2004. The Journal of Arachnology 32:193–207

LIFE HISTORIES OF FOUR SPECIES OF SCORPION IN THREE FAMILIES (BUTHIDAE, DIPLOCENTRIDAE, VAEJOVIDAE) FROM ARIZONA AND NEW MEXICO

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ABSTRACT. Although scorpions are common and potentially ecologically important members of arid ecosystems throughout the world, basic life history information is lacking for most species. In the current study I examined reproductive investment patterns in four species of scorpion (*Centruroides exilicauda, Vaejovis spinigerus, Diplocentrus peloncillensis,* and *Pseudouroctonus apacheanus*) from southeastern Arizona and southwestern New Mexico during 1996–1998. *Vaejovis spinigerus* invested more in reproduction, in both absolute (total litter mass, TLM) and relative (TLM divided by female mass) terms, than did the other species, and produced the largest litters. Offspring of *D. peloncillensis* were the largest, weighing over twice as much as the next largest juveniles. Female size was uncorrelated with offspring size in any species, but positive correlations were found between female size and both litter size and total litter mass for *C. exilicauda* (marginally significant) and *V. spinigerus* (after removal of an outlier). Greater reproductive investment, measured as TLM, was used to make more offspring (in all species but *P. apacheanus*) but not larger offspring. A marginally significant trade-off between offspring size and number was found in *V. spinigerus*; there was no size-number trade-off in the other three species. Overall, then, my results suggest that (1) larger females do not produce larger offspring, (2) larger females may produce more offspring and invest more into a reproductive bout, and (3) the allocation strategy of these species appears to be to invest reproductive resources into production of as many offspring as possible of a relatively fixed size.

Keywords: reproductive investment, scorpions, offspring size, litter size, trade-offs

One of the primary goals of life history studies is to understand how females allocate energy into reproduction, both within a single reproductive event and across their lifespan (Roff 1992, 2002; Stearns 1992). A female's allocation strategy for a single clutch may be thought of in terms of two ‘‘decisions.’’ First, she must choose how much of her available resources to devote to reproduction (i.e., reproductive effort or investment). Second, she must decide how to allocate that resource fraction into offspring (i.e., per-offspring investment; Bernardo 1996). The latter decision is generally modeled as a trade-off between making a few large or many small offspring, and a number of studies in various taxa have demonstrated such a trade-off (reviews in Roff 1992; Stearns 1992). Reproductive effort and per-offspring investment have usually been assumed to evolve independently (e.g., Smith & Fretwell 1974; Roff 1992, 2002; Stearns 1992), although recent theoretical and empirical evidence suggest they are likely linked evolutionarily (Winkler & Wallin 1987; Caley et al. 2001). Thus, reproductive effort, litter size, and offspring size potentially covary at the phenotypic level. Furthermore, these three traits often vary with female size, which itself is often under strong selective pressure (Roff 1992, 2002; Stearns 1992).

Based on the above, reproductive allocation patterns are best understood when multiple traits are measured for each of a number of females within a species. For scorpions, such studies are unfortunately rare (Francke 1981; Bradley 1984; Benton 1991a, b; Formanowicz & Shaffer 1993; Brown & Formanowicz 1995, 1996; Lourenço et al. 1996). These studies indicate that, with a few exceptions, female size is unrelated to offspring size. However, larger females generally produce larger litters and have a greater reproductive investment, measured as total litter mass, than smaller females, although these trends do not hold for all species or even all populations of a single species (Brown 2001). Females with greater investment most often simply increase the number of offspring produced, although in

Table 1.—Descriptive statistics (mean ± SE) for life history traits in *Centruroides exilicauda*, *Vaejovis spinigerus*, *Diplocentrus peloncillensis*, and *Pseudouroctonus apacheanus* from Arizona and New Mexico. CL = carapace length. CV = coefficient of variation. A dash indicates that a variable was unmeasured. Masses are in mg. Carapace lengths are in mm. Instar 1 duration is in days.

	Female mass	Female CL	Mean offspring mass	Mean offspring CL	Litter size
1996 *C. exilicauda*	425.2 ± 16.1	4.75 ± 0.06	9.4 ± 0.3	1.57 ± 0.02	16.4 ± 1.4
1997 *C. exilicauda*	373.3 ± 9.7	4.79 ± 0.03	10.3 ± 0.4	—	12.7 ± 1.1
1996 *V. spinigerus*	882.8 ± 96.1	6.41 ± 0.21	9.8 ± 0.5	—	49.2 ± 4.6
All *V. spinigerus*	828.4 ± 64.8	6.39 ± 0.14	9.4 ± 0.4	—	48.4 ± 4.0
D. peloncillensis	897.2 ± 57.9	5.42 ± 0.09	23.8 ± 1.5	—	13.0 ± 1.1
P. apacheanus	153.4 ± 17.9	3.66 ± 0.13	1.6 ± 0.2	—	27.8 ± 4.2

some cases (Formanowicz & Shaffer 1993; Brown & Formanowicz 1995) larger offspring are also made. Finally, most species do not exhibit an offspring size-number trade-off, and for those that do the strength and direction of the trade-off can vary among populations or years (Brown 2001).

The life history of scorpions is virtually unique among terrestrial arthropods (Polis & Sissom 1990). They are often long-lived and relatively large at maturity. Females give birth to live young, potentially producing multiple litters over a number of years, and provide parental care through at least the first molt. Scorpions are also potentially ecologically important predators in many arid and tropical ecosystems (Polis 2001), and knowledge of their life histories should help us explain their ecological effects in these habitats. In this paper I report reproductive data, collected in 1996–1998, on four species of scorpion from southwestern Arizona and southeastern New Mexico: one buthid, *Centruroides exilicauda* (Wood 1863); one diplocentrid, *Diplocentrus peloncillensis* Francke 1975; and two vaejovids, *Pseudouroctonus apacheanus* (Gertsch & Soleglad 1972) and *Vaejovis spinigerus* (Wood 1863). For all, I examined relationships among female size, offspring size, litter size and reproductive investment. I also examined coefficients of variation in offspring size and their relationship to these traits, since offspring size variation may itself be under selection in certain conditions (Kaplan & Cooper 1984; McGinley et al. 1987).

METHODS

Study sites and natural history.—Female scorpions were collected from three sites during 1996 (19–28 May), 1997 (29 June–7 July), and 1998 (21–30 May). All *D. peloncillensis* and *C. exilicauda* were collected from Geronimo Pass (elevation 1770 m) in the Peloncillo Mountains, Hidalgo County, New Mexico, approximately 59 km ENE of Douglas, Arizona (hereafter the Geronimo Pass population, Site 1). All *P. apacheanus* and some *V. spinigerus* were collected in the vicinity of the Southwestern Research Station of the American Museum of Natural History, located in the Chiricahua Mountains southwest of Portal, Cochise County, Arizona (hereafter the SWRS population, Site 2). Elevations ranged from 1620–1800 m. The remainder of the *V. spinigerus* were collected from a stretch of Portal Road (elevation 1370–1420 m) approximately 2–5 km east of Portal (hereafter the Portal population, Site 3). Sites 1 and 2 are primarily Madrean evergreen woodland [Brown 1994a; see Francke (1975) for a further description of the Geronimo Pass site], while site 3 is semidesert grassland (Brown 1994b). Records from SWRS show mean annual precipitation from 1978–1996 was 571 mm, with the wettest months being July and August and the driest months April and May; Geronimo Pass likely shows a similar pattern (Brown 1994a).

