ESSAY

REPRODUCTIVE BEHAVIOUR IN THE URUGUAYAN SUBSOCIAL SPIDER *Anelosimus vierae*: A REVIEW

Carolina Rojas Buffet[1,2] & Carmen Viera[1,2*]

[1] Sección Entomología, Facultad de Ciencias, Universidad de la República, Iguá 4225, 11400 Montevideo, Uruguay. [2] Laboratorio de Ecología del Comportamiento, IIBCE, Av. Italia 3318, 11600 Montevideo, Uruguay.
* Corresponding author: Carmen Viera - anelosimus@gmail.com

ABSTRACT

This paper aims to review the studies on the reproductive behaviour of the endemic Uruguayan subsocial spider *Anelosimus vierae*. We framed the reproductive behaviour of this species referring to the most important aspects of his life history. We show the sperm induction behaviour performed necessarily by males to transfer sperm from their genitalia to the copulatory organs in their pedipalps. Subsequently, the behaviours involved in sexual behaviour, courtship, pseudocopulation and mate of males and females are described, as well as the reproductive strategies in relation to the social context. We address aspects of maternal behaviour and cooperative behaviour among siblings as a main goal to evaluate their reproductive success. Finally, we discuss some perspectives and future studies about these behaviours.

Key words: spider, *Anelosimus vierae*, sexual behaviour.

RESUMEN

Comportamiento reproductor de una araña subsocial uruguaya *Anelosimus vierae*: una revisión. El presente trabajo tiene como objetivo recapitular los estudios acerca del comportamiento reproductor de una araña subsocial, endémica de Uruguay *Anelosimus vierae*. Enmarcamos el comportamiento reproductor de la especie mencionando los aspectos más relevantes de su historia de vida. Analizamos el comportamiento de inducción espermática, necesario en los machos para poder transferir el esperma desde su genitalia hasta los órganos copuladores ubicados en los pedipalpos. Posteriormente, describimos las conductas involucradas en el comportamiento sexual, considerando cortejo, pseudocópula y cópula, así como las estrategias reproductivas de machos y hembras según el contexto social en el que se encuentren. Para completar la visión de la reproducción en esta especie, analizamos aspectos sobre el comportamiento maternal y cooperativo entre hermanos que constituyen una parte fundamental al momento de evaluar el éxito reproductor. Finalmente, discutimos algunas perspectivas y estudios a futuro sobre estos comportamientos.

Palabras clave: araña, *Anelosimus vierae*, comportamiento sexual.

INTRODUCTION

Social behaviour and its evolution have been studied with great emphasis by many entomologists, mainly from the 1970s (Wilson, 1971). This is because insects are an excellent model given that some species have complex societies with castes and division of labour. Many years later, other arthropods with different types of sociality in relation to insects have also been studied (Kullman, 1972; Uetz & Hieber, 1997; Lubin & Bilde, 2007; Foelix, 2011).

Social behaviour in spiders has attracted attention because the vast majority are solitary, territorial and cannibalistic. Approximately 60 species, of 45.674 described (World Spider Catalog, 2015), live in some kind of sociality (Avilés, 1997, Uetz & Hieber, 1997). Most of the studies on social spiders have focused on cooperative behaviours such as parental care, nest building and prey capture (Brach, 1975; Christenson, 1984; Gundermann, 1997; Ebert, 1998; Jones & Parker, 2002; Ghione *et al.*, 2004).

However, there are few studies on sexual behaviour and reproductive aspects of social spiders (Lubin, 1986; Smith, 1997; Erez *et al.*, 2005; Klein *et al.*, 2005; Pruitt & Riechert, 2009, 2011; Pruitt *et al.*, 2011, Viera, 2011). This may be because at first glance the sexual behaviour of social spiders may be boring when compared to solitary spiders. In solitary species there may be high risk of mortality through their predacious potential mate; males may be killed by the female during courtship, copulation or after copulation (Schneider & Andrade, 2011). So, in this scenario, the courtship of solitary spiders males may be prolonged, involve bridal gifts and males may copulate while females are eating (Schneider & Andrade, 2011). However, in social spiders the male courtship behaviour does not involve inhibition of aggressive females because social spiders have tolerant habits (Kullman, 1972; Buskirk, 1981; Bilde & Lubin, 2011).

