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LITTER SIZE IN MICRO-BUTHOID SCORPIONS (CHELICERATA, SCORPIONES)

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Abstract: All available information about litter size in buthoid scorpions is presented in tabular form. Selected examples concerning species of micro-buthoid scorpions are given. The possible factors responsible for litter-size variation in these species are discussed. It is concluded that (i) reduction of litter size in these species is independent of ecological factors, (ii) litter size is directly proportional to the size of the female and inversely proportional to the size of the young, (iii) large body size of pro-juveniles at birth seems to be associated with a more 'complete' embryonic development, (iv) post-embryonic development is achieved with a smaller number of instars, (v) morphometric growth values are higher than those observed for other buthoids.
Key words: Scorpiones, micro-buthoids, litter size, evolutionary factors.

El tamaño de la camada en los escorpiones microbutoides (Chelicerata, Scorpiones)
Resumen: Se presenta, tabulada, toda la información disponible sobre el tamaño de la camada en los escorpiones butoides. Se incluyen ejemplos escogidos de especies de escorpiones microbutoides. Se discuten los posibles factores que determinan el tamaño de las camadas, y se concluye que (i) la reducción en el tamaño de la camada de estas especies es independiente de factores ecológicos, (ii) el tamaño de la camada es directamente proporcional al tamaño de la hembra e inversamente proporcional al tamaño de las crías, (iii) el nacimiento de pro-juveniles de gran tamaño parece ir asociado a un desarrollo embrionario más "completo", (iv) el desarrollo postembrionario se lleva a cabo en un menor número de estadios, (v) los valores del crecimiento morfométrico son más altos que los que se observan en otros butoides.
Palabras clave: Scorpiones, micro-butoides, tamaño de las camadas, factores evolutivos.

Introduction

Scorpions are unusual among terrestrial arthropods in several traits of their life-history. Because of this, many aspects of the reproductive biology of scorpions were poorly understood by early authors (see Polis & Sissom, 1990 for details). However, some precise studies on scorpion embryology had already been carried out by the end of the 19th century (Laurie, 1890, 1891, 1896a,b) and these were followed by the publications of Pavlovsky (1924, 1925) and Pflugfelder (1930).

Since the mid-1970s, there has been a renewal of interest in the reproductive biology of scorpions and, in particular, their post-embryonic development. Research on this subject was increased during the 1980s and continued throughout the 1990s. Little attention, however, was paid to the aspect of litter size in scorpions and only a few isolated publications have provided additional information. A pioneering work was that of Francke (1981), who attempted to explain the factors involved in litter size of scorpions of the family Diplocentridae. According to this author, litter size in diplocentrids is directly proportional to the size of the female and inversely proportional to the size of the young. Thus, the size of the mother and the size of the young were found to account for 81 percent of the variation in litter size between the species of this family. Polis & Sissom (1990) briefly re-discussed this matter, but referred to Francke's (1981) results as being intuitive. The syntheses proposed by Polis & Sissom (1990) and Lourenço (1991, 2002a) only resume the known data about litter size in scorpions, without further discussion about the factors that might be responsible for its variability.

Subsequent to the publications by Polis & Sissom (1990) and Lourenço (2002a), new data on litter size of several species of buthoid scorpions have become available. These are summarized in Table I, with special attention being given to micro-buthoid species (sensu Lourenço, 2000), including members the families Buthidae Koch and Microcharmidae Lourenço.

Many, if not most, of these small species of buthids and microcharmids show strongly reduced 'average litter size', in most cases with numbers less than 10 and in others less than 7 juveniles. It is important to note that small broods have also been observed for large species of buthids, and that these numbers are frequently reported as 'standard' numbers by several authors (Polis & Sissom, 1990). In fact, this kind of situation can be observed for females of any species which arrive to the end of their life cycle, when the number of follicles starts to decline (Lourenço, 1979). These numbers should not be retained as 'average' values.

Here I will focus on selected examples for which precise life history data, or at least life history predictions, are available.

Selected examples

Microtityus Kjellesvig-Waering

Armas (1974) and González-Sponga (1984) provided some biological data about *Microtityus* species, respectively showing that the litter sizes of *Microtityus fundorai* Armas and *Microtityus joseantonioi* González-Sponga were particularly small, comprising only 6 or 7 juveniles on average.