Scorpions were collected from under rocks or other surface debris during day searches, or while active on the surface at night by using portable flashlights equipped with ultraviolet bulbs. All females were gravid when collected except for seven *C. exilicauda* found in 1997 with first (n = 5) or second (n = 2) instars on the back. Of the four species studied, *D. peloncillensis* is the only obligate burrower, and was found under rocks at or near the burrow

Table 1.—Extended.

Total litter mass	Relative litter mass	CV of offspring mass	Instar 1 duration	% Survival
153.2 ± 13.3	0.37 ± 0.03	10.1 ± 1.9	7.4 ± 0.2	76.4 ± 7.0
130.7 ± 13.3	0.35 ± 0.04	7.9 ± 1.0	7.2 ± 0.6	89.7 ± 4.9
472.9 ± 46.1	0.56 ± 0.04	9.1 ± 1.1	8.6 ± 0.6	99.7 ± 0.3
440.7 ± 35.7	0.55 ± 0.04	9.6 ± 1.0	8.9 ± 0.4	98.7 ± 1.0
310.0 ± 35.9	0.35 ± 0.03	10.4 ± 1.4	13.3 ± 0.8	92.8 ± 3.0
44.1 ± 8.3	0.30 ± 0.05	11.2 ± 3.3	7.8 ± 0.5	100 ± 0

entrance. *Vaejovis spinigerus* is also known to burrow, and at my collecting sites was captured under rocks with and without obvious burrows. The remaining two species inhabit depressions under rocks. *Pseudouroctonus apacheanus* was found only under rocks containing moist soil, and was never captured at night. Conversely, *C. exilicauda* and *V. spinigerus* did not exhibit any noticeable moisture preference and were captured in both day and night searches. Voucher specimens of all species have been deposited at the Denver Museum of Nature and Science.

Maintenance and data collection.—Following capture, females were returned to a laboratory at the University of Texas at Arlington, where they were housed individually in 18.5 x 7.5 x 9 cm plastic containers filled with ~0.5 cm of sand. I placed a crumpled paper towel in each container to serve as a refuge; this was kept moistened to increase humidity levels and replaced if it became moldy. I offered each female one adult cricket, *Acheta domestica* (Linnaeus 1758), every third week while gravid (1–2 juvenile crickets for *P. apacheanus*); females carrying offspring were not fed. The laboratory was kept on a 14:10 h light:dark cycle at a mean temperature of 26 °C (range 24–31 °C). Additional heat was provided by heat lamps (100 W incandescent bulbs with a parabolic metal flashing) attached above the shelves holding the plastic containers. I rotated containers daily along the lengths of the shelves to minimize potential effects of temperature variation on embryo development. Previous work (Brown 1998) has demonstrated that using this additional heat source increases parturition success of females and offspring survival to dispersal in the laboratory.

Following birth, first instar juveniles climb onto the female's back, where they undergo their first molt and subsequently disperse. I therefore checked containers daily for the presence of newborns, newly molted second instars or dispersed offspring. For each litter, all offspring molted or dispersed within a single 24 h period. Immediately following dispersal, I weighed the female and all live offspring individually to the nearest 0.1 mg on an analytical balance (Denver Instruments M-220). Litter size equaled the number of living and dead juveniles. Females were then killed by heat shock and preserved in 75% ethanol, after which I measured carapace length (CL), to the nearest 0.1 mm, using a dissecting microscope (American Optical) equipped with an optical micrometer. Using the same procedure I also measured offspring CL on a subset of *C. exilicauda* litters from 1996.

For my measure of reproductive investment I calculated total litter mass (TLM) by summing individual offspring masses. I also calculated a size-corrected measure of investment, relative litter mass (RLM), as TLM divided by female mass. Both TLM and RLM will be underestimated by using masses of second, rather than first, instars, as scorpions lose weight between birth and dispersal (Formanowicz & Shaffer 1993). This is more likely to affect interspecific comparisons since mass loss rates probably vary more among than within species, although the degree to which this is true is unknown. As a measure of within-litter variation in offspring mass I calculated coefficients of variation (CVs) using the bias correction of Sokal & Rohlf (1995:58). Finally I calculated percent survival of offspring until dispersal as the number of juveniles alive at the time of weighing divided by litter size.

Data analyses.—Because they have more space in which to store embryos or are better at obtaining resources, larger females often are predicted to produce more or larger offspring and to have greater reproductive investment. Thus, I examined relationships between female size (CL; see Results) and offspring size, litter size, or TLM using least-squares regression. For the remaining relationships I calculated correlation coefficients (Pearson's *r*), as I had no a priori basis for cause and effect. The trade-off between offspring size and number was examined in the following manner to statistically control for variation in female size. I first regressed offspring mass or litter size against female CL and obtained residuals. I then used these residuals in a correlation analysis. For each species separately, I initially set $\alpha = 0.05$ and then made adjustments using the sequential Bonferroni procedure (Rice 1989) to account for multiple ($n = 10$) significance tests. Regression and correlation results were combined within species for this correction. When *P* values were less than 0.05 but nonsignificant after Bonferroni correction, I also report adjusted α values.

For *C. exilicauda* I collected sufficient data to make comparisons between years using analysis of variance. Because of statistical problems associated with ratios (Packard & Boardman 1987), in this ANOVA I used the residuals from a regression of TLM on female mass as a measure of RLM. For all analyses reproductive variables were $\log_{10}$-transformed to meet assumptions of parametric tests. Data analysis was carried out using Statistica for Windows version 4.5 (StatSoft 1993).

