Substrate vibrations in the scorpion *Centruroides margaritatus* (Scorpiones: Buthidae) during courtship

R.D. Briceño[1] & F. Bonilla[2]

1. Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria Rodrigo Facio, 11501-2060, San José, Costa Rica.
2. Instituto Clodomiro Picado, Universidad de Costa Rica, 11501-2060, Ciudad Universitaria Rodrigo Facio, Costa Rica.

Received 03-X-2007. Corrected 20-VIII-2009. Accepted 26-X-2009.

Abstract: Mating behavior in *Centruroides margaritatus*, as in other scorpion species, includes a series of rapid rocking or shaking movements of the male ("juddering"). It has been suggested that substrate vibrations are generated by juddering and that females respond to them by approaching the male, but its functional significance remains little studied. For the first time, substrate vibrations produced by males during courtship in *Centruroides margaritatus* are documented. The male started juddering after his first physical contact with the female and only one type of male vibratory signal was registered. The signal is produced during a series of rapid shaking of the male's body from front to rear and consists of multiple short pulses. Each pulse is called a judder and several judders "a series". The average duration of each judder was 0.018±0.009s (n=50) with an interval of 0.028±0.013s (n=50); the average duration of each series of judders was 4.2±3.5s with an interval between series of 3.5±6.3s and a rate of 0.21±0.17 series per second. The females responded in 72% of the time to the males juddering. Rev. Biol. Trop. 57 (Suppl. 1): 267-274. Epub 2009 November 30.

Key words: *Centruroides margaritatus*, scorpions, juddering, Costa Rica.

Communication through substrate vibrations has been recognized for a long time, but has received very little attention in comparison with sounds transmitted through the air. Nevertheless, in recent years, it has become clear that these signals play a crucial role in many groups of insects, spiders and crustaceans, in transmitting information related to sexual behavior, alarm, defensive behavior, and to coordinate complex actions in groups and social interactions (Aicher & Tautz 1990, Schüch & Barth 1990, Hill 2001, Elias *et a.l* 2003).

Vibration can be used in predator prey interactions, and scorpions have evolved a high sensitivity to information that is received through the surface. Brownel & Farley (1979 a,b,c.) demonstrated that *Paruroctonus mesaensis* is capable of responding to substrate vibrations up to half a meter away and can use vibrations in sand to determine both direction and distance of prey species. In turn the burrowing cockroach, *Arenivaga investigata*, uses vibration to detect and avoid the approach of the scorpion species (Brownell 1977). Vibrations can also provide a channel of communication between males and females during mating. Mating behaviors have been described for about 30 species of scorpions (Polis & Sissom 1990) and usually interactions between sexes are often complicated by conflicting stimuli which simultaneously produce incompatible tendencies to flee, attack and mate (Tinbergen 1953, Morris 1956)

Centruroides margaritatus (Gervais, 1841), belongs to the family Buthidae, the most numerous and widely distributed group of modern scorpions, and includes about 45 of the total of 115 genera (39%) and 600 of 1200 described species (50%) (Escobar & Ochoa 2003). *Centruroides margaritatus* is about 5 to

8cm long including the telson, and is native to Mexico, Central America and Northern South America (Venezuela, Colombia and Ecuador) (Escobar & Ochoa 2003) and with unintentional introductions in parts of West Africa and Japan (Armas 1977, 1981). In Costa Rica it is distributed from the lowlands of the tropical dry forest on the Pacific coast to the Central Valley (1300m). Studies on scorpion life histories, however, are few in number. The lack of data is due in part to difficulties in rearing scorpions in captivity (Francke 1976, 1979a, 1981, Polis & Farley 1979) therefore it is no surprising how little is known about behavior general biology of this species.

This paper represents the first description of substrate vibrations during sexual interactions in *Centruroides margaritatus* and its characterization.

MATERIALS AND METHODS

All scorpions studied were from a stock maintained in rearing conditions at the Instituto Clodomiro Picado (Universidad de Costa Rica), from specimens collected in a tropical dry forest at Parque Nacional Santa Rosa, Guanacaste, in 2006/07. The scorpions were keep individually in round plastic boxes with a diameter of 15 cm, with multiple holes for ventilation, with humid cotton and crumpled paper as a refuge. The animals were maintained at room temperature between 20-24°C, and relative humidity between 62-70%. The scorpions were fed every 15 days, with insects such a cockroaches *(Periplaneta americana, Blaberus giganteus)*, crickets (*Acheta domesticus)* and larvae of tenebrionids beetles (*Tenebrio molitor*) reared in the laboratory.

