are given above the diagonal, p-values below the diagonal (* indicates significance following Bonferroni correction). For correlations involving coefficient of variation of mean offspring mass within litters (V^*), values represent results of Spearman rank-order correlation analysis (r_s); all other values represent Pearson's r (TLM total litter mass)

	Female mass	Offspring mass	Litter size	TLM	V^*
A. Decatur					
Female mass	—	0.22	0.18	0.32	0.03
Offspring mass	0.16	—	-0.26	0.46	-0.53
Litter Size	0.27	0.1	—	0.74	0.47
TLM	0.04	0.002*	<0.001*	—	0.09
V^*	0.84	0.0004*	0.002*	0.59	—
B. Independence Creek					
Female mass	—	0.3	0.41	0.65	-0.12
Offspring mass	0.27	—	-0.41	0.57	-0.65
Litter size	0.13	0.13	—	0.51	0.38
TLM	0.009*	0.03	0.05	—	-0.31
V^*	0.68	0.008*	0.16	0.26	—
C. Kickapoo					
Female mass	—	0.25	0.62	0.73	-0.08
Offspring mass	0.34	—	-0.19	0.39	0.03
Litter size	0.008*	0.46	—	0.83	-0.02
TLM	0.001*	0.12	<0.001*	—	-0.09
V^*	0.75	0.92	0.93	0.72	—

Fig. 1a-d Significant relationships among reproductive variables for the Decatur population ($n = 41$). **a** The relationship between mean offspring mass and total litter mass (TLM). **b** The relationship between litter size and TLM. **c** The relationship between within litter variability in offspring mass (V^*) and litter size. **d** The relationship between V^* and mean offspring mass



Again, significant differences existed ($F_{(2,69)} = 8.73$, $P = 0.0004$). Kickapoo females had significantly smaller offspring than females from Independence Creek (as indicated by a conditional Tukey-Kramer test; $CV = 0.143$, $P < 0.05$), a result similar to that found when controlling for among population variation in female mass.

Variation within populations

The within-population correlations for the reproductive variables are given in Table 3. For the Decatur population, a

significant positive correlation occurred between mean offspring mass and TLM (Fig. 1a). No significant correlations existed between female mass and mean offspring mass or litter size; the correlation between female mass and TLM was marginally nonsignificant (power = 0.30). Litter size and mean offspring mass were not significantly correlated, but litter size was significantly positively correlated with TLM (Fig. 1b). There was a significant positive correlation between V^* and litter size (Fig. 1c) and a significant negative correlation between V^* and mean offspring mass (Fig. 1d). Coefficient of variation of offspring mass was not significantly correlated with female mass or with TLM.

In the Independence Creek population larger females had significantly larger TLM (Fig. 2a), but there were no significant correlations between female mass and mean offspring mass or litter size. Mean offspring mass was not significantly correlated with litter size. The correlations between TLM and litter size (power = 0.28) and mean offspring mass (power = 0.39) were marginally nonsignificant. Coefficient of variation of offspring mass was significantly negatively correlated with mean offspring mass (Fig. 2b), but not with female mass, litter size, or TLM.

In the Kickapoo population larger females had both significantly larger litters (Fig. 3a) and larger TLM (Fig. 3b). There was also a significant positive correlation between litter size and TLM (Fig. 3c). The correlations between mean offspring mass and either female mass, litter size, or TLM were all nonsignificant. Coefficient of variation of offspring mass was not significantly correlated with female mass, mean offspring mass, litter size, or TLM.

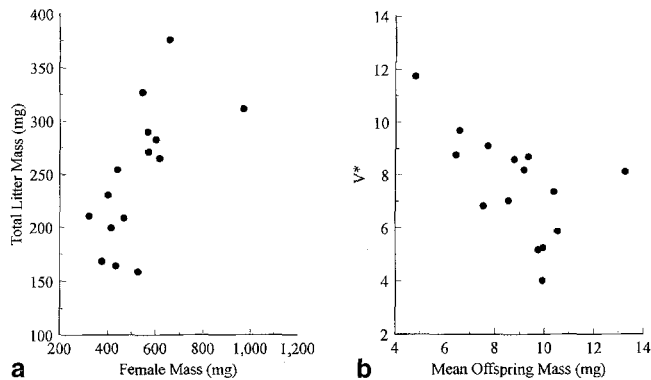
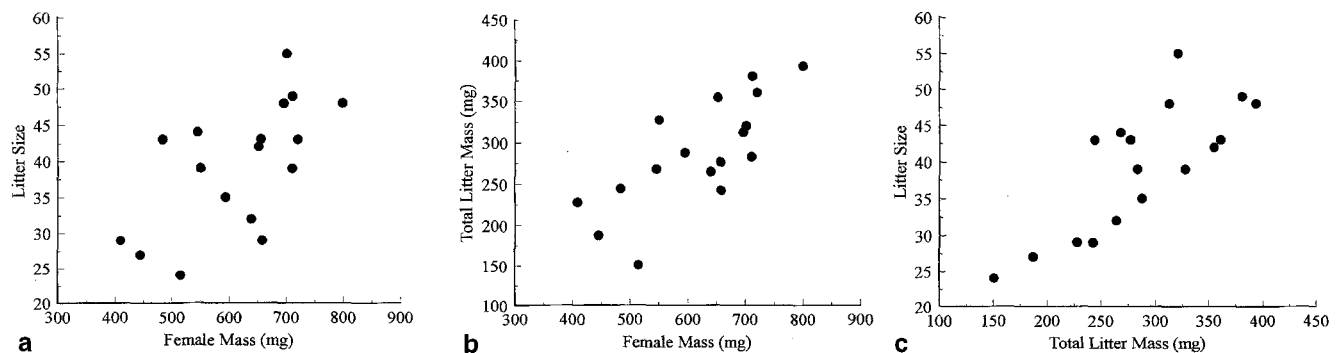