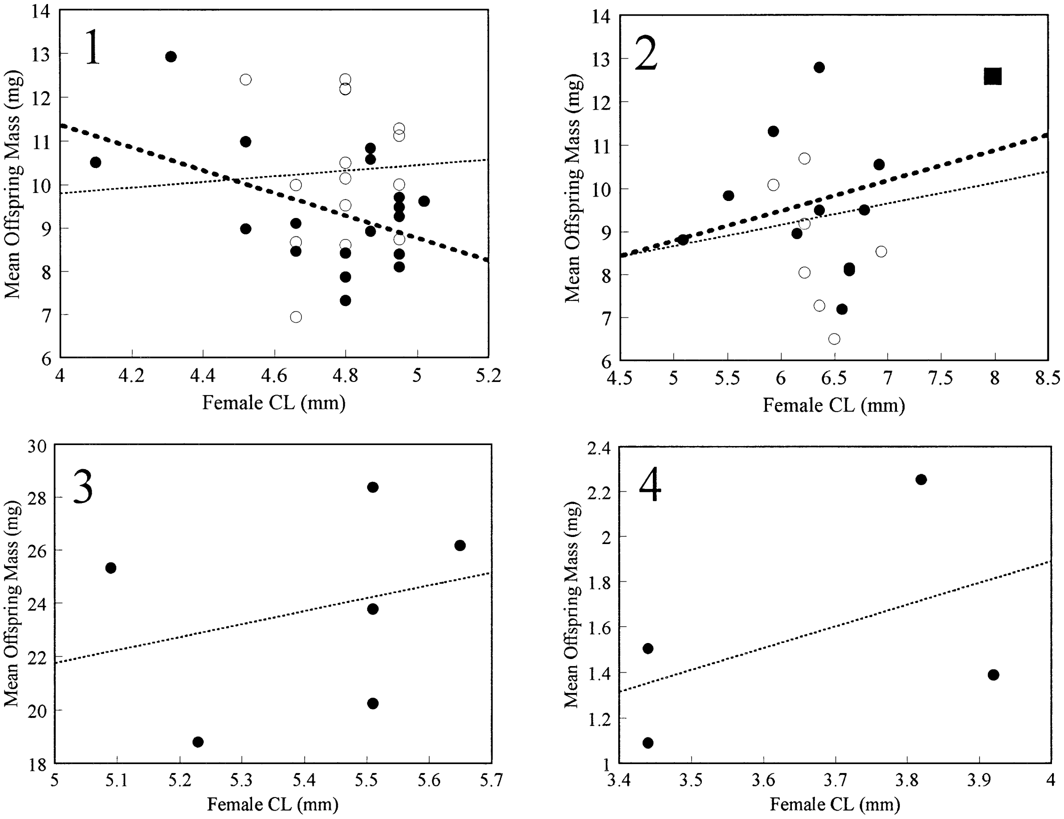
RESULTS

I obtained data from 63 females, as follows: 33 *C. exilicauda* (1996: $n = 18$; 1997: $n = 15$), 19 *V. spinigerus* (1996 SWRS: $n = 3$; 1996 Portal: $n = 12$; 1997 SWRS: $n = 2$; 1997 Portal: $n = 2$), six *D. peloncillensis* (1996, $n = 4$; 1997: $n = 2$), and five *P. apacheanus* (1996: $n = 1$; 1997: $n = 3$; 1998: $n = 1$). Since relationships among reproductive variables can vary over space or time (e.g., Brown & Formanowicz 1995; Brown 2001), it is preferable to use data from a single population and breeding season. I have therefore examined each year separately for *C. exilicauda* and have calculated two sets of means for *V. spinigerus*, one using all data and one using only 1996 Portal data (which had the largest sample size). For *D. peloncillensis* and *P. apacheanus* I lacked enough individuals in any one year, and so combined data across years. Summary statistics for each species are presented in Table 1.

Centruroides exilicauda females gave birth between 13 June–14 July in 1996 and from 1–9 July in 1997. Parturition in both *D. peloncillensis* (16 August–3 September) and *P. apacheanus* (29 July–18 August) occurred later in the season. Portal *V. spinigerus* had the most protracted birthing period, from 30 June–10 August in 1996 (both 1997 females gave birth in mid July). *Vaejovis spinigerus* from SWRS gave birth later than Portal females in both 1996 (10–26 August) and 1997 (2–17 August).

Diplocentrus peloncillensis and *V. spinigerus* were similar in mass and the largest species in this study, weighing about twice as much as *C. exilicauda* and 5–6 times more than *P. apacheanus*. However, these differences in female size were not necessarily reflected in other life history traits (Table 1). Offspring of *D. peloncillensis* averaged twice the mass of *V. spinigerus* offspring, while *C. exilicauda* and *V. spinigerus* offspring were similar in mass despite their two-fold difference in adult size. However, *V. spinigerus* had 3–4 times as many offspring as either *D. peloncillensis* or *C. exilicauda*. The smallest species, *P. apacheanus*, also had litters 1.7–2 times larger than *D. peloncillensis* or *C. exilicauda*, albeit with much smaller offspring. Combining offspring size and litter size, *V. spinigerus* invested more in reproduction than the other species, both in absolute (TLM) and relative (RLM) terms. The remaining species, while differing substantially in total investment, had similar RLM values. The per-litter percentage of offspring surviving until dispersal was very high ($\geq 90\%$), with the exception of *C. exilicauda* in 1996. Dead offspring were most often first instars, many of which had died while molting.

Centruroides exilicauda did not differ between years in female CL ($F_{1,31} = 0.38$, $P =$



Figures 1–4.—Linear regressions of mean offspring mass against female carapace length for four species of scorpion from Arizona and New Mexico. Regression equations are given in Table 2. Dashed lines indicate a nonsignificant regression. (1) 1996 (filled circles, heavy line) and 1997 (open circles, light line) *Centruroides exilicauda*. (2) 1996 Portal (filled circles, heavy line) and all (filled + open circles, light line) *Vaejovis spinigerus*. The square indicates an outlier (see text). (3) *Diplocentrus peloncillensis*. (4) *Pseudouroctonus apacheanus*.

0.54), offspring mass ($F_{1,31} = 2.71$, $P = 0.11$), litter size ($F_{1,31} = 3.25$, $P = 0.08$), TLM ($F_{1,31} = 1.21$, $P = 0.28$), RLM ($F_{1,31} = 0.42$, $P = 0.52$) or within-litter variation in offspring mass ($F_{1,31} = 1.23$, $P = 0.28$). However, female mass was significantly greater in 1996 ($F_{1,31} = 5.83$, $P = 0.02$). Repeating the above analyses using female mass as the covariate in an ANCOVA again revealed no significant differences among years (results not shown).

Female mass and CL were strongly positively correlated in *V. spinigerus* (1996 Portal: $r = 0.87$, $P < 0.001$, $n = 12$; all females: $r = 0.94$, $P < 0.001$, $n = 19$), *P. apacheanus* ($r = 0.96$, $P = 0.04$, $n = 4$), and *C. exilicauda* in 1996 ($r = 0.83$, $P < 0.001$, $n = 18$). The relationship between these variables was also positive, but not significant, for *D. peloncillensis* ($r = 0.60$, $P = 0.21$, $n = 6$) and *C. exilicauda* in 1997 ($r = 0.19$, $P = 0.49$, $n = 15$). I therefore used CL as my measure of female size because it is less subject to fluctuations (e.g., due to feeding history) than is mass. Results using female mass were qualitatively similar unless otherwise noted. Mass and CL were also significantly positively correlated for *C. exilicauda* offspring in 1996 ($r = 0.75$, $P = 0.01$, $n = 10$), and I therefore report only correlations involving mass (using CL gave similar results) to be consistent with the 1997 data.

