Invertebrate Zoology, 2023, 20(1): 90–96

Reproductive investment in the Brazilian scorpion *Tityus pusillus* Pocock, 1893 (Scorpiones: Buthidae): Do larger females produce better offspring?

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ABSTRACT. Large females are usually associated with substantial provisioning of offspring. However, the finitude of resources generally results in a trade-off between investment in offspring size and number in many taxa. Such incidences are poorly investigated in iteroparous species, which produce multiple broods throughout their lifespan. Thus, we produced a model to predict how maternal traits (female size and mass) are associated with offspring traits (number and mass) in an iteroparous scorpion. To this end, we used a sample of 166 juveniles from 20 *Tityus pusillus* Pocock, 1893 females collected from a fragment in the Brazilian Atlantic rainforest. Our results showed that maternal traits (e.g. size and mass) were not correlated with provisioning, and no statistical correlation was found between total offspring mass and offspring size. Similar to congeneric species, *T. pusillus* appears to invest in more rather than heavier newborns. In addition to the deferred fertilization exhibited by this species, such reproductive traits have the potential to ensure reproductive success and high population abundance.
How to cite this paper: Dionisio-da-Silva W., Albuquerque C.M.R., de, Lira A.F. de A. 2023. Reproductive investment in the Brazilian scorpion *Tityus pusillus* Pocock, 1893 (Scorpiones: Buthidae): Do larger females produce better offspring? // Invert. Zool. Vol.20. No.1. P.90–96. doi: 10.15298/invertzool.20.1.04

KEY WORDS: body size; litter size; offspring fitness; resource allocation; size-number tradeoff.

Репродуктивный вклад у бразильского скорпиона *Tityus pusillus* Pocock, 1893 (Scorpiones: Buthidae): Производят ли более крупные самки лучшее потомство?

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РЕЗЮМЕ. Крупных самок обычно ассоциируют с существенным обеспечением потомства. Тем не менее, ограниченность ресурсов в общем случае приводит во многих таксонах к компромиссу между вкладом в размер потомства и его количеством. Эти аспекты слабо исследованы у итеропарных (повторнородящих) видов, которые многократно приносят потомство в течение своего жизненного цикла. Предложена модель, предсказывающая соотношение материнских свойств (размер и масса самки) и свойств потомства (число и масса) у повторнородящего скорпиона. Изучены 166 ювенилей из 20 самок *Tityus pusillus* Pocock, 1893, собранных в дождевом тропическом лесу приатлантической Бразилии. Наши результаты показали, что материнские свойства (т.е. размер и масса) не коррелируют со свойствами потомства, также не обнаружена корреляция между массой и размером потомства. Оказалось, что, подобно другим видам рода, *T. pusillus* вкладывает в большее количество новорожденных, чем в более тяжелое потомство. В дополнение к отмеченному у этого вида отложенному оплодотворению, такие особенности размножения обеспечивают репродуктивный успех и высокую численность популяции.
Как цитировать эту статью: Dionisio-da-Silva W., Albuquerque C.M.R., de, Lira A.F. de A. 2023. Reproductive investment in the Brazilian scorpion *Tityus pusillus* Pocock, 1893 (Scorpiones: Buthidae): Do larger females produce better offspring? // Invert. Zool. Vol.20. No.1. P.90–96. doi: 10.15298/invertzool.20.1.04

КЛЮЧЕВЫЕ СЛОВА: размер тела; размер выплода; пригодность потомства; распределение ресурсов; компромисс между размером и количеством.

Introduction

Maternal investment in offspring fitness is one of the most important issues in reproductive and evolutionary biology (reviewed in Bernardo, 1996; Fox, Czesak, 2000). Body size, age, and environmental conditions are some of the main features recognized to affect offspring number, litter mass, survival, and developmental time (e.g. Metcalfe, Monaghan, 2001; Skow, Jakob, 2003; Iida *et al*., 2016; Ma *et al.*, 2018; Herlin *et al*., 2019). However, the role of female size in offspring production remains inconclusive because of the different results obtained in many studies (Oberhauser, 1997; Kishi, 2014; Rollinson, Rowe, 2016). For many species, such as the butterfly *Danaus plexippus* (L. 1758), egg weight is positively correlated with maternal size (Oberhauser, 1997). However, female size in the dung beetle *Onthophagus atripennis* Waterhouse, 1875 is not correlated with egg size, although it can provide larger brood balls than small females, which supplies more food for their larvae (Kishi, 2014).