Anelosimus (Family: Theridiidae) is one of the genus that include solitary, subsocial and quasisocial species. In subsocial spiders the offspring of a female keep together in a common nest part of their life cycle and at some point they disperse, while in the quasisocial spiders they stay together throughout their life cycle (Avilés, 1997). The general accepted hypothesis is that quasisocial spiders evolutionarily derived from subsocial ones (Avilés, 1997). The genus *Anelosimus* contains species of different degree of sociality, from solitary to social ways of life. Therefore, subsocial *Anelosimus* spiders are an appropriate model for the evolutionary study of sociality.

In Uruguay lives the endemic subsocial spider *Anelosimus vierae* Agnarsson, 2012. Research on this species has included studies of cooperative, maternal and sexual behaviour (Ghione *et al*., 2004; Albo *et al*., 2007; Viera *et al*., 2007a, 2007b; Viera & Albo, 2008; Cayafa *et al*., 2011; Lorieto *et al*., 2010 Gómez *et al*., 2015; Da Rocha Dias & Viera, in prep.). This revision aimed to update the reproductive behaviour and also provide original data of the Uruguayan subsocial spider *A. vierae*. This update will be useful to detect the gaps in our knowledge about the sexual behaviour of this species and will be the starting point to compare it with that of species with different grades of sociality.

Fig. 1. Nest of *Anelosimus vierae*.

Anelosimus vierae LIFE HISTORY

A. vierae is a subsocial spider from Uruguay. Its taxonomic status was problematic until recently; it was called *Anelosimus* cf. *studiosus* because is morphologically similar to *Anelosimus studiosus*, its North American congener (Levi 1956 and 1963). Agnarsson (2012) resolved it status as a new species based on molecular analysis and behavioural data.

A. vierae builds nests in the lower part of the evergreens with dried leaves and silk (Fig. 1). Each nest is composed of a mother and her first and second offspring that live during the summer and part of the autumn (December-May) (Viera *et al.*, 2007a). The mother cares for the young, and juveniles show lack of aggressiveness and cooperate in different activities in the natal nest (Viera *et al.*, 2007b).

Fig. 2. Male (A) and female (B) of *Anelosimus vierae*.

Individuals remain in the communal nest until they reach adulthood at the end of the spring. They have a 2:1 secondary sex ratio (operative) biased towards females (Viera *et al*., 2007a). It takes a variable number of moults to reach adulthood according to the gender, until eight moults in females and six in males (Fig. 2A, B). So, males mature and die earlier than females, while the latter mature asynchronously (Viera *et al.*, 2007a). The reproductive period occurs in the months of October and November (Viera *et al*., 2007a). Egg-sacs and spiderlings are present in summer and females die in late fall (Viera *et al*., 2007a, 2007b).

SPERM INDUCTION

After the maturation of male spiders, they go in search of females to mate, but previously they have to charge their copulatory organs, that are in the pedipalps, with the sperm that is produced in the gonads located in the abdomen. So, they engage in a process called sperm induction. First they build a sperm web, which varies in size and shape depending on the spiders families. Second, they deposit a droplet of semen from their gonopore on the web, and then takes up the semen in their pedipalps (Foelix, 2011).

Under laboratory conditions, we contacted an adult male with an adult female of *A. vierae* (N= 30) and filmed for two hours the occurrence and characteristics of male's sperm induction (Rojas Buffet & Viera, in press.). Results show that just after mating several males performed sperm induction. Within the two hours of experience, there was no re-mating.

The sperm induction of this species consists of several stages that we describe as follows. The males remain suspended with the ventral zone up in the female´s web, build a scaffolding of the sperm web that consists of two nearly parallel threads connected with the female's web. Then, males begin to lay a swath of threads between the parallel threads following several abdomen movements and laying threads in certain points of the parallel threads. The sperm web is a horizontal hourglass shaped web. Once the sperm web is finished, immediately, males move repeatedly the abdomen up and down until a drop of sperm emerge and is deposited on the thin middle portion of the sperm web. Then they place the tip of one pedipalp on the sperm drop with fast vibratory movements and absorb it; and repeat the same process with the other pedipalp. The duration of the entire process of sperm induction (sperm web construction + emergence of sperm drop + filling the pedipalps) takes approximately 5 min (Rojas Buffet & Viera, in press.).