For *C. exilicauda*, *D. peloncillensis*, and *P. apacheanus*, female size was uncorrelated with offspring size, litter size, or total investment following Bonferroni correction (Table 2; Figs. 1, 3–5, 7–9, 11, 12). For *C. exilicauda*, marginally significant positive correlations were found between female size and litter size

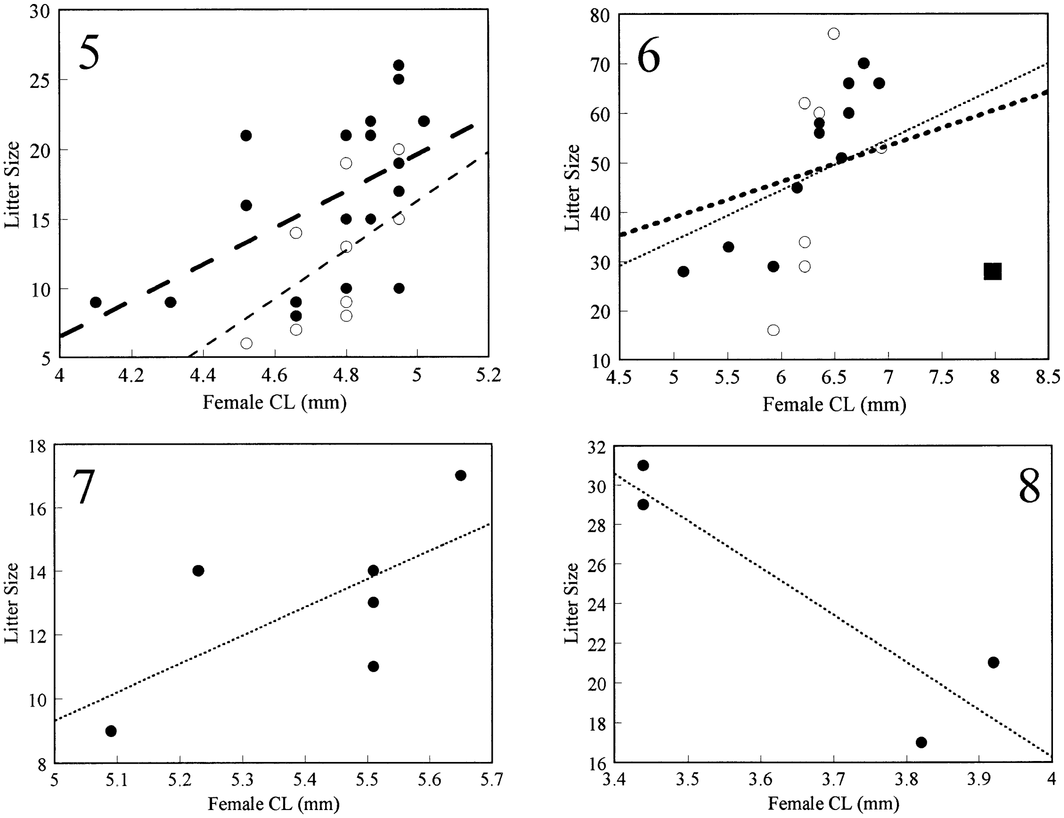
Table 2.—Linear regression statistics for the relationship between female size (carapace length) and offspring mass (OM), litter size (LS), or total litter mass (TLM) for four species of scorpion from Arizona and New Mexico. All variables were log-transformed prior to analysis. df = degrees of freedom for the *F*-test.

Species	Variable	Slope	Intercept	R^2	F	P
1996 *C. exilicauda*	OM	−1.17	4.06	0.21	4.28	0.055
df = 1, 16	LS	4.10	−3.67	0.31	7.08	0.017
	TLM	2.93	0.39	0.15	2.80	0.11
1997 *C. exilicauda*	OM	0.54	1.47	0.007	0.10	0.76
df = 1, 13	LS	7.62	−9.46	0.32	5.99	0.029
	TLM	8.16	−7.99	0.31	5.83	0.031
1996 Portal *V. spinigerus*	OM	0.36	1.61	0.05	0.56	0.47
df = 1, 10	LS	1.16	1.70	0.13	1.56	0.24
	TLM	1.51	3.30	0.25	3.32	0.10
All *V. spinigerus*	OM	0.20	1.85	0.01	0.18	0.68
df = 1, 17	LS	1.73	0.60	0.15	2.88	0.11
	TLM	1.93	2.45	0.22	4.79	0.042
D. peloncillensis	OM	1.11	1.29	0.08	0.33	0.60
df = 1, 4	LS	3.86	−3.98	0.47	3.60	0.13
	TLM	4.97	−2.68	0.49	3.84	0.12
P. apacheanus	OM	2.24	−2.49	0.26	0.70	0.49
df = 1, 2	LS	−3.64	7.89	0.79	7.51	0.11
	TLM	−1.40	5.39	0.21	0.53	0.54

in both years (1996: $P = 0.017$, adjusted $\alpha = 0.0056$; 1997: $P = 0.029$, adjusted $\alpha = 0.0056$) and between female size and TLM in 1997 ($P = 0.031$, adjusted $\alpha = 0.0063$). The regressions involving litter size and TLM for *C. exilicauda* in 1997 were in the same direction when female mass was used in place of CL, but were much weaker and not significant (log litter size = 1.4 + 0.18*log female mass, $R^2 = 0.002$, $F_{1,13} = 0.03$, $P = 0.86$; log TLM = 2.9 + 0.32*log female mass, $R^2 = 0.007$, $F_{1,13} = 0.09$, $P = 0.77$). Surprisingly, both litter size and TLM declined with increasing female size in *P. apacheanus*.

Female size was also uncorrelated with reproductive traits in *V. spinigerus* after Bonferroni correction (Table 2; Figs. 2, 6, 10), although there was a marginally significant relationship between female size and TLM when using data from all litters ($P = 0.042$, adjusted $\alpha = 0.0063$). However, one data point (the square in Figs. 2, 6, 10) was determined to be an outlier. With this removed there was no change in the relationship between female size and offspring mass (results not shown), but both litter size and TLM were now significantly positively correlated with female size (litter size: 1996 Portal: log litter size =−2.13 + 3.28*log female CL, $R^2 = 0.84$, $F_{1,9} = 44.9$, $P < 0.0001$; all females: log litter size = −3.02 + 3.72*log female CL, $R^2 = 0.48$, $F_{1,16} = 14.5$, $P = 0.002$; TLM: 1996 Portal: log TLM = 0.41 + 3.12*log female CL, $R^2 = 0.69$, $F_{1,9} = 19.8$, $P = 0.002$; all females: log TLM = −0.05 + 3.31*log female CL, $R^2 = 0.43$, $F_{1,16} = 12.0$, $P = 0.003$).

Reproductive investment, measured as TLM, was uncorrelated with offspring mass in all species (Table 3; Figs. 13–16), although greater investment tended to be associated with larger offspring in *D. peloncillensis* and *P. apacheanus*. Offspring number was significantly positively correlated with TLM in *C. exilicauda* and *V. spinigerus*, and the correlation between these traits was marginally positive in *D. peloncillensis* ($P = 0.04$, adjusted $\alpha = 0.005$; Table 3; Figs. 17–20). I found no evidence of a trade-off between offspring size and number (Figs. 21–24) in *C. exilicauda* (1996: $r = 0.21$, $P = 0.40$, $n = 18$; 1997: $r = -0.12$, $P = 0.68$, $n = 15$), *P. apacheanus* ($r = -0.74$, $P = 0.26$, $n = 4$), or *D. peloncillensis* ($r = -0.18$, $P = 0.73$ $n = 6$). There was also no trade-off in the 1996 Portal *V. spinigerus* ($r = -0.45$, $P = 0.14$, $n = 12$), although a marginally significant trade-off was found when including all data ($r = -0.50$, $P = 0.03$, adjusted $\alpha = 0.0056$, $n =$