The observations carried out on *M. consuelo* and *M. rickyi* (Lourenço *et al.,* 1999) confirm this biological aspect. In both species, the broods are composed of very small numbers: 3 to 5 for *M. consuelo* and 4 to 6 for *M. rickyi*

(Fig. 1). In contrast, the size of pro-juveniles at birth is large. For example, in *M. rickyi* the female body size (prosoma + mesosoma) averages 7 mm in length while pro-juveniles body size averages 2.5 mm in length.

The duration of embryonic development ranged from 3 to 4 months, while the acquisition of adulthood took place at an average of 229 days for *M. consuelo* and 249 days for *M. rickyi*. These developmental periods are not very different from those in other buthids, but the growth rate values observed between different instars are globally higher in comparison with those of other species of Buthidae studied.

Morphometric growth values of the different instars for both the species of *Microtityus* studied are higher on average than those of other studied species of the family Buthidae. This aspect can probably be explained by the following factors: the number of molts necessary to reach adulthood is only 4, as opposed to the 5 or 6 observed for other buthid species (Lourenço, 2002a); the initial body size of *Microtityus* pro-juveniles at birth is much larger (in relation to mother's body size), than those observed for species belonging to other buthoid genera (Lourenço, 2002a). I suggest at present that the large body size of pro-juveniles at birth could be associated with a more 'complete' embryonic development. This factor 'may' facilitate a strategy of post-embryonic development with a smaller number of instars.

The theoretical morphometric growth value (constant) defined by Dyar (1890) and Przibram & Megusar (1912) for the development of arthropods is 1:26. The values observed for several species of buthoids vary from 1:22 to 1:33, depending on the parameter (segment) measured (Lourenço, 1979, 2002a). For both *Microtityus consuelo* and *Microtityus rickyi* the observed growth values were: carapace length 1:31 and 1:28; metasomal segment V length 1:55 and 1:50; movable finger length 1:28 and 1:31.

***Tityus* (*Caribetityus*) *elii* (Armas & Marcano Fondeur)**

With a total length of 30-35 mm, this species should not really be ranged among micro-buthoid scorpions. However, some of its biological traits show similarities with micro-buthoids and are therefore presented here.

The broods obtained for *Tityus* (*Caribetityus*) *elii* were composed of 10 to 12 individuals. These numbers are lower than those observed in most *Tityus* species, but are similar to the values observed for some small species of the subgenus *Tityus* (*Archaeotityus*) Lourenço (see Table I). In contrast, the size of pro-juveniles at birth is rather large in *T.* (*C.*) *elii* (Fig. 2).

The duration of embryonic development ranged from 3 to 4 months, while the acquisition of adulthood took place at an average of 447 days. These developmental periods are not very different from those found in *Tityus* species or other genera of Buthidae, but the observed growth rate values in the different instars are slightly greater than those of the other Buthidae that have been studied.

The analysis of the reproductive characteristics observed for *Tityus* (*Caribetityus*) *elii* shows that several traits are similar while others are distinct from those observed in other species of *Tityus* (Rouaud *et al*., 2002). The number of molts necessary to reach adulthood in *T.* (*C.*) *elii* is only 4, compared with 5 or 6 observed in *Tityus* species (Lourenço 1979, 2002a). Litters contain a smaller number of young: 10-12, compared with an average of 15-25 in most species of *Tityus*. Only a few species of the subgenus *Archaeotityus* have similarly low numbers. The initial body size of pro-juveniles at birth is slightly larger (in relation to the mother's body size) than that observed in other species of *Tityus*. This more complete embryonic development may be correlated with the smaller number of post-embryonic instars.

The average growth rates observed for different instars are similar to those observed for several species of *Tityus*. For males and females of *T.* (*C.*) *elii*, the growth rates were: carapace length 1.22 and 1.28; metasomal segment V length 1.28 and 1.29; movable finger length 1.24 and 1.26.

***Microbuthus fagei* Vachon**

Observations carried out on *M. fagei* showed that broods are composed of very small numbers, 3-4 (Lourenço, 2002b). In contrast, the size of pro-juveniles at birth is very large. Female body length averages 8.4 mm, while pro-juveniles body length averages 4.2 mm.

No precise data are available on the embryonic and postembryonic development of the species. However, using indirect methods and the morphometric values of juveniles collected in nature, the number of molts necessary to reach adulthood can be estimated to be 4.

