THE LIFE HISTORY OF *EUSCORPIUS FLAVICAUDIS* (SCORPIONES, CHACTIDAE)

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Abstract. The life-history of an English population of the scorpion, *Euscorpius flavicaudis,* was studied using morphometric measures of over 300 specimens. The study hypothesizes seven instars. Evidence strongly suggests that there are two instars of adults: some males and females mature at the sixth instar and some at the seventh. Larger scorpions may have a higher per-season reproductive success but may have fewer reproductive seasons owing to the extra time needed to mature.

Studies of scorpion life-histories face several major difficulties. Firstly, scorpions are relatively long-lived compared to other terrestrial arthropods. For example, the Australian scorpion *Urodacus yaschenkoi* (Birula) grows to maturity in four years and may live an additional six (Shorthouse & Marples 1982). Secondly, scorpions can be very difficult to rear in the laboratory, often suffering high mortality at molting (Francke & Sissom 1984; Williams 1987; pers. obs.). Additionally, laboratory conditions may differ sufficiently from those in the field to produce inaccurate data. For example, Smith (1966) found that the duration of the first instar of *U. manicatus* (Thorell) was strongly influenced by the temperature at which the animals were maintained. Field studies of scorpion life-history can be equally problematical, as marked individuals lose their marks with each molt.

Many studies have resorted to estimating the number of instars from measurements of many specimens taken in the field (Polis & Sissom 1990). This method is approximate, but allows the tentative calculation of the life-history parameters of the scorpion under study.

The chactid scorpion, *Euscorpius flavicaudis* (de Geer) is a widespread southern European species that has successfully colonized a port in southern England. This colony at Sheerness, Kent (51°26′N: 0°45′E), has existed for about 120 years (Benton in press a). Over a two year period the ecology and behavioral ecology of this species was studied (Benton 1990) and enough data were collected to allow investigation of the life-history of *E. flavicaudis.* The prime purpose of this paper is to present data which strongly suggest that there is more than one instar of sexually mature adult in this population. The concurrent studies allow, for the first time, the evolutionary significance of a scorpion life-history polymorphism to be discussed.

METHODS

Between September 1987 and September 1989, a total of 317 specimens of *Euscorpius flavicaudis* were measured. Two methods of measuring were used: (1) 208 live animals were measured in the laboratory using a binocular microscope with optical micrometer, and (2) 109 animals were measured in the field using dial calipers accurate to 0.1 mm. These latter scorpions were subdued mechanically by using a modified 50 ml syringe. The nozzle end was replaced by a fine nylon mesh and the plunger was sheathed in cotton-wool. Scorpions were placed in the barrel of the syringe and pressed against the mesh. A small hole was cut through the mesh to allow a pedipalp to be pulled out. Thus immobilized, the pedipalp could be measured quickly and accurately without damaging the animal.

Most of the scorpions measured were adults or sub-adults ($N = 287$). Measurements made were: length and width of pedipalpal chela, length of prosoma (taken along midline), width of sternite V, weight and approximate whole-body length. In some analyses, the two measures of chela size were combined as the Chela-size Index (CSI). CSI is used in preference to chela length alone, as the ecological importance of chela size is most likely related to their strength (Benton in press b) and therefore volume. This is better approximated by the CSI.
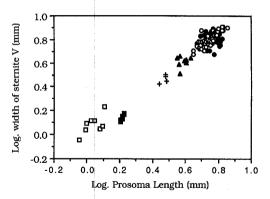
Figure 1.—A log-log bivariate morphometric plot, showing the 5 juvenile instars in the scorpion, *Euscorpius flavicaudis* ($N = 163$). Instars determined either by morphological differences (e.g., first and second instars) or cluster statistics (adults and fifth instars). White squares = first instar; black squares = second; cross = fourth; black triangle = fifth; white circle = adult females; black circle = adult males. Regression equation of this relationship (including all instars other than 1st): $y = 1.139x - 0.079$, $R^2 = 0.974$, $N = 155$.
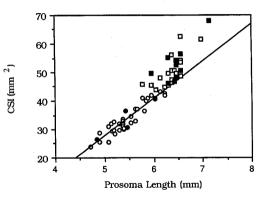

Figure 2.—Relationship between chela-size index (CSI = length of chela × width) and prosoma length in adult males. Data have been separated into two instars (see text), sixth (circles) and seventh (squares). Regression line fits the relationship in the sixth instar: seventh instar males have allometrically larger chelae. Regression line: $y = 12.9x - 37.1$, $R^2 = 0.88$. Males known to have deposited a spermatophore (filled symbols) occur in both instars.