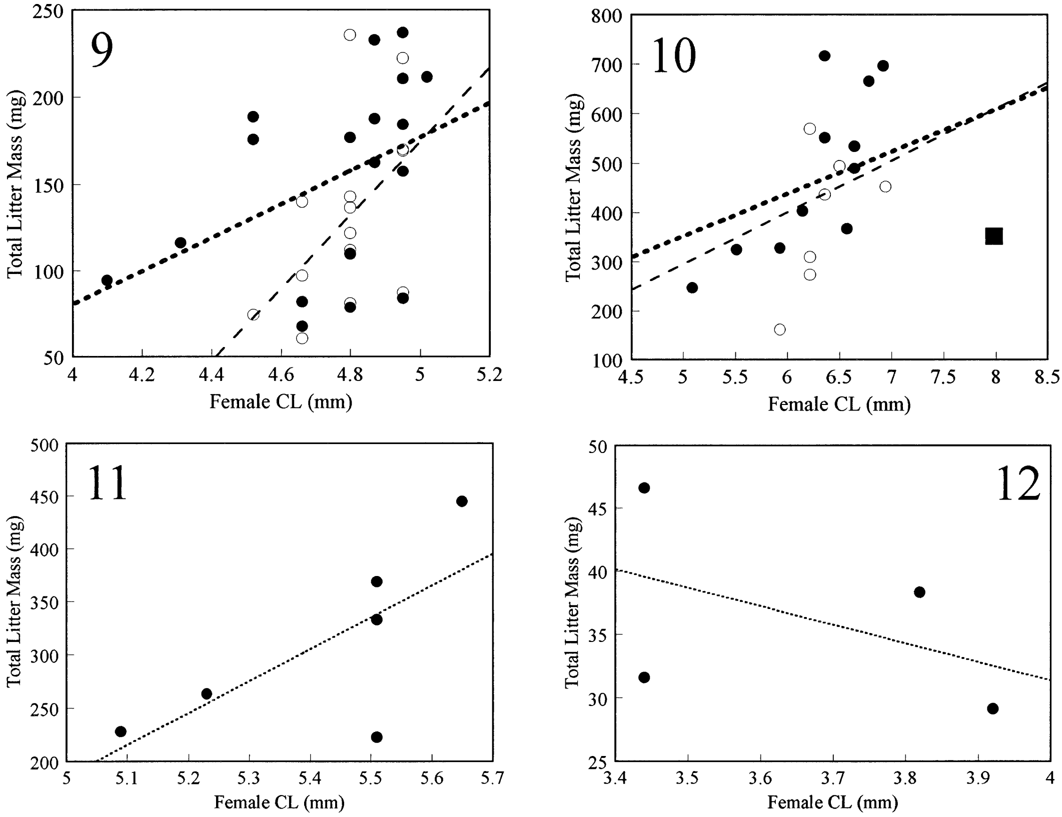


Figures 5–8.—Linear regressions of litter size against female carapace length for four species of scorpion from Arizona and New Mexico. Regression equations are given in Table 2. Short dashed lines indicate a nonsignificant regression, long dashed lines a marginally significant regression. Symbols as in Figure 1. (5) *Centruroides exilicauda*. (6) *Vaejovis spinigerus*. (7) *Diplocentrus peloncillensis*. (8) *Pseudouroctonus apacheanus*.

19). Within-litter variation in offspring mass (CV) was uncorrelated with other traits in most species (Table 3); the only exceptions were marginally negative correlations between CV and litter size ($P = 0.044$, adjusted $\alpha = 0.0063$) or TLM ($P = 0.026$, adjusted $\alpha = 0.0056$) for the 1996 Portal *V. spinigerus*. No obvious trends were found in CV patterns across species. Removal of the outlier for *V. spinigerus* qualitatively altered none of the above results (results not shown).

Captivity is suspected to affect scorpion reproduction because of differences in prey availability or environmental parameters between the field and laboratory (Polis & Sissom 1990). Therefore, for each species I examined correlations between days in captivity (the time between capture and parturition) and female mass, offspring mass, litter size, and total litter mass, the traits most likely to be affected by laboratory conditions. Within a species, these traits tended to either all increase or all decrease (Table 4), although there was no consistent overall pattern across species. Only two correlations were marginally significant: litter size of *V. spinigerus* (all litters; $P = 0.05$, adjusted $\alpha = 0.0125$), and mass of female *C. exilicauda* in 1997 ($P = 0.04$, adjusted $\alpha = 0.0125$), declined with time spent in captivity. The results for *C. exilicauda* are likely unimportant, as all litters had dispersed within 18 days of capture.

Both *C. exilicauda* females captured in 1997 carrying second instar juveniles gave birth in the laboratory to a second litter. The times between dispersal of the first litter and birth of the second were 109 and 341 days. Both females increased substantially (93–94



Figures 9–12.—Linear regressions of total litter mass against female carapace length for four species of scorpion from Arizona and New Mexico. Regression equations are given in Table 2. Short dashed lines indicate a nonsignificant regression, long dashed lines a marginally significant regression. Symbols as in Figure 1. (9) *Centruroides exilicauda*. (10) *Vaejovis spinigerus*. (11) *Diplocentrus peloncillensis*. (12) *Pseudouroctonus apacheanus*.

mg) in post-dispersal mass and produced larger second litters (first litter/second litter: 8/18 and 13/14). Mean offspring mass in the second litter increased for one female and decreased for the other (10.1 mg/8.9 mg and 10.5 mg/11.8 mg, respectively, for the litter sizes above). Neither female had access to males after capture, but I do not know whether females had remated in the field while gravid or whether sperm from a single mating was used for both litters.

DISCUSSION

Based on data summarized in Polis & Sissom (1990) and Brown (2001), *V. spinigerus* had larger litters than other species in the family Vaejovidae [mean = 27.5 (*n* = 22)] or the genus *Vaejovis* [mean = 29.0 (*n* = 10)]. Previous authors have reported litter sizes of 13–69 for *V. spinigerus* (*n* = 4 litters; McAlister 1960; Stahnke 1966; Williams 1969); two Portal females had litters larger than this maximum (70 and 76 juveniles). First instar duration was shorter than the family mean of 12.6 d (*n* = 8), but slightly longer than the duration reported for *V. spinigerus* by McAlister (1960; 7–8 d).