Maternal size is often a proxy of nutritional conditions and female potential of reproductive investment, with large females that are generally healthier and better nourished giving birth to better offspring (Fox, Czesak 2000; Rollinson, Rowe, 2016). However, several studies have indicated a trade-off between offspring quality and quantity (e.g. Lim *et al*., 2014; Stahlschmidt, Adamo, 2015). Maternal investment in offspring number can have the opposite effect on offspring size, wherein the female produces a greater number of lighter individuals (Skow, Jakob, 2003; Lim *et al*., 2014). A possible explanation for the number-size trade-off stems from the finitude of resource allocation, which prevents pregnant females to increase number without decrease size of offspring and vice versa, as long as nutrient resources are limited (Stearns, 1992; Fox, Czesak, 2000; Lim *et al*., 2014). In a meta-analytical study involving vertebrate and invertebrate taxa, Lim et al. (2014) investigated the relationship between female size, offspring body size, and offspring number in 231 animal species. These authors found that intraspecifi-

cally, female size could be positively correlated with both litter traits, although offspring body size and number were negatively correlated when analyzed using a multi-taxa approach.

These trade-offs are less apparent in offspring from females that use adult-acquired resources, females that have parental care and iteroparous females (i.e., females that allocate resources through several broods) because such reproductive strategies make it difficult to quantify variations provided by reproductive investment (Fox, Czesak, 2000). This reproductive strategy is commonly found in scorpion species (Warburg, 2011; Stockmann, Flay, 2010; Albuquerque, Lira, 2016). In addition, different species from this taxon have shown great variation in adult size and offspring traits (offspring number and mass) (Brown, Formanowicz, 1995; Myers, 2001). Such a reproductive mechanism is profitable for animals with reproductive success that is usually associated with availability of resources and climatic conditions (Polis, Sissom, 1990; Dionisio-da-Silva *et al.*, 2018). Some species are also capable of storing sperm and producing multiple broods from a single insemination (e.g. Outeda-Jorge *et al*., 2009; Rodríguez-Cabrera *et al*., 2015; Albuquerque, Lira, 2016), which is advantageous for reproduction when environmental conditions are more suitable.

To further understand the female reproductive investment in scorpions, using *Tityus pusillus* Pocock, 1893 as a study organism, this research investigated the relationships between female body size and offspring number and size, as well as the number-size trade-off. Because of their high abundance, stable taxonomy, easy rearing in the laboratory, and some previous knowledges regarding reproduction and development (Albuquerque, Lira, 2016; Dionisio-da-Silva *et al*., 2018), *T. pusillus* seems a good species for investigating reproductive investment in iteroparous species. For instance, *T. pusillus* can store sperm, producing up to three litters from a single insemination with four to 12 offspring per litter (Albuquerque, Lira, 2016). According to Brown (2001, 2004) number-size trade-offs are not an observed pattern and more empirical studies are needed to determine how common they could be in scorpions. Therefore, we hypothesize that larger females produce more offspring rather than larger offspring, like the congeneric species *T. stigmurus* (Thorell, 1876) and *T. colombianus* (Thorell, 1876) (Lourenço *et al*., 1996; Aguiar *et al*., 2008). Finally, we expected a trade-off between offspring size and number, resulting in numerous small offspring.

Material and methods

Data collection

Twenty pregnant *T. pusillus* females were collected from a fragment of Atlantic rainforest belonging to the Trapiche mill in the municipality of Sirinhaém, Pernambuco State, northeastern Brazil (08°35′27″S, 35°06′58″W) in October 2012. These individuals giving birth in 1-2 weeks in laboratory, because *T. pusillus* females were field-caught, we were unable to precisely determine their age or reproductive history. In the laboratory, the animals were identified following Lourenço (2002) and individually separated in plastic containers (9.5 cm in diameter and 7.5 cm in depth) with a water supply for hydration. The scorpions were fed with a cockroach nymph of *Nauphoeta cinerea* (Olivier, 1789) every week and reared at 28 ± 3 °C under a 12:12 h light/dark photoperiod. As in previous studies of scorpion ontogeny, only the carapace length of females was measured by Lira AFA using a digital caliper under a stereomicroscope as a proxy for female size (FS) (e.g. Lourenço, 1979; Benton, 1991; DeSouza *et al*., 2016; Albuquerque, Lira, 2016; Seiter, Stockmann, 2017). Following the procedures of Brown (2003) and Aguiar *et al*. (2008), the body mass of females was measured every week until parturition and after birth and dispersal of neonates to estimate female mass (FM). After parturition, the offspring number (ON) was also recorded by counting all individuals on the dorsum of females, and after dispersal, all living and dead neonates were counted, except for those cannibalized. Total offspring mass (TOM) was measured as the mass of all individuals in a brood and as a proxy of neonate size. Therefore, TOM was measured by the difference between mass of female scorpions in the last week before parturition by mass of female scorpions after neonates' dispersal. All masses were measured to four decimal places using a precision analytical balance.