The apparent objectivity of using cluster statistics in taxonomy has been frequently criticized (e.g., Ridley 1986), so in my analyses I only use cluster statistics to clump data when the number of clusters has been determined, or hypothesized, by some other method. The method of clustering was to use "average neighbor distance" (see Norusis 1985) using the package SPSSx (SPSS Inc., Chicago, IL 60611). As two different methods of measuring the scorpions were used, it is likely that their associatied errors were different. Due to this, in each analysis, care was taken to use only those scorpions that had been measured using the same method.

RESULTS

Number of juvenile instars.—The bivariate morphometric plot of prosomal carapace length vs. width of the sternite on mesosomal segment V, using all available data, reveals four clumps of scorpions other than the adults (Fig. 1). These clumps correspond to the first, second, fourth and fifth instars. No third instars were measured as a result of sampling error. Progression factors for the juvenile molts were calculated (Table 1), assuming that the third instar would clump midway between the second and fourth. Data are only available on the masses of the first and second instars: 0.0084 ± 0.0025 g ($N = 10$) and 0.0070 ± 0.0013 g ($N = 5$) respectively. The

reduction in mass between the first and second instar is due to the mass of the exuvium.

Number of adult male instars.—Sexually mature males can be distinguished on the basis of two secondary sexual characteristics: the possession of a notch in the pedipalpal fingers and their relatively longer pectines. The size-range of these adult males is large. However, the largest male and the second smallest deposited spermatophores, confirming their sexual maturity (Fig. 2).

During the course of field observations it became apparent that a dimorphism in the size of the pedipalpal chelae of adult males existed. Some males had chelae comparable in size to adult females; whereas others had disproportionately large chelae (mean adult male CSI = 42.5 ± 9.2 mm², range 24.3–66.6, $N = 113$; mean adult female CSI = 33.6 ± 7.3 mm², range 18.6–51.4, $N = 78$). To investigate this apparent dimorphism, the frequency distribution of chela lengths was compared to the expected normal distribution. The observed distribution of chela sizes differs significantly from normal ($\chi^2 = 21.1$, $df = 7$, $P < 0.001$; χ^2 test of normality, Zar 1984:89) (Fig. 3). The distribution is, in fact, bimodal, indicating the population of adult males occurs in two size-classes for chela length. The distribution of prosoma lengths of these 114 males also differs from normality ($\chi^2 = 17.2$, $df = 7$, $N = 80$, $P < 0.025$).
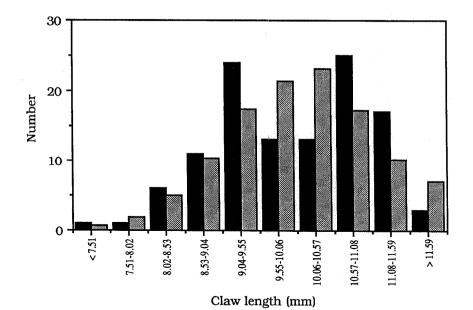
Having determined the existence of two size-

Figure 3.—The observed (filled bars) and expected (stippled bars) distributions of chela-lengths of 114 male scorpions from Sheerness. The expected distribution is a normal distribution given the mean and standard deviation of the observed. The distributions differ significantly ($\chi^2 = 21.1$, $df = 7$, $P < 0.001$). The two modes of the observed distribution correspond to two instars.

classes, cluster analysis was conducted on 66 males for which measures of prosoma length, chela width and chela length were available, in order to divide the adults more exactly. Figure 2 shows that the analysis splits the males into two groups based on different relationships between the prosoma length and the chela-size index. Large males have disproportionately large chelae.

The determination of the boundaries of the clusters by the above analysis allows calculation of the average weights and body size (prosoma + mesosoma, measured as one unit). Large males are, on average, 145% heavier than small males

Table 1.—Progression factors (PFs) in *E. flavicaudis*. A PF is the multiplicative increase in dimensions between instars. The first instar is atypical due to its incompletely sclerotized exoskeleton. The mean PFs for the other instars are 1.30 ± 0.09 (prosoma length) and 1.34 ± 0.11 (width of sternite V). As there are no data for the third instar, the PFs for the second–third and third–fourth molts are estimated by taking the square-root of the increase between the second and fourth instars. Final instars often show a lower PF than earlier instars (e.g., Polis & Farley 1979).