In contrast, both *C. exilicauda* and *D. peloncillensis* had smaller litters on average than other confamiliars [Buthidae mean = 22.8 (*n* = 33), Diplocentridae mean = 24.6 (*n* = 8)] or congeners [*Centruroides* mean = 37.5 (*n* = 7), *Diplocentrus* mean = 24.8 (*n* = 6)]. Geronimo Pass *C. exilicauda* had litters intermediate in size to those of inland (mean = 10.1) and coastal (mean = 18.2) *C. exilicauda* from Baja California [Myers 2001; however, this likely represents a distinct species from the New Mexico population (Gantenbein et al. 2001)], but smaller than the mean of 20 for

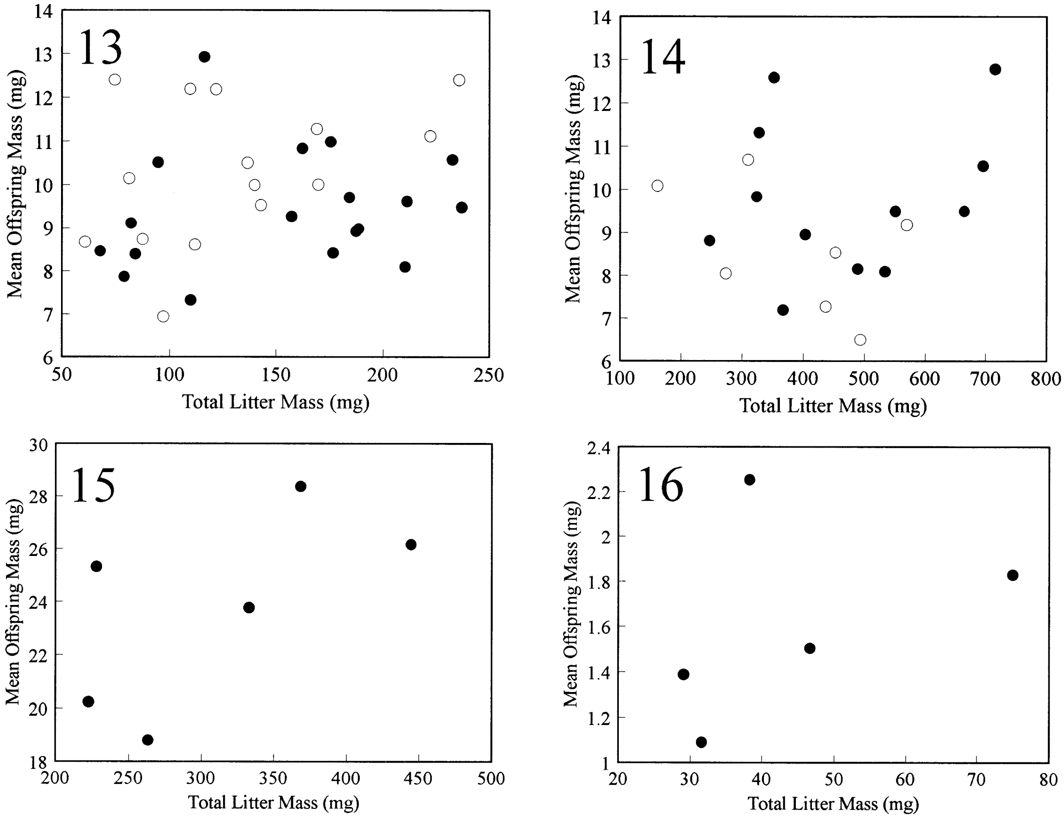
Table 3.—Correlations (Pearson's *r*) between reproductive traits in four species of scorpion from Arizona and New Mexico. FCL = female carapace length. All other abbreviations are defined in Tables 1 and 2. * $P < 0.05$, *** $P < 0.001$.

	Correlation between:					
	TLM-OM	TLM-LS	CV-FCL	CV-OM	CV-LS	CV-TLM
1996 *C. exilicauda* (*n* = 18)	0.24	0.94***	0.37	−0.36	−0.20	−0.31
1997 *C. exilicauda* (*n* = 15)	0.38	0.90***	0.40	−0.07	0.06	0.03
1996 Portal *V. spinigerus* (*n* = 12)	0.17	0.88***	−0.29	−0.05	−0.59*	−0.64*
All *V. spinigerus* (*n* = 19)	0.004	0.90***	−0.20	−0.34	−0.13	−0.30
D. peloncillensis (*n* = 6)	0.61	0.83*	−0.20	0.04	0.17	0.15
P. apacheanus (*n* = 5)	0.48	0.71	−0.32	−0.86	0.13	−0.52

this species (Polis & Sissom 1990). First instar duration was similar to family means for *C. exilicauda* [mean = 6.5 d (*n* = 20)] and *D. peloncillensis* [mean = 14.4 d (*n* = 4)], and for *C. exilicauda* was within the range previously reported for this species (6–15 d: Stahnke 1966; Williams 1969). *Pseudouroctonus* life history data are available for only a single litter of *P. reddelli* (Gertsch & Soleglad 1972). This species is much larger than *P. apacheanus* and has larger litters and a slightly shorter first instar duration (Brown 1997).

With the exception of *V. spinigerus*, relative litter mass was lower than in any sexually reproducing scorpion (range 0.44–0.55: Benton 1991a; Formanowicz & Shaffer 1993; Brown & Formanowicz 1995, 1996; Lourenço et al. 1996). Such low relative investment might occur if females cannibalize some newborns, decreasing observed litter sizes. However, no females in this study were observed feeding on juveniles. Low food levels might also lead females to invest fewer resources in reproduction, or to resorb some embryos (Polis & Sissom 1990). If precipitation levels can be used as a proxy for arthropod prey availability, then reduced investment might be expected in 1996, when only 27.4 mm of precipitation had fallen by the end of May when scorpions were collected. However, RLM was as low in 1997 (e.g., for *C. exilicauda*), when > 7 times as much rain (202.4 mm) had fallen in the same period. Conditions in the laboratory might also have been more stressful than in the field, leading to decreased investment in reproduction (lower TLM), maintenance (lower female mass), or both, as time spent in captivity increased. If so, low RLM should primarily reflect declines in TLM, a trend not supported by my data for any species. Thus, relatively low reproductive investment in *C. exilicauda*, *D. peloncillensis*, and *P. apacheanus* may simply reflect an adaptive response by these species to specific environmental conditions, such as a decrease in the length of the growing season or lower prey availability, in lower montane woodlands. Obviously, more comparative investment data for scorpions from various habitats are required to assess this hypothesis.

For *C. exilicauda* and *D. peloncillensis*, more detailed comparisons can be made to *C. vittatus* (Say 1821) and *D. lindo* Stockwell & Baldwin 2001. The latter two species occur sympatrically at Chandler Independence Creek Preserve in west Texas (Brown & Formanowicz 1995, 1996), which differs in elevation (~700 m) and habitat (Chihuahuan desert scrub) from Geronimo Pass. Reproductive data were obtained for the Texas species in 1992 (Brown & Formanowicz 1995, 1996) and 1996–1997 (Brown unpub. data). *Diplocentrus* females are similar in size, while *C. vittatus* females are ~30% larger by mass than *C. exilicauda* females. For the other reproductive traits, the same pattern emerged for each



Figures 13–16.—Correlations between total litter mass and mean offspring mass for four species of scorpion from Arizona and New Mexico. Correlation coefficients are given in Table 3. Symbols as in Figure 1. (13) *Centruroides exilicauda*. (14) *Vaejovis spinigerus*. (15) *Diplocentrus peloncillensis*. (16) *Pseudouroctonus apacheanus*.

congener pair: Texas scorpions had larger litters, smaller offspring, and larger total and relative investment than New Mexico scorpions (part of this trend was relaxed for *D. lindo* in 1997, as TLM and RLM were just slightly larger than comparable values for *D. peloncillensis*).