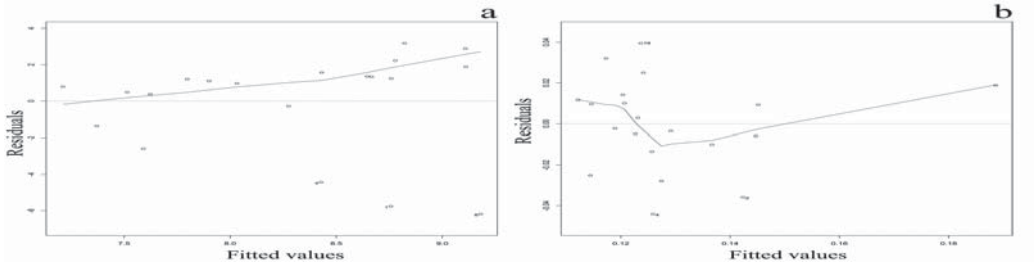

Fig. 1. Residuals vs Fitted values from Generalized Linear Models of: A — offspring number and B — total offspring mass in function of female traits of *Tityus pusillus* Pocock, 1893.
Рис. 1. Остаточные/подобранные значения генерализованных линейных моделей: A — количества потомства и B — общей массы потомства как функции свойств самок *Tityus pusillus* Pocock, 1893.

Statistical analyses

Initially the data normality was verified using the Shapiro-Wilk test. We performed generalized linear models (GLMs) for normal distribution with a post-hoc Bonferroni correction to evaluate the influence of maternal body size and mass on ON and mass (Neter *et al*., 1983; Benjamin, Hochberg, 1995; Walker *et al*., 2003). In model 1, we used ON as the dependent variable, and model 2 used TOM as the dependent variable. We used FS and FM as independent variables in both models. Next, the residual values of ON and TOM generated by the models were used to evaluate the correlation between these offspring traits through Spearman's correlation between these variables (Brown, 2003; Walker *et al*., 2003). TOM rather than mean offspring mass was used because this latter is a ratio between TOM and ON, what would cause a correlation resulted by statistical artifact. All analyses were conducted using the stats and Hmisc package in R Studio v. 1.1.463 (Harrel, 2019; RStudio Team, 2019).

Results and Discussion

In this study, we investigated the reproductive investment of the scorpion *T. pusillus* through the relationship between female body conditions and offspring traits. Furthermore, we evaluated whether there was a trade-off between ON and mass. A total of 166 juveniles were used, between 3–12 individuals per litter (mean 8.3 ± 0.62) and the female traits (size and mass) were 3.91 ± 0.06 mm and 183.27 ± 7.58 mg, respectively (n = 20). Our results showed that maternal body conditions (FM and FS) were not correlated with offspring quantity (GLM for TOM: $r_s = –0.1273$, adjusted-$P = 1$; Fig. 1A) or quality (GLM for ON: $r_s = 0.2593$, adjusted-$P = 0.1018$; Fig. 1B). Statistical summaries of the models are plotted in Figure 2. Similarly, previous studies have also found no correlation between maternal condition and offspring fitness in different taxa, such as ephemeropterans, isopterans, and also scorpions (e.g. Corkum *et al*., 1997; Dangerfield, 1997; Aguiar *et al*., 2008). In addition, Silva-Júnior et al. (2022) found that nutritional stress causes changes in the progeny of inadequately fed *T. pusillus* females. According to these authors, less-fed females produce a litter with more juveniles than well-fed females. Therefore, the lack of relationship found in our study between maternal body condition and offspring traits may be related to mother physiological condition. For some scorpion species, the physiological condition of the female is a more relevant factor in determining litter traits than body size (Warburg, 2001).