TWO SCENARIOS FOR SEXUAL ENCOUNTERS IN *A. vierae*

Females can show one of two reproductive tactics according to the availability of resources (Ferreira, 2015). They con remain in the maternal nest sharing the web with other sisters (multi-female nest) or disperse as subadults and build individual nests (uni-female nest) (Viera *et al*., 2007a). So, when males disperse from their natal nest they can find multi-female nest with many subadult and adult females or with a uni-subadult-female nest. The scenarios determine the sexual strategies and preferences of males. (Viera & Albo, 2008; Rojas Buffet, 2011). Viera and Albo (2008) made an experimental design simulating a multi-female nest of *A. vierae* that allowed males to choose between females of different age and reproductive status (Fig. 3). These multi-female nests consist of one mature female, one recently moulted female and one subadult (penultimate) female. The authors found that all males courted at least one female, and no courtship was observed towards subadult females. Although recently moulted and mature females were receptive and attractive and males courted both simultaneously, males preferred to copulate with the mature males.

Albo *et al*. (2007) also reproduced the uni-subadult-female nest. In this scenario, the subadult female was exposed to two males. Subadult females were very attractive to males, which located their refuges, courted and fought with other males. Many subadult females actively vibrated and touched males and elicited pseudocopulations. The adoption of adult mating posture and the prolonged pseudocopulation shown by subadult females was described in this work for the first time in spiders.

COURTSHIP, COPULATION AND PSEUDOCOPULATION

Albo *et al*. (2007) and Rojas Buffet & Viera (unpublished data) found that when males arrive to an adult or subadult female web, they perform courtship walking and they move their pedipalps alternately and vibrate their body. When they reach a female they touch legs and abdomen with legs I and pedipalps.

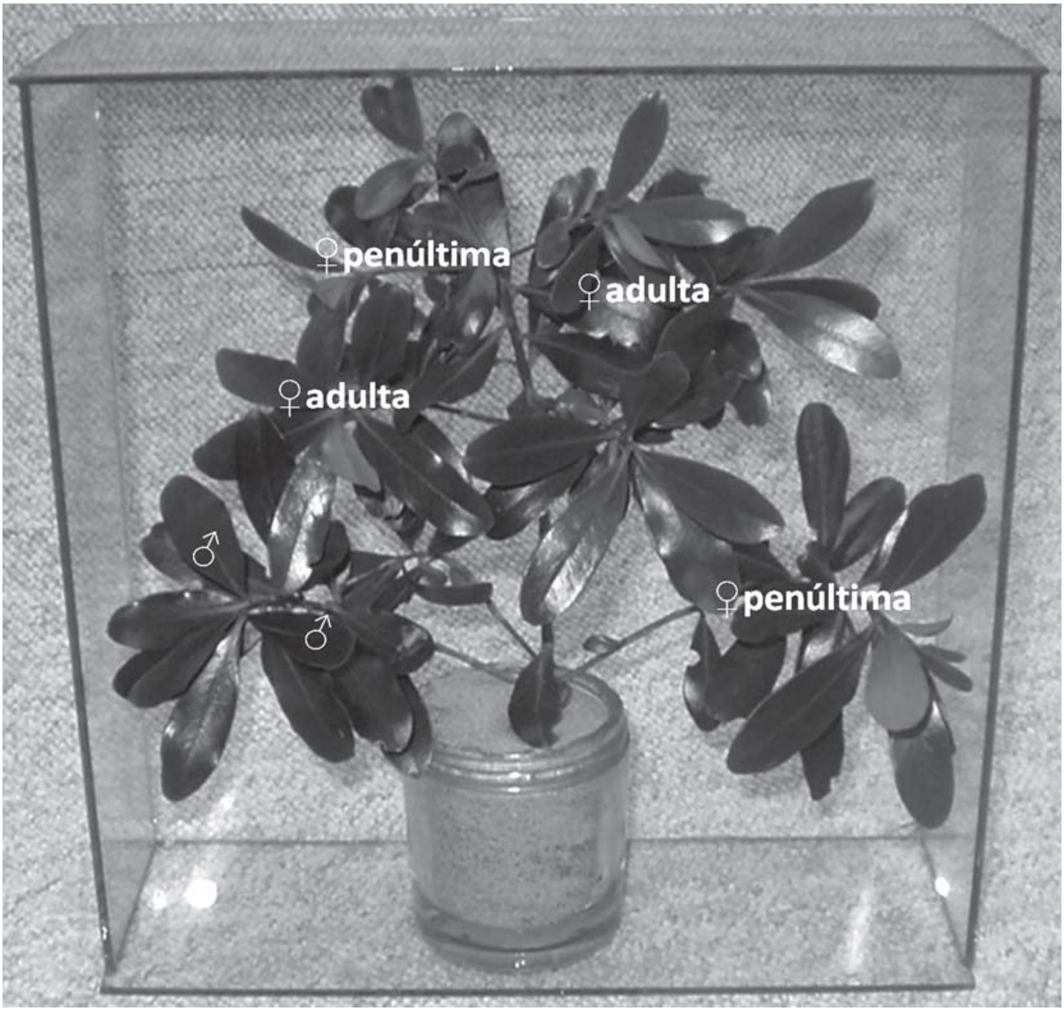

Fig. 3. Flowerpot used as experimental design using two adult males and four females of different reproductive stages.