A total of 10 pairs of scorpions were used. A mature female was placed in an aquarium (29.5cm high, 24cm wide and 50cm long) filled with river sand, and once she became calm a male was introduced. If mating was not initiated within half an hour, one or both members of the pair were replaced. If courtship began a vibration sensor was located approximately 2-5mm from the juddering male (Fig 1). Each mating pair was recorded once for an entire hour. The recordings were made during the day in a dark room under laboratory conditions with a ICP acceleration sensor® (model 352C65) and a signal conditioner® (amplifier, model 480E09 PCB Piezotronics), connected to a video camera Sony DCR-TRV 80 equipped with night shot and +6 close up lenses. The signals were digitized (22 kHz, 16 bits mono), stored on the hard disk and analyzed with the computer program Avisoft®. For the signal analysis we used an equal number of measurements per individual. The variables analyzed for each song were: pulse duration, interval between pulses, maximal frequency and amplitude. Means are followed by ± one standard deviation.

RESULTS

As have been observed in sexual interactions in other species (after Polis & Sissom, 1990) four behavior sequences can be distinguish in *C. margaritatus*: initiation, *promenade a deux*, sperm transfer and insemination, detailed in next paragraphs.

Initiation: Males usually initiated courtship after he detected the female's presence and approached her, making searching movements with his chelae extended and opened. During the search the pectines are spread wide and swept across the substrate. Males may rock or judder in the presence of the female and it appears that this occurs only during sexual interactions. During searching the male begins with a series of rapid shaking of his body from front to rear (juddering). These vibrations also occurred when the male was otherwise immobile in front of the female, after making physical contact, or at a "certain distance". The male´s pectines were usually spread and his legs firmly planted on the substrate. Juddering also occurred during the *promenade* phase (mating dance or *promenade a deux*, Maccary, 1810), and when male and female were touching each other with their chelicera.