Instar	Prosoma length [mm ± SD (*n*)]	Progression factor	Width [mm ± SD (*n*)]	Progression factor
1st	1.10 ± 0.14 (8)		1.24 ± 0.24 (8)	
2nd	1.65 ± 0.04 (12)	1.50	1.42 ± 0.08 (12)	1.16
4th	2.96 ± 0.14 (4)	1.34^2	2.95 ± 0.24 (4)	1.44^2
5th	3.86 ± 0.26 (8)	1.30	4.14 ± 0.40 (8)	1.40
Female 6th	5.11 ± 0.37 (20)	1.32	5.94 ± 0.59 (20)	1.43
Female 7th	6.15 ± 0.38 (19)	1.20	7.24 ± 0.45 (19)	1.22
5th				
Male 6th	5.47 ± 0.39 (38)	1.42	5.34 ± 0.56 (49)	1.29
Male 7th	6.39 ± 0.28 (28)	1.17	6.53 ± 0.35 (30)	1.20

(0.658 ± 0.124 g cf. 0.428 ± 0.115 g; Mann-Whitney $U_{20,23}$ = 36.5, P = 0.0001), and their body length averages 117% longer (18.9 ± 1.6 mm cf. 16.2 ± 1.7 mm; Mann-Whitney $U_{20,23}$ = 45, P = 0.0001).

Perhaps the most parsimonious explanation for this dimorphism is that two instars of adult males exist within the population. The mean lengths of the males in each cluster allow the calculation of putative progression factors (Table 1).

Number of adult female instars.—As with males, females known to be mature (because they gave birth in the laboratory) show a wide range in size (Fig. 4). Animals assumed to be adult females have a larger range of sizes than that of adult males (prosoma length 4.46–7.22 mm of 5.07–7.14 mm in males). However no obvious dimorphism is apparent within females, as they do not have an allometric relationship between chela size and body size. For all available variables there are no significant departures from normality in the frequency distributions (χ^2 = 5.7, df = 7, N = 80, P > 0.50 for chela length; χ^2 = 10.26, df = 7, N = 79, P > 0.10 for chela width; χ^2 = 2.11, df = 6, N = 40, P > 0.90 for prosoma length). It is however possible that there are two instars of adult females, but the frequency distributions overlap more than males making females difficult to separate.

To investigate this further, cluster statistics were used to divide adult females into two size-classes (using the variables prosoma length and CSI). The means of the clumps were then used to calculate hypothetical progression factors (Table 1) which agree well with what would be predicted if there were two instars.

Resightings of marked individuals in the field suggest that adults can live for at least two years (Benton in press a) and growth to maturity may take three or more years. As post-maturation molts are unknown in scorpions (Polis & Sissom 1990), adult sixth instars do not become adult seventh instars, so we might expect females maturing at the seventh instar to have a reproductive benefit. A higher per-season reproductive success is the most obvious reason that natural selection may favor the delay of female maturity for several months and an extra instar. Under laboratory conditions built to mimic closely the scorpions' habitat in England, 16 females gave birth to viable broods (Benton in press b). Within these females (where data are available) a sig-
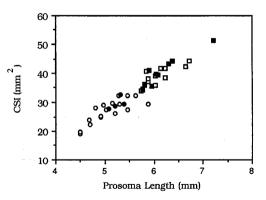

Figure 4.—Relationship between chela-size index (CSI = length of chela × width) and prosoma length in adult females. Data have been separated into two putative instars (see text), sixth (circles) and seventh (squares). Females known to have given birth (filled symbols) occur in both instars.

nificant relationship exists between female prosoma size and the weight of her brood (R^2 = 0.36, $F_{1,10}$ = 5.6, P < 0.05), and a positive relationship exists between female size and number of young (R^2 = 0.23, $F_{1,11}$ = 3.29, P = 0.10). Using the size criteria, determined by the earlier cluster analysis, to separate these females into two groups, it can be shown that a "small" female has on average 30 ± 5 young (range 26–38, N = 5) weighing 0.237 ± 0.048 g (range 0.196–0.315, N = 5); whereas a large female has 36 ± 9 young (range 25–51, N = 10) weighing 0.327 ± 0.063 g (range 0.210–0.420, N = 9). The difference in brood weights is significant (Mann-Whitney $U_{5,9}$ = 6, P < 0.05), the difference in brood sizes is not ($U_{5,10}$ = 15, P = 0.2).

DISCUSSION

From data reviewed in Francke and Sissom (1984) the mean number of instars in scorpions is 7.0 ± 1.2 (N = 57). In the present study there appear also to be seven instars of *Euscorpius flavicaudis*.