Our results also indicated that *T. pusillus* females may balance the investment in each offspring to optimize offspring fitness through the absence of correlation between ON and TOM. A weakly correlation was found between the ON and TOM residuals (Spearman's correlation: $r_s = 0.409$, $P = 0.07453$; Fig. 3). However, such result can be a false positive because it does not attend at significant level of 0.05 and it was interpreted with caution herein. Such result could be associated with two non-exclusive explanations. First, female investment in ON is profitable when offspring survival is low (Forbes, 1991). Second, breeding multiple times is a better strategy to increase the population rather than breed only once, as do semelparous organ-

Dependent variable	Predictor variable	Std. Error	t	*P*
Offspring number	Female size	13.8687	-0.072	0.944
	Female mass	299.3621	-0.088	0.931
	Female size + mass	76.7528	0.136	0.894
Total offspring mass	Female size	1.768	1.814	0.0962
	Female mass	1.273	-2.45	0.2211
	Female size + mass	-1.456	-1.456	0.1646

Fig. 2. Relationship between *Tityus pusillus* Pocock, 1893 female body traits (mass and size) and offspring traits.
Рис. 2. Взаимоотношение между свойствами тела самки *Tityus pusillus* Pocock, 1893 (масса и размер) и свойствами потомства.

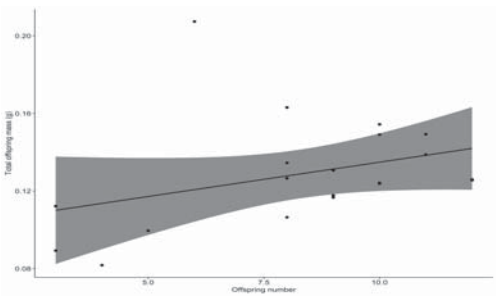

Fig. 3. Spearman's correlation among offspring traits of *Tityus pusillus* Pocock, 1893.
Рис. 3. Корреляция по Спирмену между свойствами потомства *Tityus pusillus* Pocock, 1893.

isms (Morris 2009). Such profitability may occur because juvenile survival is generally low because they are potential prey for adult conspecifics and larger species (Fonseca *et al.*, 2018; Marques *et al.*, 2018). This is also realistic for scorpions with age-size-structured populations, where cannibalism and interspecific predation are common (Polis, McCormick, 1987). Thus, a large investment in ON throughout multiple broods by one or more intercourse appears to be a successful tactic for the high abundance of *T. pusillus* populations found in their natural habitats (e.g. Dionisio-da-Silva *et al*., 2018; Lira *et al.*, 2019).

Finally, we cannot disregard other mechanisms that may influence *T. pusillus* maternal conditions. Among them, maternal age generally has a negative effect on offspring provisioning (reviewed in Bernardo, 1996; Fox, Czesak, 2000). In most arthropods, ON decreases with maternal age, as seen in lepidopterans and coleopterans (reviewed in Fox, Czesak, 2000). However, some organisms have evolved an offsetting mechanism, such as the spined soldier bug *Podisus maculiventris* (Say, 1832), whose older females produce larger eggs with shorter development time than eggs of younger females (Mohaghegh, *et al*., 1998). In the current study, pregnant females were collected from the natural environment; therefore, their age was unknown. However, the influence of maternal age on offspring provisioning has revealed controversial results in scorpions with reduced ONs in subsequent litters of many buthid species: *T. serrulatus*, *T. bahiensis*, *T. kuryi* (Lourenço, 1997), *T. obscurus* (Gervais, 1843), and *T. stigmurus*. However, no difference or the opposite trend has been observed in other buthids, such as *Troglorhopalurus lacrau* (Lourenço et Pinto-da-Rocha, 1997), *T. costatus* (Karsch, 1879), and *T. silvestris* (Outeda-Jorge *et al.*, 2009). Therefore, it is difficult to attribute our results to this factor because there is no general trend for the influence of maternal age on the offspring size of scorpions.