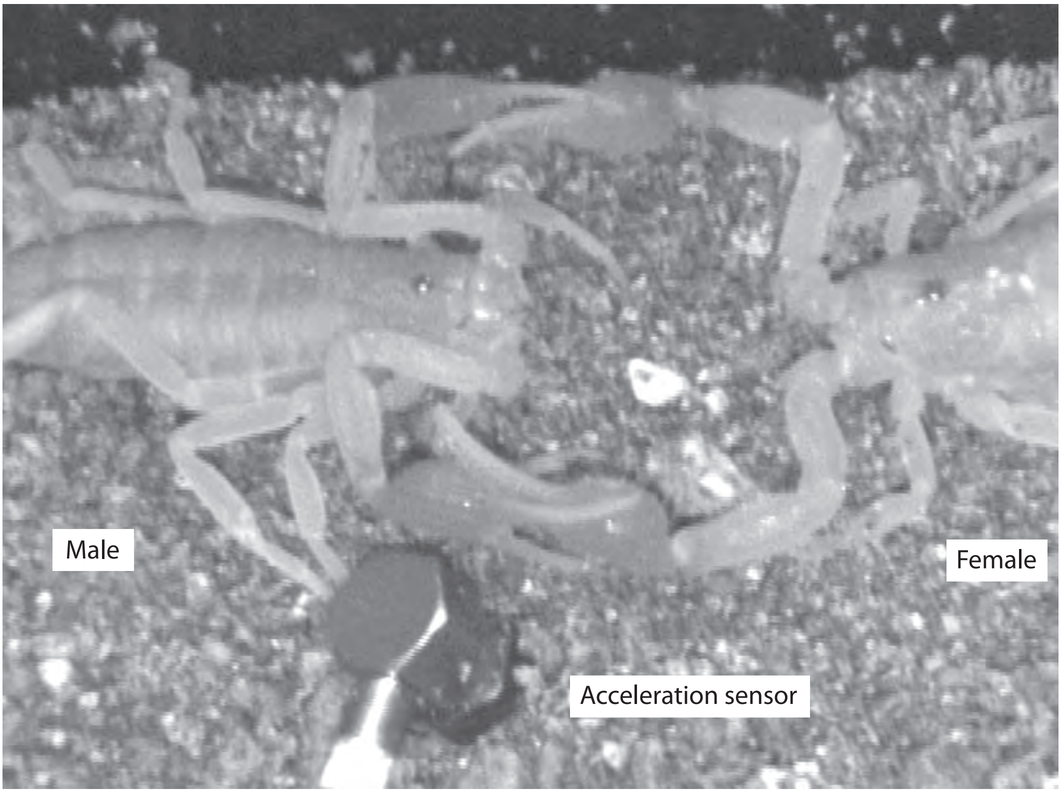

Fig. 1. *Centruroides margaritatus,* courtship initiation: the male lunges and seizes the female with his pedipalps and starts juddering. The ICP acceleration sensor was located close to the male.

During this initial contact, the male appeared to grasp the female's tail and club her with his tail, while the female moved toward the male, grasped and released his body with her chelae, clubbed or attempted to sting him with her metasoma, and then retreated. Polis & Farley (1979) called this the female's "mating attack behavior". Clubbing is defined as hitting with the metasoma while the sting is tucked away (McAlister 1966). The male then began to "strut defensively" (Stahnke 1966). During this behavior, the male stilted on his legs, his metasoma is raised parallel to the ground, and he remained still or moved intermittently while his pectines slowly swept the substrate.

Occasionally females participated in the initiation by approaching the male. A receptive female will approach a male with raised pedipalps and either bump or walk over the male until he responds with a lunge and grasps her as described above.

***Promenade a deux**:* Once the male grasped the female's chelae with his own, the pair started to move together for short periods (4.4±3.1min, n=8) back and forth. The male was the most active of the pair and guided this *promenade*. During this dance the male raised his first walking legs and moved them very rapidly in front of the female. Usually the pair eventually touched each other's chelicerae (6.3±4.2min, n=9), and they stayed immobile in this position for long periods, in some cases for the entire day.

Sperm transfer and insemination: Once a suitable substrate was encountered during tandem movement, the male lowered his mesosoma until the genital aperture touched the ground and extruded the spermatophore. After extrusion, the male repeatedly jerked rearward, eventually succeeding in pulling the female over the spermatophore. In one of matings the female avoided the male´s spermatophore.

Substrate vibrations: We observed a total of 20 interactions with an average duration of 3.7±5.4 min of which in 73% of the occasions the males started juddering prior to grasping the female with his chelae. Only 40% (n=8) of the total interactions ended in female grasping, and in all cases the males continued juddering. The average number of series while grasping the female with his chelae was 13.6±21 (n=20), and 14.2±14.3 (n= 6) when not grasping the female. In an encounter that lasted 42 minutes, we observed that juddering is an activity that occurred frequently, especially at the beginning and end of the interaction (Fig. 2), coordinated with other activities such as *promenade* and cheliceral contact. The male started juddering 5.8±6.2s after his first physical contact with the female.

Only one type of male vibratory signal was registered during the juddering behavior; it was of low amplitude, and not audible. The signal is produced during a series of rapid shaking of the male's body from front to rear, and consists of multiple short pulses. Each pulse is called a judder and several judders a series of judders (Fig. 3B). The temporal structure and spectrogram of a burst of juddering is shown in Fig. 3A. The average frequency of the signal was 486.6±36.1Hz at 117.5±17.5 db (10 pairs, n=200). The average duration of each judder was 0.018±0.009s (n=50) with an interval of