Fig. 2a,b Significant relationships among reproductive variables for the Independence Creek population ($n = 15$). **a** The relationship between total litter mass and post-dispersal female mass. **b** The relationship between within-litter variability in offspring mass and mean offspring mass

Fig. 3a-c Significant relationships among reproductive variables for the Kickapoo population ($n = 17$). **a** The relationship between litter size and post-dispersal female mass. **b** The relationship between TLM and post-dispersal female mass. **c** The relationship between litter size and TLM



Discussion

Variation among populations

Our results indicate that the scorpion *Centruroides vittatus* shows considerable variation in reproductive investment among the three populations studied. Such variation may result from differences among these populations in total resources available for reproductive investment, differences in the manner in which investment was apportioned into offspring, or both (Wilbur 1977). We estimated relative investment in reproduction by females using RCM; this trait did not vary among populations. In other viviparous species (snakes and lizards), RCM varies little across populations or years (Vitt and Price 1982; Seigel and Fitch 1984, 1985; Brodie and Ducey 1989; Ford and Seigel 1989). It has been suggested (Vitt and Congdon 1978; Vitt 1981; Vitt and Price 1982) that RCM in snakes and lizards is affected by foraging and predator-escape behaviors as well as by food availability and habitat utilization. These factors may influence RCM in scorpions as well, although the specific effect of any is unknown. If all females obtain sufficient resources for reproduction, as has been suggested for one species of scorpion (Bradley 1984), then RCM may also be affected by available space within the female for developing offspring (Sinervo and Licht 1991).

Because relative investment was consistent among populations, the variation in reproductive investment appears to be the result of differences in how investment was apportioned among offspring. At Kickapoo, females produced smaller offspring and larger litters than females at Independence Creek or Decatur; this was also found when adjusting for female mass or TLM. This variation may be due to one or more of several factors. First, there may exist genetic variation among populations for these life history traits. Second, there may be differences in the environment experienced by each population, such as differences in: resource abundance or utilization, competition for resources, degree of variability (or stressfulness), abiotic factors such as temperature or precipitation, or predation risk (Stearns 1976). Third, there may be differences in the number of clutches produced during a reproductive season (Polis and Sissom 1990), although there is no evidence for this in *C. vittatus* maintained long-term (> 1 year) in our laboratory.

Differences in predation risk may be important in these populations for two reasons. First, intraguild predation [by other species of scorpions (Polis and McCormick 1987), arachnids, or centipedes (Polis and McCormick 1986)] and cannibalism (Polis 1981) are thought to be important in structuring scorpion populations. Females may produce larger offspring in habitats where the risk of predation is high, because the results of intra- or interspecific interactions are often determined by the relative size of the individuals (Polis 1981; Polis and McCormick 1987). We have observed cannibalism in each population, but the degree to which it or other intraspecific interactions affect reproductive decisions is not known. Intraguild predation could explain differences in reproductive investment between Independence Creek and Kickapoo females (four to seven scorpion species are sympatric with *C. vittatus* at Independence Creek, while two sympatric species occur at Kickapoo, one uncommon and much smaller than *C. vittatus* and the other found only in caves), but this hypothesis predicts that Decatur females should invest similarly to Kickapoo females, since *C. vittatus* is the only scorpion at Decatur. That they do not indicates the risk of intraguild predation may not be the primary explanation for these differences. Second, predation risk could alter the foraging behavior, and hence energy acquisition, of females. Polis (1980) has suggested that scorpions are "time minimizers" (*sensu* Schoener 1971) and may decrease time spent actively foraging as the risk of predation increases; this will in turn lead to a decrease in energy available for reproduction.