Receptive adult females respond to male courtship by performing body vibrations and touching males with forelegs. Then the couple adopts the receptive posture, the male suspends horizontally in the female web, with ventral side up, and the prosoma towards the female; and the female faces down and the body axis is approximately inclined 45º. In this position, the male begins to make several attempts to insert their copulatory organs performing drumming behaviour with both pedipalps on the female epigynum, until one achieves the pedipalpal insertion. He makes several ejaculations with that pedipalp and then changes the pedipalp and starts again the same routine with the other pedipalp. The total duration of the copulation is more than one hour. The end of the copulation can be given by both sexes, when the male withdraws the copulatory organ voluntarily or when the female repeatedly twists her body until it is released from the male copulatory organ (Albo *et al*., 2007; Rojas Buffet & Viera, unpublished data).

Male courtship when they are exposed to subadult females is longer than against adult females (Rojas Buffet & Viera, unpublished data). In some cases, subadult females accept male courtship and adopt the typically adult receptive posture. In this position the male pedipalps face the area of the female epigynum. The male makes several attempts to insert the copulatory organs, drumming with his pedipalps alternately (right and left, either) the female epigynum, but cannot insert any of them because of a mechanical impediment given that females do not have fully developed epigynum (Albo *et al.,* 2007; Rojas Buffet, 2011). The drumming of the male pedipalps on the female epigynum is not a continuous behaviour; the male stops this movement and before he continues with a new cycle of drumming, he remains quiescent or moves away. This behaviour powerfully attracted our attention and therefore we are currently assessing the implications for both sexes of having it (Rojas Buffet & Viera, unpublished data).

CONFLICT BETWEEN MALES

When two males arrive to a female web they engage in agonistic behaviour. Behavioural patterns involved in male-male conflicts are: silk thread tension, vibration, persecution, ritualised fighting and grapple. The two last behaviours occur in few cases and when both males have similar body condition. In the ritualised fighting, the males confront venter-to-venter and facing upwards, contacting leg tarsi and vibrating intensively their bodies, but causing no damages. In the grapple, males face each other, crossing legs and biting each other chelicerae to chelicerae, finishing with injuries or death of one of the individuals (Albo *et al.,* 2007; Rojas Buffet, Gómez & Viera, unpublished data).

The winner male mates with the female firstly. However, the loser male remains as «satellite» probably because the adult females re-mate easily; she can accept the loser male then. Therefore, it is expected that both males have a percentage of paternity of the female's offspring.

Lorieto *et al.* (2010) did not found a pattern of sperm priority using the sterile male technique. Both the first male that copulates and the second one show highly variable percentages of paternity, including total paternity of the first male and total paternity of the second male, suggesting that other factors have greater importance and that there may be cryptic female choice in this species.

ASPECTS OF BREEDING THAT INFLUENCE THE FUTURE REPRODUCTIVE SUCCESS

Regurgitation from adult females towards juveniles is a well-known phenomenon in social spiders (Lubin & Bilde, 2007). In the subsocial spider *A. vierae* maternal regurgitation to offspring plays an important role in the survival of the colony (Ghione *et al.,* 2004). However, food transfer between large juveniles also occurs in this species. Viera *et al.* (2005) experimentally tested if well fed penultimate females were capable of regurgitating fluids to starved males, and if well fed penultimate males were capable of regurgitating fluids to starved females. They concluded that both well fed penultimate males and females can feed other starved subadults, but when given access to members of the opposite sex, males benefit more from females than females with males. Later, in Gómez *et al*. (2015), we investigated if this regurgitation exchange among subadults could contribute somehow in the adult male's fitness. In this study, we examined the effects of supplementary food on the subadult male's development towards maturity. We carried out two types of trial: groups of subadult males and females siblings and non-siblings were weighed, and cephalothorax and leg I in adult males were measured. Our results suggest that the supplementary food obtained by males from sisters allows the acquisition of larger size. Besides weight gain, males fed by females reached larger sizes of leg I femur and tibia. As we said previously, leg I plays an important role in intrasexual competition, given that males with larger legs are more likely to win agonistic encounters and mate in first place. Although Lorieto et al (2010) did not found a pattern of sperm priority, more studies using molecular tools, are necessary to elucidate the cryptic female choice.