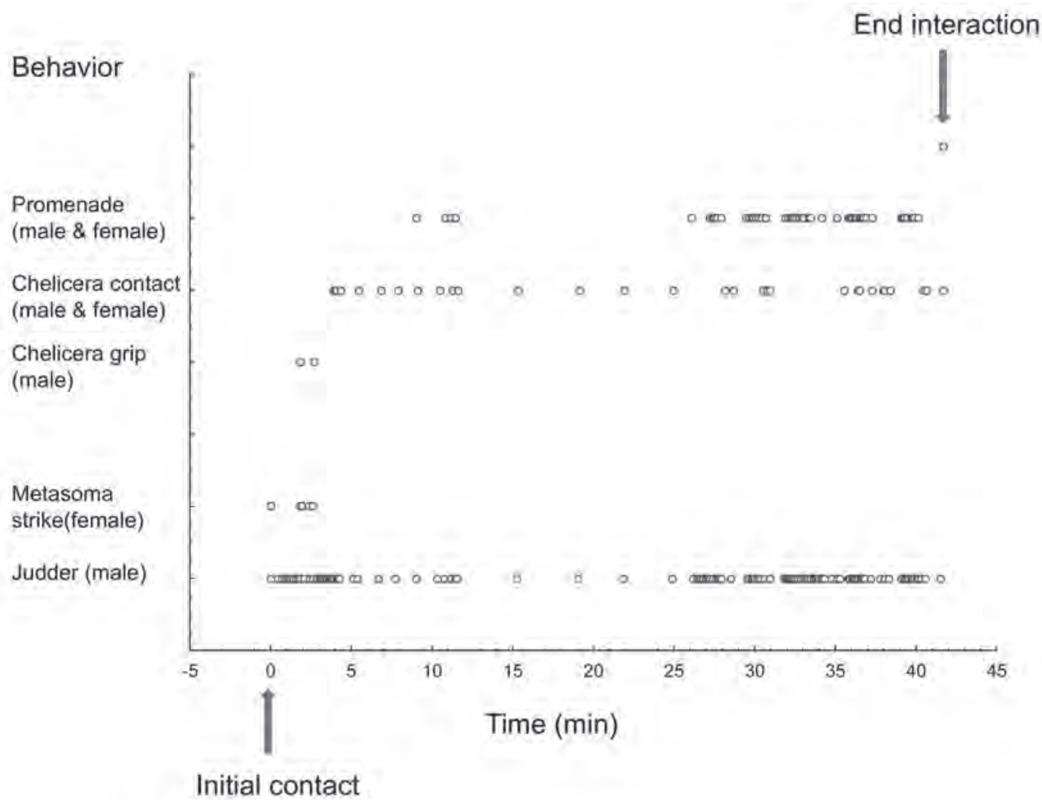

Fig. 2. Behaviors observed by male and female of *Centruroides margaritatus* during a sexual interaction that lasted 42 minutes.

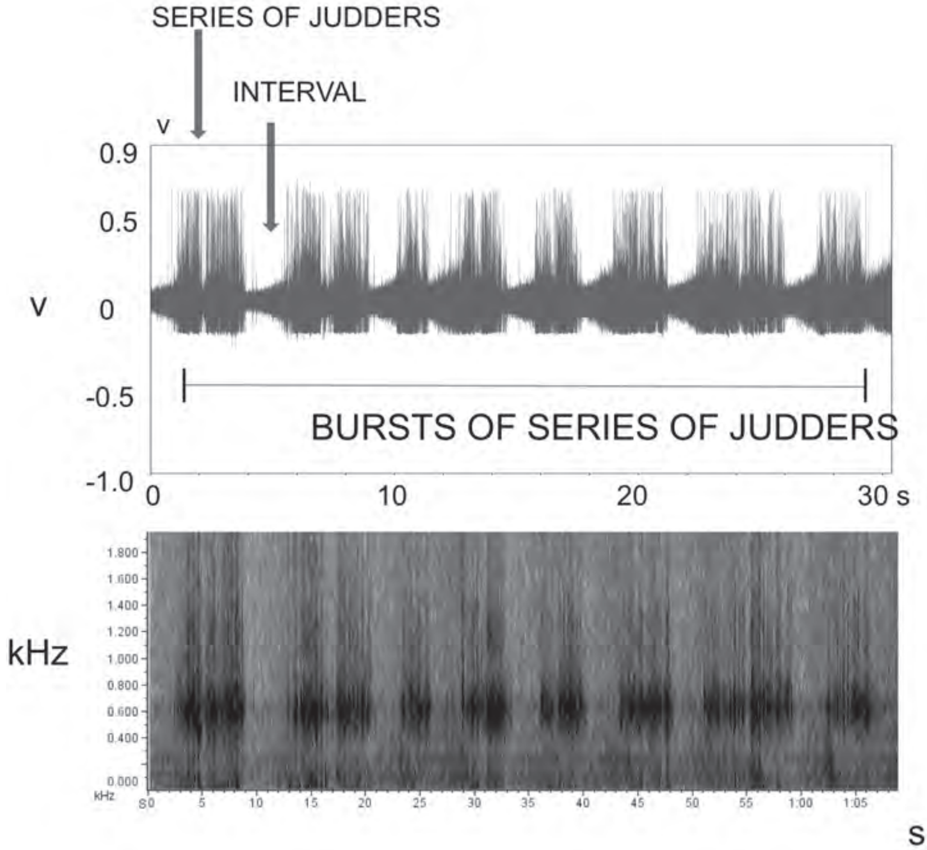

Fig. 3. A). *Centruroides margaritatus,* burst of series of judders, the temporal structure of the song ranges from 450-562 Hz (spectrogram) [amplitude (v) vs. time (s)] and vs. frecuency (Hz)].