***Orthochirus* Karsch**

Observations carried out on both *Orthochirus negebensis* (Shulov & Amitai, 1960) and an undescribed species of *Orthochirus* from Africa showed that broods are composed of very small numbers, 5-9 (Fig. 3). In contrast, the size of pro-juveniles at birth is very large. In both species, female body length averages 11.5 mm, while pro-juveniles body length averages 4.4 mm.

No precise data are available on the embryonic and postembryonic development of *Orthochirus* species. However, using indirect methods and the morphometric values of juveniles collected in nature, the number of molts necessary to reach adulthood can be estimated to be 4.

***Ananteris coineaui* Lourenço**

Although many different species of the genus *Ananteris* Thorell have been described in recent years, almost nothing is known about the life cycles of members of this genus. Observations carried out for a single species, *Ananteris coineaui*, show that the average number in a brood is 15 (Lourenço & Cuellar, 1999). In contrast to the pro-juveniles of other small species, those of *Ananteris coineaui* are rather small in size. Female body length in this species averages 11.8 mm, while pro-juvenile body length averages 3.1 mm.

No precise data are available on the embryonic and postembryonic developments of *A. coineaui*. However, using indirect methods and the morphometric values of juveniles collected in nature, the number of molts necessary to reach adulthood can be estimated to be 5, as in many other buthid species.

***Microcharmus variegatus* Lourenço, Goodman & Fisher**

Microcharmids represent a depauperate group of humicolous scorpions, endemic to Madagascar (Lourenço et al., 2006). Up to now, almost nothing was known about their life cycles. Preliminary observations carried out on *Microcharmus variegatus* showed that broods are composed of

Fig. 1. *Microtityus rickyi*, female with pro-juveniles (photo D. Huber). **Fig. 2.** *Tityus* (*Caribetityus*) *elii*, female with pro-juvenils (photo D. Huber). **Fig. 3.** *Orthochirus negebensis*, female with pro-juveniles (photo E. Ythier). **Fig. 4.** *Compsobuthus werneri schmiedeknechti*, female with first instar juveniles (photo A. Tietz).

very small numbers, 2-3 pro-juveniles. In contrast, the size of pro-juveniles at birth is large. Female body length averages 7 mm, while pro-juvenile body length averages 3 mm.

No precise data are available on the embryonic and postembryonic developments of the *M. variegatus*. However, using indirect methods and the morphometric values of juveniles collected in nature, the number of molts necessary to reach adulthood can be estimated to be 4.

Conclusions

The observations carried out for several micro-buthoid species allow the following conclusions:

1. The reduction of litter size in these species is independent of ecological factors, since some of the species are humicolous or live in rain forests while others inhabit arid environments and even deserts.

2. In all cases, as already proposed by Francke (1981), litter size is directly proportional to the size of the female and inversely proportional to the size of the young.

3. It can be suggested that the large body size of pro-juveniles at birth could be associated with a more 'complete' embryonic development. This factor 'may' permit a strategy of post-embryonic development with a smaller number of instars.

4. Morphometric growth values observed in micro-buthoids species are higher than those observed for other buthoids.

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Table I. Litter size in buthoid scorpions

[Data (sometimes modified) from Polis & Sissom (1990), Lourenço (1991, 2002a) and E. Ythier & W.R. Lourenço (unpublished)]

Species	Distribution	Litter Size
Ananteris coineaui Lourenço	South America	15
Androctonus amoreuxi (Audouin)	North Africa	23–27
Androctonus australis (Linnaeus)	North Africa	30–40
Androctonus bicolor Ehrenberg	Africa/Middle East	30–40
Androctonus mauritanicus (Pocock)	North Africa	38–75
Babycurus jacksoni (Pocock)	Africa	14–35
Butheoloides maroccanus Hirst	North Africa	8–10
Buthus occitanus (Amoreux)	Europe	20–50
Buthus malhommei Vachon	North Africa	35
Centruroides arctimanus Armas	Caribbean	14
Centruroides barbudensis (Pocock)	Caribbean	22–25
Centruroides exilicauda (Wood)	North America	20(7–42)
Centruroides gracilis (Latreille)	Americas	47(26–91)
Centruroides insulanus (Thorell)	Caribbean	50(6–105)
Centruroides margaritatus (Gervais)	Americas	39(26–70)
Centruroides pococki Sissom & Francke	Caribbean	27
Centruroides vittatus (Say)	North America	31(13–47)
Compsobuthus werneri schmiedeknechti Vachon	Middle East	5–14