CONCLUSIONS AND FUTURE PERSPECTIVES

This review collects information on sexual behaviour in *A. vierae*. This species has shown very striking features in reproductive terms such as stereotyped male-male fighting and sexiness of juvenile females for males, and not only that but also, the surprising response of these females similar to the behaviours shown by adult females. Such reproductive characteristics, like other features of their life history, match with the evolutionary position of this species between solitary and more social spiders. Studies on the reproductive mechanisms in subsocial and quasisocial spiders are scarce and we believe that many more studies are needed to understand how the sexual selection operates in social species.

Given that one of the advantages of group living is to increase reproductive success, the study of the reproductive mechanisms is a key point to understand how sociality has evolved in spiders. The solitary, subsocial and quasisocial species may have different characteristics regarding sexual behaviour. So, the study of sexual interactions will let us understand how sexual selection works in spiders with different degree of social behaviour. Our future studies aim to understand the causes and possible benefits of the pseudocopulatory behaviour for one or both sexes of *A. vierae*, and in particular to comprehend how it affects future sexual encounter in the couples involved. In addition, considering the available behavioural data, it would be interesting to test thorough experimentation male mate choice and cryptic female choice hypotheses in this species.

ACKNOWLEDGEMENTS

We would like to thank all the co-authors of papers of *A. vierae* and two anonymous reviewers for their suggestions and comments.

REFERENCES

Avilés L. 1997. Causes and consequences of cooperation and permanent sociality in spiders. Pp. 476-498. *In:* Choe J. C. & Crespi B. (Eds.). The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press.

Albo M. J., Viera C. & Costa F.G. 2007. Pseudocopulation and male-male conflict elicited by subadult females of the subsocial spider *Anelosimus* cf. *studiosus* (Theridiidae). Behaviour, 144: 1217-1234.

Bilde T. & Lubin Y. 2011. Group living in spiders: cooperative breeding and coloniality. Pp. 275-306. *In:* Herberstein M. E. (Ed.). Spider Behaviour: Flexibility and Versality. Cambridge University Press.

Brach V. 1975. The biology of social spider *Anelosimus eximius* (Araneae: Theridiidae). Bulletin of the Southern California Academy of Sciences, 74: 37-41.

Buskirk R. E. 1981. Sociality in the Arachnida. Pp. 282-367. *In:* Hermann, H.R. (Ed.) Social Insects II. Academic Press. New York.

Cayafa M., Viera C. & Costa F.G. 2011. ¿Los machos de la araña subsocial *Anelosimus vierae* son capaces de orientarse por el olor de nidos coespecíficos? Boletín de la Sociedad Zoológica del Uruguay (2ª época), 20: 1-10.

Christenson T. E. 1984. Behavior of colonial and solitary spiders of the theridiid species *Anelosimus eximius*. Animal Behaviour, 32: 725-734.

Ebert D. 1998. Behavioral asymmetry in relation to body weight and hunger in the tropical social spider *Anelosimus eximius* (Araneae, Theridiidae). Journal of Arachnology, 26: 70-80.

Erez T., Schneider J. M. & Lubin Y. 2005. Is male cohabitation costly for females of the spider *Stegodyphus lineatus* (Eresidae)? Ethology, 111: 693-704.

Ferreira L. 2015. Factores que influyen en la dispersión de la araña subsocial *Anelosimus vierae* (Araneae, Theridiidae). Tesis de Maestría, Facultad de Ciencias, UdelaR. Montevideo.

Foelix R. F. 2011. Biology of spiders. Oxford, University Press, 3rd edition. 419 pp.

Ghione S., Viera C. & Costa F. G. 2004. Ability to capture prey in early instars of the subsocial spider *Anelosimus studiosus* (Henz, 1850) from Uruguay (Araneae, Theridiidae). Bulletin of the British Arachnological Society, 13: 60-62.

Gómez D., Rojas-Buffet C. & Viera C. 2015. The influence of regurgitation by sister on male’s growth in the subsocial spider *Anelosimus vierae* (Araneae, Theridiidae). Arachnology, 16: 252-254.