In conclusion, our results indicated no relationship between maternal body conditions and offspring provisioning (number or mass) or between offspring number and mass. However, the absence of a relationship between TOM and offspring number (or a marginal effect) suggests that *T. pusillus* females may balance the

investment between more and heavier newborns. Such a balance may also result from the combination of seasonal reproduction and food availability during this period. Such a mechanism combined with the production of multiple broods and sperm storage (Albuquerque, Lira 2016) may be an important factor in the abundance and distribution of these scorpions in the northeastern Brazilian Atlantic rainforest, as recorded by Lira *et al*. (2014, 2019). Further advances in studies of maternal investment in iteroparous species could enhance current information and methods of investigation to produce a general theory regarding the life history traits of these organisms.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

Acknowledgements

We are grateful to Fundação de Apoio à Pesquisa do Estado da Paraíba (FAPESQ) for granting a doctoral scholarship to W. Dionisio-da-Silva (519/18). We are grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and FAPESQ for post-doctoral scholarship to AFAL (PDCTR – 300104/2022-7).

Reference list

Albuquerque C.M.R., Lira A.F.A. 2016. Insights into reproductive strategies of *Tityus (Archaeotityus) pusillus* Pocock, 1893 (Scorpiones, Buthidae) // C. R. Biol. Vol. 339. No.5-6. P.179–184. https://doi.org/10.1016/j.crvi.2016.03.003

Aguiar A.P.N., Santana-Neto P.L., Souza J.R.B., Albuquerque C.M.R. 2008 Relationship between litter characteristics and female size in *Tityus stigmurus* (Scorpiones, Buthidae) // J. Arachnol. Vol.36. No.2. P.464–468. https://doi.org/10.1636/CSH07-130.1

Benton T.G. 1991. The life history of *Euscorpius flavicaudis* (Scorpiones, Chactidae) // J. Arachnol. Vol.19. No.2. P.105–110.

Bernardo J. 1996. Maternal effects in animal ecology // Am. Zool. Vol.36. No.2. P.83–105. https://doi.org/10.1093/icb/36.2.83

Brown C.A. 2001. Allometry of offspring size and number in scorpions // V. Fet, P.A. Selden (eds.). Scorpions 2001 in memorian Gary A. Polis. Burnham Beeches (UK): British Arachnological Society. P.307–315.

Brown C.A. 2003. Offspring size-number trade-offs in scorpions: an empirical test of the van Noordwijk and de Jong model // Evolution. Vol.57. No.9. P.2184–2190. https://doi.org/10.1111/j.0014-3820.2003.tb00397.x

Brown C.A. 2004. Life histories of four species of scorpion in three families (Buthidae, Diplocentridae, Vaejovidae) from Arizona and New Mexico // J. Arachnol. Vol.32. No.2. P.193–208. https://doi.org/10.1636/M02-56

Brown C.A., Formanowicz D.R. 1995. Variation in reproductive investment among and within populations of the scorpion *Centruroides vittatus* // Oecologia. Vol.103. No.2. P.140–147. https://doi.org/10.1007/BF00329073

Corkum L.D., Ciborowski J.J., Poulin R.G. 1997. Effects of emergence date and maternal size on egg development and sizes of eggs and first-instar nymphs of a semelparous aquatic insect // Oecologia. Vol.111. No.1. P.69–75. https://doi.org/10.1007/s004420050209

Dangerfield J.M. 1997. Growth and survivorship in juvenile woodlice: is birth mass important? // Ecography. Vol.20. No.2. P.132–136. https://doi.org/10.1111/j.1600-0587.1997.tb00355.x

DeSouza A.M., Neto P.D.L.S., Lira A.F.A., Albuquerque C.M.R. 2016. Growth and developmental time in the parthenogenetic scorpion *Tityus stigmurus* (Thorell, 1876)(Scorpiones: Buthidae) // Acta. Sci. Biol. Sci. Vol.38. No.1. P.85–90. https://doi.org/10.4025/actascibiolsci.v38i1.28235

Dionisio-da-Silva W., Lira A.F.A., Albuquerque C.M.R. 2018. Distinct edge effects and reproductive periods of sympatric litter-dwelling scorpions (Arachnida: Scorpiones) in a Brazilian Atlantic forest // Zoology. Vol.129. P.17–24. https://doi.org/10.1016/j.zool.2018.06.001

Fonseca M.M., Pallini A., Lima E., Janssen A. 2018. Ontogenetic stage-specific reciprocal intraguild predation // Oecologia. Vol.188. No.3. P.743–751. https://doi.org/10.1007/s00442-018-4256-6