Species	Distribution	Litter Size
Grosphus flavopiceus Kraepelin	Madagascar	30–40
Grosphus ankarafantsika Lourenço	Madagascar	30–50
Grosphus ankarana Lourenço & Goodman	Madagascar	20–30
Grosphus goudoti Lourenço & Goodman	Madagascar	24
Grosphus hirtus Kraepelin	Madagascar	25–40
Hottentotta caboverdensis Lourenço & Ythier	Cabo Verde	23–52
Hottentotta hottentotta (Fabricius)	Africa	12–21
Hottentotta judaicus (Simon)	Middle East	15–18
Hottentotta trilineatus (Peters)	Africa	12
Isometrus besucheti Vachon	Sri Lanka	10–17
Isometrus maculatus (DeGeer)	Ubiquitous	12–21
Leiurus quinquestriatus (Ehrenberg)	North Africa/Middle East	12–43
Liobuthus kessleri Birula	Middle East	20–25
Lychas mucronatus (Fabricius)	Asia	14–16
Mesobuthus caucasicus (Nordmann)	Asia	12–14
Mesobuthus eupeus (Koch)	Asia	23
Mesobuthus gibbosus (Brullé)	Europe/Middle East	12–40
Mesobuthus tamulus gangeticus (Pocock)	India	25–31
Microbuthus fagei Vachon	North Africa	3–4
Microtityus consuelo Armas & Marcano Fondeur	Caribbean	4–6
Microtityus fundorai Armas	Caribbean	7
Microtityus joseantonioi González-Sponga	Venezuela	6–7
Microtityus rickyi Kjellesvig-Waering	Trinidad	3–6
Odonturus dentatus Karsch	Africa	16–19
Orthochirus innesi Simon	North Africa	6–8
Orthochirus negebensis Shulov & Amitai	Middle East	5–9
Orthochirus scrobiculosus (Grube)	Middle East	5–12
Orthochirus sp.	North Africa	5–7
Parabuthus mossambicensis (Peters)	Africa	68
Parabuthus transvaalicus Purcell	Africa	40–95
Rhopalurus crassicauda Caporiaccoa	Guyana/Brazil	13–15
Rhopalurus garridoi Armas	Caribbean	19(14–27)
Rhopalurus princeps (Karsch)	Caribbean	15–30
Rhopalurus rochai Borelli	Brazil	28–49
Tityus (*Tityus*) *bahiensis* (Perty)	South America	15–25
Tityus (*Archaeotityus*) *bastosi* Lourenço	South America	10–12
Tityus (*Atreus*) *cambridgei* Pocock	South America	15–25
Tityus (*Archaeotityus*) *columbianus* (Thorell)	Colombia	13
Tityus (*Atreus*) *falconensis* González-Sponga	Venezuela	11–24
Tityus (*Tityus*) *fasciolatus* Pessôa	Brazil	15(1–26)
Tityus (*Atreus*) *fuehrmanni* Kraepelin	Colombia	13–16
Tityus (*Caribetityus*) *elii* (Armas & Marcano Fondeur)	Caribbean	10–12)
Tityus (*Atreus*) *insignis* (Pocock)	Caribbean	17–20
Tityus (*Brazilotityus*) *lokiae* Lourenço, Adis & Araújo	Brazil	10
Tityus (*Archaeotityus*) *mattogrossensis* Borelli	South America	12
Tityus (*Tityus*) *melanostictus* Pocock	South America	13–16
Tityus (*Atreus*) *metuendus* Pocock	South America	25–35
Tityus (*Archaeotityus*) *pusillus* Pocock	Brazil	10
Tityus (*Tityus*) *serrulatus* Lutz & Mello	South America	20–25
Tityus (*Tityus*) *strandi* Werner	Brazil	12
Tityus (*Atreus*) *trinitatis* Pocock	Trinidad	28
Tityus (*Atreus*) *ythieri* Lourenço	Peru	13–25
Uroplectes insignis Pocock	Africa	12–14
Uroplectes lineatus (Koch)	Africa	8–12
Uroplectes planimanus (Karsch)	Africa	26
Zabius fuscus (Thorell)	Argentina	12–35
Microcharmus variegatus Lourenço, Goodman & Fisher	Madagascar	2–3