Variation among populations in the time spent by offspring on the female's back suggests that females may differ in post-birth investment (parental care) as well as pre-birth investment. This may not affect foraging ability (we have observed females carrying offspring foraging and feeding in the field and in the lab) but may have a profound effect on anti-predator behaviors. Gravid and non-gravid females flee from threats of predation, while females carrying offspring instead exhibit a defensive posture (L. Shaffer, personal communication). If surviving an encounter with a predator is dependent on flight, carrying offspring may represent an important cost to the female.

Variation within populations

The classical assumption in life history theory is that number of offspring should be negatively correlated with offspring size; in none of the populations studied was this found to be true. Instead, two patterns emerged. For Independence Creek and Decatur, larger females had more resources to invest in reproduction and produced larger offspring, larger litters, or both; smaller litters and litters with larger offspring had offspring more uniform in size. Thus, females investing in more offspring produced more variably sized offspring, while females investing in larger offspring had offspring more uniform in

size. However, low power (due perhaps to low sample sizes) for the "marginal" correlations urges caution in interpreting patterns for these populations. For Kickapoo, larger females had more resources to invest in reproduction than did smaller females, and produced more, but not larger, offspring. Within-litter variability in mean offspring mass was uncorrelated with all reproductive traits for this population.

One explanation for the trends at Independence Creek and Decatur is that females were unable precisely to partition resources to developing embryos (Meffe 1990); within-litter variability in offspring mass is then expected to increase as litters become larger, as is the case for these two populations. Alternatively, females may tightly control resource partitioning but utilize one of two tactics: for small litters, offspring are provisioned equally at a given level N , while for larger litters some are provisioned at N and others at values greater or less than N (a bet-hedging strategy; Stearns 1976). Differences in resource availability or acquisition among females within each population may also explain the trends observed. Schultz (1989, cited in Seigel and Ford 1992) suggests that, because low resource availability should have more deleterious effects on smaller offspring, females encountering low resource levels should produce more uniformly sized offspring to increase the probability of offspring survival. Finally, the trends may be explained by the fractional clutch hypothesis (Ricklefs 1968); if energy available for reproduction is not evenly divisible by the minimal energy required to make one offspring, a female can choose between using excess reproductive energy to make one more (smaller) offspring or to make each offspring larger. In the former case offspring size should be more variable than in the latter.

The relationships for *C. vittatus* differ from those found in other scorpions. In *Paruroctonus utahensis*, female mass was uncorrelated with litter size or offspring size and negatively correlated with TLM (Bradley 1984). The explanation for the latter correlation was that females were weighed following offspring dispersal and those with large litters had lost a high proportion of their gravid weight. The same protocol was used in our study with opposite results. In diplocentrid scorpions, Francke (1981) found that female size was positively correlated with litter size and offspring size; he also found a positive correlation between litter size and offspring size but a negative regression coefficient, making it difficult to determine the true relationship between these two variables. Formanowicz and Shaffer (1993), in a study of the Decatur population of *C. vittatus* in 1991, found results similar to those reported here for this population, with the additions that larger females had larger litters and females with a larger TLM (but not smaller litters) had less variable offspring.

Formanowicz and Shaffer (1993) predicted that *C. vittatus* females were producing uniform, perhaps optimally, sized offspring. Although Bradley (1984) does not consider this question, his data (no correlation between offspring size or litter size and female mass, low within-

litter variance in offspring mass) indicate that *P. utahensis* females may also produce uniform-sized offspring. We found no significant correlations between mean offspring mass and female mass, which could suggest a uniform offspring size within each population. This scenario is more plausible for Independence Creek and Decatur, as we found a decrease in within litter variation in offspring mass as mean offspring mass increases. However, for these populations, this was confounded by the increase in mean offspring mass with increasing TLM, suggesting that females with more to invest in reproduction produced larger offspring. The fact that females do produce variably sized offspring was suggested (Capinera 1979; Crump 1981; Kaplan and Cooper 1984) to be an adaptive response to environmental uncertainty or unpredictability. It is difficult to determine whether this is true for *C. vittatus*, since there is no indication of what levels of variation should be expected in such environments (Brodie and Ducey 1989), nor in what sense the environment is unpredictable.

It has been strongly advocated (Stearns 1976; Tinkle 1979; Seigel and Fitch 1985) that, because life history traits often show profound variation across years and among populations, long-term studies, ideally including multiple populations throughout a species' range, are needed to understand fully the life history of any species. As with most organisms, such studies are lacking for scorpions. Reproductive characteristics are known to vary over time (Polis and Farley 1979a,b, 1980), but it has not been demonstrated previously that such variation exists among populations of a species. Our work, in combination with that of Formanowicz and Shaffer (1993), suggests that for *C. vittatus* knowledge of both geographic and temporal variation is important, as differences in reproductive investment can be influenced by both location and time.

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