Forbes L.S. 1991. Optimal size and number of offspring in a variable environment // J. Theor. Biol. Vol.150. No.3. P.299–304. https://doi.org/10.1016/S0022-5193(05)80429-1

Fox C.W., Czesak M.E. 2000. Evolutionary ecology of progeny size in arthropods // Annu. Rev. Entomol. Vol.45. No.1. P.341–369. https://doi.org/10.1146/annurev.ento.45.1.341

Harrell F.E., Jr. 2019. Hmisc: Harrell Miscellaneous. R package version 464 4.2-0. https://CRAN.R-project.org/package= Hmisc. Accessed 05 Sep 2019

Herlin W., Yoshimura H., Yamada Y.Y. 2019. Large mothers produce progeny with high survival rates during the immature stage and large sizes at adulthood in a parasitoid species // Sci. Nat. Vol.106. No.9. P.1–6. https://doi.org/10.1007/s00114-019-1648-3

Iida H., Kohno K., Takeda M. 2016. Seasonal fluctuations in offspring body size in the wolf spider, *Pardosa astrigera* (Araneae: Lycosidae) // Appl. Entomol. Zool. Vol.51. No.1. P.125–131. https://doi.org/10.1007/s13355-015-0381-4

Kishi S. 2014. Brood ball size but not egg size correlates with maternal size in a dung beetle, *Onthophagus atripennis* // Ecol. Entomol. Vol.39. No.3. P.355–360. https://doi.org/10.1111/een.12102

Lim J.N., Senior A.M., Nakagawa S. 2014. Heterogeneity in individual quality and reproductive trade-offs within species // Evolution. Vol. 68. No.8. P.2306–2318. https://doi.org/10.1111/evo.12446

Lira A.F.A., Rego F.N.A.A., Albuquerque C.M.R. 2014.

How important are environmental factors for the population structure of co-occurring scorpion species in a tropical forest? // Can. J. Zool. Vol.93. No.1. P.15–19. https://doi.org/10.1139/cjz-2014-0238

Lira A.F.A., Salomão R.P., Albuquerque C.M.R. 2019. Pattern of scorpion diversity across a bioclimatic dry-wet gradient in Neotropical forests // Acta. Oecol. Vol. 96. P.10–17. https://doi.org/10.1016/j.actao.2019.02.004

Lourenço W.R. 1979. Le scorpion Buthidae*: Tityus mattogrossensis* Borelli, 1901 (Morphologie, ecologie, biologie et développement postembryonnaire) // Bull. Mus. Natl. Hist. Nat. Vol.1979. No.1. P.95–117.

Lourenço W.R., Cuéllar O., Méndez de la Cruz F.R. 1996. Variation of reproductive effort between parthenogenetic and sexual populations of the scorpion *Tityus columbianus* // J. Biogeogr. Vol.23. No.5. P.681–686. https://doi.org/10.1111/j.1365-2699.1996.tb00028.x

Ma L., Lin Z.H., Gao J.F., Li H., Ji X., Lu H.L. 2018. Maternal thermal effects on female reproduction and hatchling phenotype in the Chinese skink (*Plestiodon chinensis*) // Asian. Herpetol. Res. Vol.9. P.250–257.

Marques R.V., Sarmento R.A., Oliveira A.G., Rodrigues D.D.M., Venzon M., Pedro-Neto M., Pallini A., Janssen A. 2018. Reciprocal intraguild predation and predator coexistence // Ecol. Evol. Vol.8. No.14. P.6952–6964. https://doi.org/10.1002/ece3.4211

Metcalfe N.B., Monaghan P. 2001. Compensation for a bad start: grow now, pay later? // Trends. Ecol. Evol. Vol.16. No.5. P.254–260. https://doi.org/10.1016/S0169-5347(01)02124-3

Mohaghegh J., DeClercq P., Tirry L. 1998. Effects of maternal age and egg weight on developmental time and body weight of offspring of *Podisus maculiventris* (Heteroptera: Pentatomidae) // Ann. Entomol. Soc. Am. Vol.91. No.3. P.315–322. https://doi.org/10.1093/aesa/91.3.315

Morris. 2009. Life history // S.A. Levin, S.R. Carpenter, H.C.J. Godfray, A.P. Kinzig, M. Loreau, J.B. Losos, B. Walker, D.S. Wilcove (eds.). The Princeton Guide to Ecology. Princeton University Press. P.72–78.