0.028±0.013s (n=50); the average duration of each series of judders was 4.2±3.5s with an interval between series of 3.5±6.3s and a rate of 0.21±0.17 series per second. The frequency of the bursts of juddering was 6.9±2.5 per min.

Female behavior when confronted with male juddering: From a total of 14 interactions in which males started juddering prior to grasping the female with his chelae, in 28% of the cases the females remained motionless, in 26% she oriented toward the male, in 16.5% she walked towards the male, in 9.3% she tried to grasp the male´s chelae, in 7.8% she hit the male with her metasoma and in 13% she moved away from the male. In total, females responded 72% of the time to the males' juddering.

DISCUSION

Scorpion courtship and mating have been described for many species (Garner & Stockman 1972), and Polis & Sissom (1990) calculated that in 59% of the species (5 families) males produced shaking movements during courtship (male juddering). But few of them have provided a detailed description of the juddering behavior.

This study has shown, for the first time, that juddering produced vibrations that are

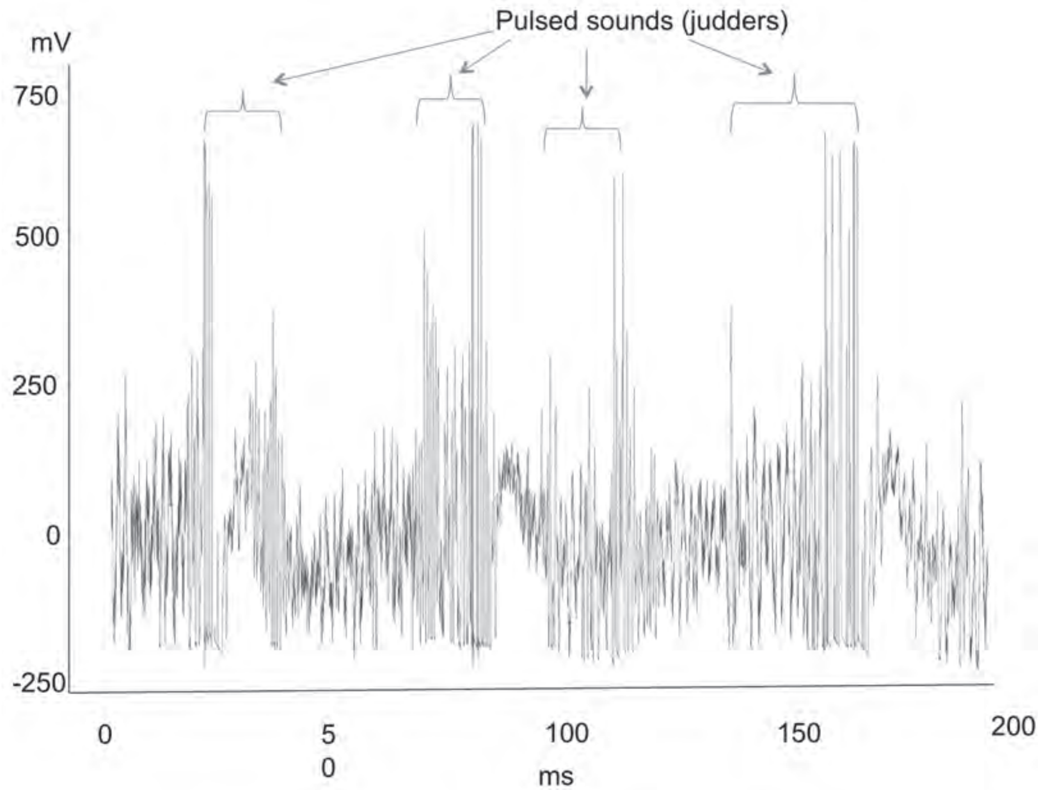

Fig. 3. B). A song consisting of a series of pulsed sounds (judders) produced by the male of *Centruroides margaritatus*.

transmitted through the substrate. Brownel & Farley (1979) showed that low-frequency surface waves, termed Rayleigh waves, and higher-frequency compression waves, could be transmitted through a sandy substrate; they also discovered that two different receptors on the legs were responding to substrate vibrations and used for prey detection.