The proximate cause of these interspecific differences is unknown, given that the two study sites differ in a number of environmental characteristics. For instance, temperature is known to affect growth rates, adult size, and reproduction in a variety of ectotherms (e.g., Li & Jackson 1996; Ernsting & Isaaks 2000). In particular, theoretical and empirical studies (e.g., Yampolsky & Scheiner 1996; Ernsting & Isaaks 2000) have demonstrated that egg/offspring size decreases, and litter size increases, with an increase in temperature. Decreases in offspring size may not balance increases in offspring number, so that total investment may be greater at higher temperatures (Ernsting & Isaaks 2000). Given that mean and maximum monthly temperatures are higher at Independence Creek than Geronimo Pass across the year [using data from the southern (NCDC 2002a) and western (NCDC 2002b) regional climate center websites, respectively], the trends for *Centruroides* and *Diplocentrus* are in the predicted direction. Alternatively, larger offspring size may be favored at Geronimo Pass if predation pressure on juveniles is greater or food availability for juveniles is lower than at Independence Creek. Under such conditions large offspring are predicted to survive better and/or develop faster than small offspring (Shine 1978; Itô & Iwasa 1981).

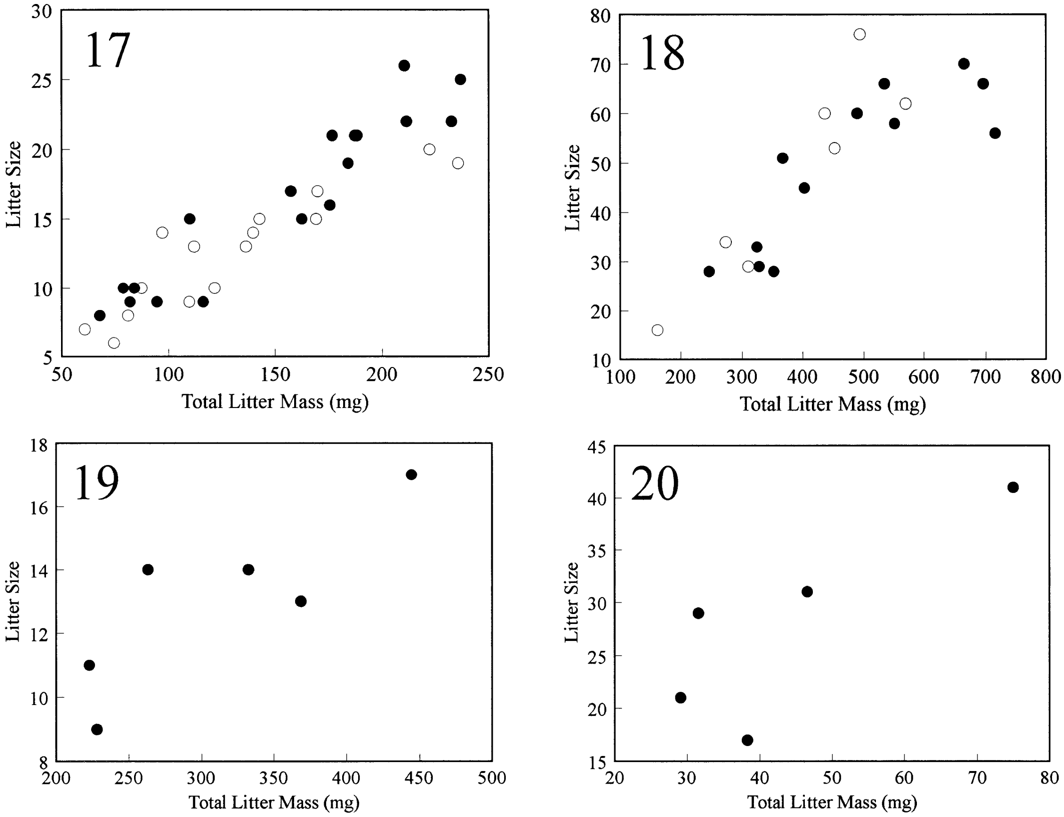
Female size had little influence on offspring size, but larger females tended to have larger

Table 4.—Correlations (Pearson's r) between days spent in captivity and selected reproductive traits in four species of scorpion from Arizona and New Mexico. All abbreviations are defined in Tables 1 and 2. * $P < 0.05$.

	Correlation between days in captivity and:			
	Female mass	OM	LS	TLM
1996 *C. exilicauda* (n = 18)	0.40	−0.14	−0.30	−0.34
1997 *C. exilicauda* (n = 15)	−0.54*	0.17	0.35	0.39
1996 Portal *V. spinigerus* (n = 12)	0.15	−0.05	−0.44	−0.48
All *V. spinigerus* (n = 19)	−0.01	0.33	−0.46*	−0.35
D. peloncillensis (n = 6)	0.75	0.47	0.40	0.58
P. apacheanus (n = 5)	0.54	0.71	0.16	0.66

litters and invest more into reproduction in all species but *P. apacheanus*. The latter two relationships are somewhat equivocal, as the correlations between female size and litter size or TLM were nonsignificant (for *D. peloncillensis*), marginally significant (for *C. exilicauda*), or significant only after removal of an outlier (for *V. spinigerus*). Nevertheless, these trends are likely to reflect real and biologically meaningful relationships, given that a positive correlation between female size and litter size or total investment is common in other taxa (reviewed in Roff 1992; Stearns 1992), including other arachnids (e.g., solifuges: Punzo 1998; spiders: Kessler 1971; Killebrew & Ford 1985; McLay & Hayward 1987; Punzo & Henderson 1999). In a recent review, Brown (2001) examined allometric relationships involving offspring size or number for 11 species of scorpion (including three of the four current species), some represented by multiple populations or years. Adding two additional sources (Formanowicz & Shaffer 1993; Myers 2001), significant positive correlations with female size (measured as mass in most cases) were found in only six of 30 cases for offspring size (with two additional significant negative correlations) and 12 of 32 cases for litter size (with one significant negative correlation). Total litter mass appears to correlate more strongly with female size for scorpions in general, as in six of eight previous cases this relationship was at least marginally significant (Bradley 1984; Benton 1991b; Formanowicz & Shaffer 1993; Brown & Formanowicz 1995, 1996). Thus, my results agree in general with those from previous studies of scorpion reproduction, although my support for an allometric effect on litter size was stronger than in Brown (2001).