Myers C. 2001. Evolution of geographic variation in body size and life-history traits // P. Brownell, G. Polis (eds.). Scorpion biology and research. Oxford (UK): Oxford University Press. P.317–333.

Neter J., Wasserman W., Kutner M.H. 1983. Applied Linear Regression Models // J. Neter (ed.). Applied statistical models. University of Michigan (USA): Richard D. Irwin, Inc.

Oberhauser K.S. 1997. Fecundity, lifespan and egg mass in butterflies: effects of male-derived nutrients and female size // Funct. Ecol. Vol.11. No.2. P.166–175. https://doi.org/10.1046/j.1365-2435.1997.00074.x

Outeda-Jorge S., Pinto-da-Rocha R., Mello T. 2009. Litter size, effects of maternal body size, and date of birth in South American scorpions (Arachnida: Scorpiones) // Zoologia. Vol.26. No.1. P.43–53. https://doi.org/10.1590/S1984-46702009000100008

Polis G.A., McCormick S.J. 1987. Intraguild predation and competition among desert scorpions // Ecology. Vol.68. No.2. P.332–343. https://doi.org/10.2307/1939264

Polis G.A., Sissom W.D. 1990. Life history // G.A. Polis (ed.). The Biology of Scorpions. California (USA): Stanford University Press. P.161–223.

Rodríguez-Cabrera T.M., Teruel R., Rodríguez L.V. 2015. Iteroparity following single insemination and largest size litter in "*Rhopalurus junceus*" (Herbst, 1800) // Rev. Iber. Aracnol. Vol.26. P.75–77.

Rollinson N., Rowe L. 2016. The positive correlation between maternal size and offspring size: fitting pieces of a life-history puzzle // Biol Rev. Vol.91. No.4. P.1134–1148. https://doi.org/10.1111/brv.12214

RStudio Team. 2019. RStudio: integrated development for R. RStudio. Inc. Boston. http:www.rstudio.com/. Accessed 05 Sep 2019

Seiter M., Stockmann, M. 2017. The life history of the parthenogenetic scorpion *Lychas tricarinatus* (Simon, 1884) from Odisha province, India and supplementary notes on *Tityus trivittatus* Kraepelin, 1898 (Scorpiones, Buthidae) // Zool. Anz. Vol.270. P.155–165. https://doi.org/10.1016/j.jcz.2017.10.003

Silva-Júnior A.O., Seiter M., Lira A.F.A., Pontes W.J.T. 2022. Effects of nutritional stress on reproductive output in the scorpion *Tityus pusillus* Pocock, 1893 (Scorpiones, Buthidae) // Invert. Reprod. Dev. Vol. 2022. P.1–6. https://doi.org/10.1080/07924259.2022.2082330

Skow C.D., Jakob E.M. 2003. Effects of maternal body size on clutch size and egg weight in a pholcid spider (*Holocnemus pluchei*) // J. Arachnol. Vol.31. No.2. P.305–309. https://doi.org/10.1636/01-85

Stahlschmidt Z.R., Adamo S.A. 2015. Food-limited mothers favour offspring quality over offspring number: a principal components approach // Funct. Ecol. Vol.29. No.1. P.88–95.

Stearns S.C. 1992. The evolution of life histories. Oxford (UK): Oxford University Press. 264 p.

Stockmann R., Flay N. 2010. Scorpions of the World. French: NAP Editions. 573 p.

Walker S.E., Rypstra A.L., Marshall S.D. 2003. The relationship between offspring size and performance in the wolf spider *Hogna helluo* (Araneae: Lycosidae) // Evol. Ecol. Res. Vol.5. No.1. P.19–28.

Warburg M.R. 2001. Scorpion reproductive strategies, potential and longevity: an ecomorphologist's interpretation // V. Fet., P.A. Selden (eds.). Scorpions 2001 in Memoriam Gary A. Polis. Burnham Beeches (UK): British Arachnological Society. P.349–358.

Warburg M.R. 2011. Scorpion reproductive strategies, allocation and potential; a partial review // Eur. J. Entomol. Vol.108. No.2. P.173–181. https://doi.org/10.14411/eje.2011.023

Responsible editor K.G. Mikhailov