Also we showed that females reacted to male juddering. Rosin & Shulov (1963) noted that female *Nebo* definitely sense the pre-*promenade* juddering of the male from a distance of several centimeters. In *Opistophthalmus latimanus* the primary releaser of courtship behavior appears to be a change in the female behavior in response to juddering by the approaching male (Alexander 1958). Polis & Farley (1979a) showed that receptive *P. mesanensis* females sense the substrate vibrations of moving males (see also Armas 1986). That means that vibrations produced during courtship probably are used as a channel of communication between males and females, but at this point, there are a few works that explore this possibility and its possible role. *C. margaritatus* also tends to produce such vibrations from a certain distance from a female after a previous contact. It is possible that these vibrations have different roles at different stages of the courtship, for example we observed that vibratory signals during searching behavior apparently are less intense than during sexual contact. Some possible functions are: sex or species recognition behavior, as a releaser of mating behavior so that the female is stimulated to cooperate and/or inhibition of aggressive and escape behaviors so that courtship can be initiated.

We cannot discard the possibility that vibratory signals during courtship serves to bias cryptic female choice to favor the male (Eberhard 1996). In jumping spiders, the importance of vibratory signals in courtship display was demonstrated in males of *H. dossenus* by comparing mating frequencies across experimentally manipulated treatments: females were significantly more likely to copulate with non-muted males than with muted males (Elias *et al*. 2005). In *Bothriurus flavidus* the female allowed the male to execute the *promenade* and deposit his spermatophore, but then, resisted the final step of spermatophore transfer. Female resistance at the final stage causes failure of sperm transfer and has been seen in other species of *Bothriurus*, *Timogensis elegans* and *Urophonius iheringi*. It is possible that these female behavior patterns were also a response to the number, intensity and/or durations in the vibratory signals produced by males during juddering. Differences between males need to be investigated.

ACKNOWLEDGMENTS

We thank William Eberhard and P. Hanson and two anonymous reviewers for suggestions to previous drafts. Thanks are also given to the Vice-presidency for Research, Clodomiro Picado Institute and the University of Costa Rica for financial support.

RESUMEN

El comportamiento de apareamiento en *Centruroides margaritatus* como en otras especies del escorpiones, incluye una serie de oscilaciones rápidas hacia adelante y hacia atrás del cuerpo del macho (juddering). Se ha especulado que tales oscilaciones generan vibraciones en el substrato y las hembras pueden responder a ellas aproximándose al macho, pero su significado funcional sigue siendo poco estudiado. Por primera vez, las vibraciones del substrato producidas por los machos durante el comportamiento de cortejo de *Centruroides margaritatus* son documentadas. El macho comenzó las vibraciones después de su primer contacto físico con la hembra y sólo se registró un tipo de señal vibratoria. La señal se produce durante una serie de rápidas sacudidas del cuerpo del macho de adelante hacia atrás y se compone de múltiples pulsos cortos. La duración media de cada pulso fue 0.018±0.009s (n = 50) con un intervalo de 0.028±0.013s (n=50); la duración media de cada serie de pulsos fue de 4.2±3.5s, con un intervalo entre las series de 3.5±6.3s y una tasa de 0.21±0.17 serie por segundo. Las hembras respondieron en un 72% del tiempo a las sacudidas de los machos. Se discute acerca de su posible función como señal.

Palabras clave: *Centruroides margaritatus*, escorpiones, vibraciones de cortejo, Costa Rica.

REFERENCES

Aicher, B. & J. Tautz. 1990. Vibrational communication in the fiddler crab, *Uca pugilator*. J. Comp. Physiol. 166: 345-353.

Alexander, A.J. 1958. On the stridulations of scorpions. Behaviour 12: 339-352.

Armas, L.F. De. 1977. Identidad subespecífica de *Centruroides margaritatus* (Scorpionida: Buthidae) de Jamaica. Misc. Zool. 6: 4.

Armas, L.F. De. 1981. El género *Centruroides* Marx, 1889 (Scorpiones: Buthidae) en Bahamas y República Dominicana. Poeyana 223: 1-21.

Armas, L.F. De. 1987. Cópula de escorpiones (Arachnida: Scorpiones: Buthidae). Poeyana 333: 1-27.