However, perhaps the most interesting aspect of this life-history study is the evidence of finding more than one instar of adults. The evidence for this is that sexually mature males are dimorphic in size. The means of the two size-classes are separated by progression factors of the expected size. If there were not two instars, a progression factor of 1.48 (for increase in prosoma length) for the fifth instar-adult male molt would be necessary. This would be higher than that previously

reported for scorpions (scorpion average = 1.28 ± 0.04, data from Polis & Farley 1979). Sexually mature females do not occur in two size-classes, but the range of female size is greater than for males. It was therefore hypothesized that two instars of adult female existed. Cluster statistics were then used to divide the range of adult females into two groups. To test the hypothesis, two predictions were made: (1) progression factors for the two groups should be within the normal range for scorpions, and (2) larger females should have a greater reproductive success per breeding attempt. Qualitatively, both these predictions were supported by data.

Life-history polymorphism is not unusual among scorpions. Francke and Sissom (1984) list 32 species for which the sexually mature instars had been determined. Of these species 47% (15) showed more than one adult instar (three species where only females mature at more than one instar, six only males and six both). The only record of a chactid scorpion with a life-history polymorphism is for *E. italicus,* where Angermann (1957) reports two instars of adult females.

No cases are known where scorpions continue to molt after they mature (Polis & Sissom 1990), so sixth instar adult scorpions are unlikely to molt a seventh time. Thus, the sixth instar of this population of *E. flavicaudis* consists of adult males and females, and sub-adult males and females. Adult males are immediately distinguishable owing to their notch in the pedipalpal fingers. However, the other categories of sixth instar are not easily distinguishable. Unfortunately the significance of the range of adult sizes was not realized until after the field study of this population had finished. In addition, the population is small and has a threatened status (Benton in press a) so I was unwilling to collect a large number of specimens for dissection. In total, 25 females (sixth and seventh instars) were preserved, and on closer inspection one of these was found to be a male without the obvious secondary sexual characteristics: he was a sub-adult. The prosoma length of this individual was 4.73 mm, with a CSI of 24.3 mm^2, putting it within the range of "adult females" (Fig. 4). Further, this sub-adult male has an average progression factor of 1.28 when compared to the average dimensions of the fifth instar scorpions which is within the normal range in this species. This makes it much more likely that this specimen is a small sixth instar male rather than a very large fifth instar.

Given the state of preservation of the specimens it was not possible to determine whether there were sixth instar immature females amongst them.

Although the observed life-history polymorphism in scorpions has previously been reported, for the first time an attempt can be made to explain its evolutionary significance. Seventh instar males are, on average, 1.20 times larger than sixth instar males; and seventh instar females 1.21 times larger than sixth (average of the progression factors for prosoma length, chela length, chela width and body width). Behavioral and ecological correlates of size do exist. In this species, the scorpion's primary offensive and defensive weapons are its chelae. Chela size predicts the outcome of fights between males for female-occupied burrows during the mating season, and large-clawed males can "persuade" otherwise unwilling females to mate (Benton in press b). It is interesting, therefore, that chela-size increases disproportionately to body size between the sixth and seventh instar adult males. Seventh instar males, therefore, have a higher per-season reproductive success than sixth instar males. In females, the benefit of being large seems also to be a greater reproductive success, in that large females have heavier (and more) offspring than smaller females. In *Paruroctonus mesaensis* rate of food intake was shown to have a significant effect on brood weights (Polis & McCormick 1987). This may result from the ability to increase food intake rate, by capturing larger prey. Larger scorpions win cannibalistic contests (Polis 1980; Benton 1990), so may obtain more food in this way.

If scorpions have a higher per-season reproductive success as seventh instar adults, why do any mature at the sixth instar? The answer to this must lie in the fact that seventh instar scorpions *delay* their maturity. In the study population in England, females give birth in late summer (Benton in press b) and the first instar lasts 7 days (Benton 1991). Second instars overwinter and molt the following spring to the third instar. The duration of subsequent instars is unknown, but laboratory studies uniformly show that instar duration increases as scorpions age (W. D. Sissom, pers. commun.), so it is plausible that seventh instar adults, by delaying maturity, miss one mating season. Adult longevity is difficult to assess, but the longest period between resightings of an adult (male) in the field is 23 months. Lon-

gevity for two or more mating seasons is probable.

Two maturation strategies exist in this population of scorpions: to mature at the sixth instar, and be small, or to delay maturity until the seventh instar and be large. It is possible that the two strategies' payoffs are frequency dependent, and occur at an equilibrium value—the Evolutionarily Stable Strategy (ESS, Maynard Smith 1982). This subject is explored further in Benton (in press b).

ACKNOWLEDGMENTS

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