Gundermann J. L., Horel A. & Roland C. 1997. Costs and benefits of maternal care in a subsocial spider, *Coelotes terrestris*. Ethology, 103: 915-925.

Jones T. C & Parker P. G. 2002. Delayed juvenile dispersal benefits both mother and offspring in the cooperative spider *Anelosimus studiosus* (Araneae: Theridiidae). Behavioral Ecology, 13: 142-148.

Klein B. A., Bukowski T. C. & Avilés L. 2005. Male residency and mating patterns in a subsocial spider. The Journal of Arachnology, 33: 703-710.

Kullman E. J. 1972. Evolution of Social Behavior in Spiders (Araneae; Eresidae and Theridiidae). Annals of Zoology, 12: 419-426.

Lorieto V., Ghione S. & Viera C. 2010. An indirect approach to study sperm precedence in a subsocial spider. Ethology, Ecology and Evolution, 22: 1-10.

Lubin Y. 1986. Courtship and alternative mating tactics in a social spider. The Journal of Arachnology, 14: 239-257.

Lubin Y. & Bilde T. 2007. The Evolution of Sociality in Spiders. Advances in the Study of Behavior, 37: 83-145.

Pruitt J. N. & Riechert S. E. 2009. Male mating preference is associated with risk of pre-copulatory cannibalism in a socially polymorphic spider. Behavioral Ecology and Sociobiology, 63: 1573-1580.

Pruitt J. N. & Riechert S. E. 2011. Nonconceptive sexual experience diminishes individuals' latency to mate and increases maternal investment. Animal Behaviour, 81: 789-794.

Pruitt J. N., Burghardt G. M. & Riechert S. E. 2012. Non-conceptive sexual behavior in spiders: a form of play associated with body condition, personality type, and male intrasexual selection. Ethology, 118: 33-40.

Rojas C. 2011. Cortejo y pseudocópula de la araña subsocial *Anelosimus vierae* (Theridiidae). Pasantia de grado, Facultad de Ciencias, UdelaR. Montevideo.

Rojas Buffet C. & Viera C. In press. Loading the male pedipalps: sperm induction in a subsocial spider. Journal of Arachnology.

Schneider J. & Andrade M. 2011. Mating behaviour and sexual selection. Pp. 215-274. *In:* Herberstein M. E. (Ed.). Spider Behaviour: Flexibility and Versality. Cambridge University Press.

Smith D. R. 1997. Notes on the reproductive biology and social behavior of two sympatric species of *Philoponella* (Araneae, Uloboridae). The Journal of Arachnology, 25: 11-19.

Uetz G. W & Hieber C. S. 1997. Colonial web-building spiders: balancing the costs and benefits of group-living. Pp. 458-475. In: Choe, J. C. & Crespi, B. (Eds.). The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press.

Viera C. 2011. Sociedades de arañas. Pp. 135-148. *In:* Viera, C. (Ed.). Arácnidos de Uruguay. Diversidad, comportamiento y ecología. Editorial Banda Oriental. Montevideo.

Viera C. & Albo M. J. 2008. Males of subsocial spider choose among females of different ages and same reproductive status. Ethology, Ecology and Evolution, 20: 35-41.

Viera C., Costa F. G., Ghione S. & Benamú M. 2007a. Progeny, development and phenology of the sub-social spider *Anelosimus* cf. *studiosus* (Araneae, Theridiidae) from Uruguay.

Studies on Neotropical Fauna and Environment, 42: 145-153.

Viera C, Ghione S. & Costa F. G. 2005. Regurgitation among penultimate juveniles in the subsocial spider *Anelosimus studiosus* (Araneae, Theridiidae): are males favored?. Journal of Arachnology, 34: 258-260.

Viera C., Ghione S. & Costa F. G. 2007b. Mechanisms underlying egg sac opening in the subsocial spider *Anelosimus* cf. *studiosus* (Araneae Theridiidae). Ethology Ecology & Evolution 19: 61-67.

Wilson E. O. 1971. The insect societies. Belknap Press, Harvard University, Cambridge. 548 pp.

World Spider Catalog. 2015. World Spider Catalog. Natural History Museum Bern, online at http://wsc.nmbe.ch, version 16.5, accessed on {18/09/2015}.

Fecha de Recepción: 22 de Setiembre de 2015
Fecha de Aceptación: 06 de Noviembre de 2015