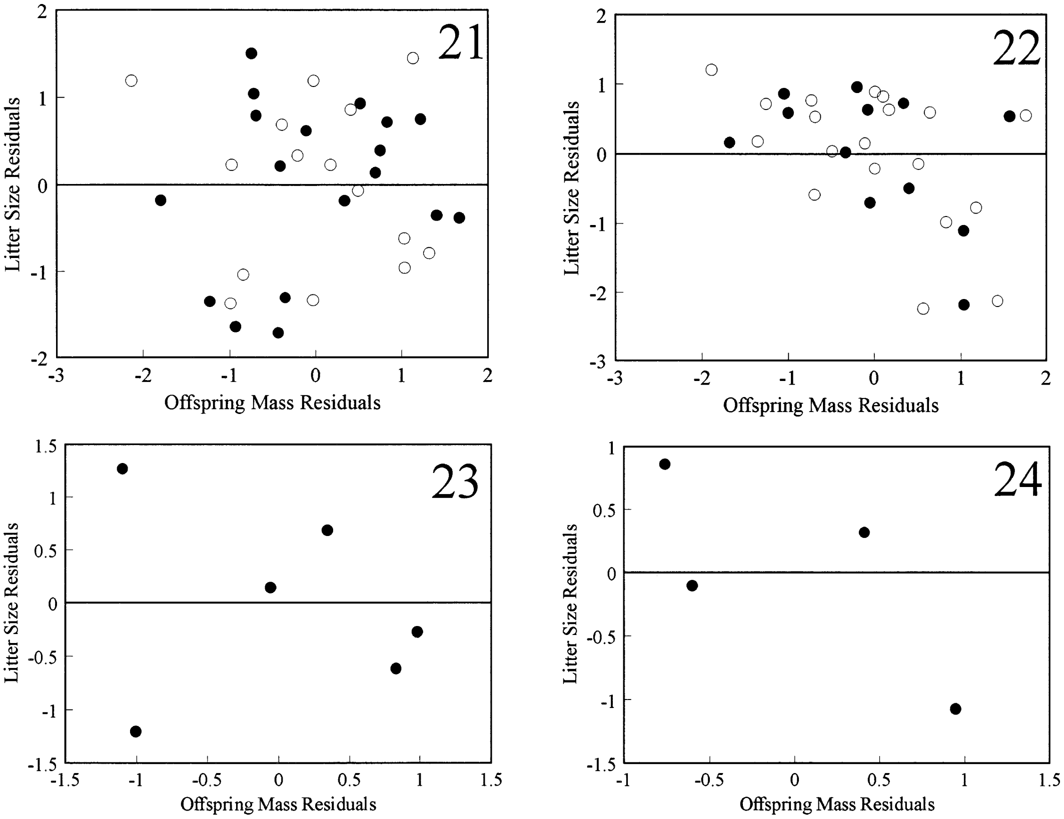
In the current study and in Brown (2001), two issues may obscure detection of significant allometric effects. First, sample sizes may be too low to reveal effects; for example, in the current study the significant or marginally significant results involving litter size and TLM came from the two species (*C. exilicauda* and *V. spinigerus*) with the largest sample sizes. The use of Bonferroni correction, although conceptually justified, may exacerbate this problem by making it harder to detect important trends. I note, however, that across species of scorpions sample size is uncorrelated with the magnitude of the correlation coefficient between female size and litter size [$r = 0.005$, using data from Brown (2001)]. Second, and perhaps more importantly, the choice of female size measure appears to alter the strength of the correlation with litter size (and TLM) in a usually consistent way. In the current study, in all cases litter size was more strongly correlated with female CL (R^2 range without removing *V. spinigerus* outlier, 0.13–0.79) than with female mass (R^2 range, 0.002–0.12), although only for 1997 *C. exilicauda* did statistical significance change. The same



Figures 17–20.—Correlations between total litter mass and litter size for four species of scorpion from Arizona and New Mexico. Correlation coefficients are given in Table 3. Symbols as in Figure 1. (17) *Centruroides exilicauda*. (18) *Vaejovis spinigerus*. (19) *Diplocentrus peloncillensis*. (20) *Pseudouroctonus apacheanus*.

trend holds in *Tityus columbianus* (Thorell 1876), where litter size is strongly correlated with female body length but weakly correlated with female mass (Lourenço et al. 1996), and *C. vittatus*, where litter size and TLM are more strongly correlated with female CL than female mass in seven of ten population-year combinations (Brown 1998). Thus, female mass may be a relatively poor measure for examining allometric relationships in scorpions, and significant correlations between litter size and female size may be more common than reported in Brown (2001).

The lack of significant relationships between offspring size and female size or TLM suggests that offspring size is relatively canalized compared to litter size. This was reflected in coefficients of variation across females; CVs of litter size (range of species means, 21.2–42.5%) were 1.5–3 times greater than CVs of offspring size (range, 14.2–27.6%). My results are consistent with those from other terrestrial ectotherms (e.g., lizards: Congdon 1989; spiders: Kessler 1971; McLay & Hayward 1987; Killebrew & Ford 1985; insects: Mappes et al. 1996; scorpions: Brown & Formanowicz 1995, 1996; Lourenço et al. 1996) indicating that increases in reproductive output result primarily from adding offspring rather than increasing offspring size. Canalization of offspring size may represent a decision by females to allocate a relatively constant amount of resources to each offspring. As suggested for spiders (Marshall & Gittleman 1994), this amount may be near the minimum necessary to ensure survival of offspring until dispersal. Variation in offspring size among or within litters might then reflect "noise" created by a female's inability to precisely allocate resources. Alternatively, the



Figures 21–24.—Correlations between residual offspring mass and residual litter size for four species of scorpion from Arizona and New Mexico. Correlation coefficients are given in the text. Symbols as in Figure 1. (21) *Centruroides exilicauda*. (22) *Vaejovis spinigerus*. (23) *Diplocentrus peloncillensis*. (24) *Pseudouroctonus apacheanus*.

relative uniformity in offspring size may reflect anatomical constraints (see e.g., Congdon & Gibbons 1987), perhaps in the structure of the ovariuterus or genital operculum, which limits egg or offspring size but is unrelated itself to female size.

I found little support for an offspring size-number trade-off in the four species studied, similar to the trend for scorpions in general (Brown 2001). Also similar to results from other arachnids (Simpson 1993; Brown 1998, 2001) was the year-to-year change in strength and magnitude of the trade-off in *C. exilicauda*. The reasons for this are unclear, as much life history theory predicts that offspring size and number will be negatively correlated if resources available for reproduction are limited (Roff 1992, 2002; Stearns 1992). Variation in acquisition of resources, which can occur if better quality females obtain more or better quality prey, has been predicted to potentially obscure trade-offs between offspring size and number (van Noordwijk & de Jong 1986). Brown (in press) has recently demonstrated that this hypothesis applies to scorpions, that is, that stronger (more significant) negative correlations between offspring size and number occur when variation among females in reproductive investment (a measure of variation in resource acquisition by females) is relatively low. A second explanation for the lack of a trade-off involves the relatively constant size of offspring. If there exists a fixed allocation strategy, that is, females use their reproductive resources to make as many offspring as possible of a given (minimal?) size, then there is no underlying basis for a trade-off.

In summary, I found little evidence for larger females to produce larger offspring for any of the species studied. However, for two of the four species (*C. exilicauda* and *V. spinigerus*) larger females produced more offspring and had a greater total litter mass, although these results were not always significant after Bonferroni correction. For each of the four species studied, females with higher reproductive investment produced more but not larger offspring than females with lower investment. Finally, no trade-off existed between offspring size and number, except when I combined data across years and populations in *V. spinigerus*. These results do not appear to be unusual among scorpions, and understanding the generality of these patterns and the factors that influence them remains a major challenge to scorpion biologists. Experiments in which environmental factors such as prey availability or temperature are manipulated and reproductive traits measured are the next critical step.

ACKNOWLEDGMENTS

I thank Dan Formanowicz, Chris Amaya, and Marina Gerson for assistance in collecting scorpions. Wade and Emily Sherbrooke, and the staff of the Southwestern Research Station, made our trips to Arizona extremely enjoyable. This work was supported by two grants (1996–1997) from the Southwestern Research Station Fund of the American Museum of Natural History.

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Manuscript received 18 October 2002, revised 27 June 2003.