Brownell, P.H. 1977. Compressional and surface waves in sand used by desert scorpions to locate prey. Science 197: 479-482.

Brownell, P.H. & R.D. Farley. 1979. Detections of vibrations in sand by tarsal sense organs of the nocturnal scorpion, *Paruroctonus mesaensis*. J. Comp. Physiol. 131: 23-30.

Brownell, P.H. & R.D. Farley. 1979b. Prey location behavior of the nocturnal desert scorpion, *Paruroctonus mesaensis*: Orientation to substrate vibrations. Anim. Behav. 27: 185-193.

Brownell, P.H. & R.D. Farley. 1979c. Orientation to vibrations in sand by the nocturnal scorpion, *Paruroctonus mesaensis*: Mechanism of target localization. J. Comp. Physiol.131: 31-38.

Brownell, P.H. & G. Polis (eds). 2001. Scorpions biology and research. Oxford University Press. Oxford, England.

Eberhard, W.E. 1996. Female control: sexual selection by cryptic female choice. Monographs in behavior and ecology. Princeton University Press, New Jersey, USA.

Elias, D.O., A.C. Mason, W.P. Madison & R.R. Hoy. 2003. Seismic signals in a courting male jumping spider (Araneae: Salticidae). J. Exp. Biol. 206: 4029-4039.

Elias, D.O., E.A. Hebets, R.R. Hoy & A.C. Mason. 2005. Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae: Salticidae). Anim. Behav. 6: 931-938.

Escobar, E. & J. Ochoa. 2003. Confirmación de la presencia de *Centruroides margaritatus* (Gervais,1841) (Scorpiones: Buthidae) en el Perú. Libro de resúmenes XII Reunión Científica ICBAR. UNMSM. Lima, Perú.

Francke, O.F. 1976b. Observations on the life history of *Uroctomes mordax* Thorell (Scorpionidae, Vaejovidae). Bull. Brit. Arachnol. Soc. 3: 254-260.

Francke, O.F. 1979. Spermatophores of some North American scorpions (Arachnida, Scorpiones). J. Arachnol. 7: 19-32.

Francke, O.F. 1981. Birth behavior and life history of *Diplocentrus spitzeri* Stalmke. Southwest. Nat. 25: 517-523.

Garner, G. & R. Stockman.1972 . Etude comparative de la paraide chez differentes espèces de scorpions et chez *Pandinus imperator.* Ann. Univ. Abdijan Ser. E (Ecologie) 5: 475-497.

Hill, P.S. 2001. Vibration and animal communication. Ann. R. Amer. Zool. 41: 1135-1142.

Morris, D.J.1956. The function and causation of courtship ceremonies. pp. 54-89 *In* P.P. Grasse. (ed.). L'Instinct dans le comportement des animaux et de l'homme. Masson Cie. Paris, France.

McAlister, W. H. 1965. The mating behavior of *Centruroides vittatus.* Tex. J. Sci. 17: 307-312.

Maccary, A. 1810. Memoire sur le scorpions qui se trouvent sur la montagne de Cette, Gabon, Paris, France.

Polis, G.A. & R.D. Farley. 1979. Behavior and ecology of mating in the cannibalistic scorpions *Paruroctomus mesaensis* Stahnke (Scorpionida: Vaejovidae). J. Arachnol. 7: 33-46.

Polis, G. & W. Sissom *1990.* Life history. The biology of scorpions. Stanford University, California, USA.

Rosin, R. & A. Shulov. 1963. Studies on the scorpion *Nebo hierochonticus*. Proc. Zool. Soc. London 140: 547-575.

Scüech, W. & F.G. Barth. 1990. Vibratory communication in a spider: female responses to synthetic male vibration. J. Comp. Physiol. 166: 817-826.

Stahnke, H. L. 1966. Some aspects of scorpion behavior. Bull. Southern California Acad. Sci. 65: 65-80.

Stürzl, W., R. Kempter & J.L. van Hemmen. 2000. Theory of arachnid prey localization. Phys. Rev. Lett. 84: 5668-5671.

Tallarovic, S.K., J.M. Melville & P.H. Brownell. 2000. Courtship and mating in the giant hairy desert scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae). J. Insect Behav. 13: 827-838.

Tinbergen, H. 1953. Social behavior in animals. Methuen Co., London, England.