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DESCRIPTION OF IMMATURE STAGES OF *MELANAETHUS CRENATUS* (HEMIPTERA: HETEROPTERA: CYDNIDAE: CYDNINAE: GEOTOMINI), WITH NOTES ON OVIPOSITION, SEED-CARRYING AND FEEDING BEHAVIORS

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ABSTRACT

Here we describe the immature stages and seed-carrying and feeding behaviors of *Melanaethus crenatus* (Signoret) (Hemiptera: Heteroptera: Cydnidae: Cydninae: Geotomini), based on 4 sampling dates from 2009 through 2011. Adult females of this species move seeds of its host plant, *Richardia scabra* L. (Rubiaceae), to small cavities under small rocks for feeding; these cavities in some cases correspond to oviposition sites where nymphs also feed on the seeds. All instars of *Melanaethus crenatus* are described and illustrated for the first time. This species is associated with dry oak forest and lives under rocks. This record probably represents an intermediate behavior between nonparental and parental care.

Key Words: seed-carrying behavior, Mexico, Rubiaceae

RESUMEN

En este estudio se describe el ciclo de vida, los comportamientos de alimentación y transporte de semillas de *Melanaethus crenatus* (Signoret). Las adultas hembras de esta especie de chinches mueven las semillas de su planta hospedera, *Richardia scabra* L. (Rubiaceae) a pequeños agujeros debajo de pequeñas rocas para poder alimentarse; estos pequeños agujeros sirven a su vez como sitios de oviposición en donde las ninfas también se alimentan de las semillas movidas por las madres. Se describen e ilustran por primera vez todos los estadios de *Melanaethus crenatus*. Esta especie está asociada a bosques secos de encinos y vive debajo de rocas. Este registro probablemente representa un estadio intermedio en el comportamiento de especies de chinches con cuidado parental y no parental.

Palabras Clave: Acarreo de semillas, Mexico, Rubiaceae

In the Hemiptera, parental care is believed to have evolved primarily in response to parasitism of eggs (Tallamy & Schaefer 1997). These extended parental behaviors range from oviposition of eggs in one mass and egg guarding to production of trophic eggs, protection of nymphs against predators and progressive provisioning. Although subsocial behavior has been reported for a number of families within the order, reports of parental care that extends to providing nymphs with a food source have only been recorded for 4 species belonging to the Cydnidae, subfamily Sehirinae; and to one species of the related Parastrachidae, despite the fact that the biology and behavior of

many species of Cydnids are unknown because most of the species live underground. Intermediate behaviors between nonparental and parental bugs rarely have been mentioned.

The bugs with extended parental behavior are: *Sehirus cinctus cinctus* (Palisot de Beauvois) (Sites & McPherson 1982; Agrawal et al. 2004, 2005); *Adomerus triguttulus* (Motschulsky) (Kudo & Nakahira 2004, 2005; Kudo et al. 2006; Nakahira & Kudo 2008); *Adomerus variegatus* (Signoret) (Mukai et al. 2010); *Canthophorus niveimarginatus* Scott (Sehirinae) (Filippi et al. 2009; Baba et al. 2011); and the most studied *Parastrachia japonensis* Scott (Parastrachidae) (Tachikawa &

Schaefer 1985; Tsukamoto & Tojo 1992; Tsukamoto et al. 1994; Filippi et al. 1995a, 1995b, 2000a, 2000b, 2001, 2002, 2005; Nomakuchi et al. 1998; Hironaka et al. 2005, 2007a, 2007b, 2007c; Tojo et al. 2005). In a laboratory experiment adults and nymphs of *Adrisa magna* Uhler were observed to carry seeds of *Sophora japonica* L. (Leguminosae) to shelter places allowing communal feeding and possible provisioning for nymphs (Takeuchi & Tamura 2000).

Melanaethus crenatus (Signoret) (Figs. 1-7, 10-12) is a true bug that belongs in the subfamily Cydninae. In the USA it has been recorded from Arizona and Texas, and in Mexico from Baja California Sur, Jalisco, Hidalgo, Puebla, Estado de Mexico, Distrito Federal, and Veracruz (Froeschner 1960; Mayorga 2002). Its host plant, rough Mexican clover, *Richardia scabra* L. (Rubiaceae) (Fig. 9) can be found in disturbed, moist, and sunny areas, common in dry forests, and less abundantly in dry thorn bush; at elevations ranging from 0 to 1,400 m. It occurs from USA to Brazil, and in Cuba and Jamaica in the West Indies. In Mexico it has been recorded from the states of Baja California Sur, Chiapas, Colima, Distrito Federal, Jalisco, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Tabasco, Tlaxcala, Veracruz, and Yucatán. *Richardia scabra* is an annual or a perennial weed with prostrate tillers, usually forming large patches. Leaves, bracts, flowers and stems have whitish hairs. Flowers have 6 triangular petals; it flowers from March to December (Rzedowski & Rzedowski 2001; Villaseñor & Espinosa 1998).

In this study we record for the first time the life history and immature stages of *M. crenatus*. In addition, we present a brief diagnosis of the adult, information on its host plant, and notes about its seed-carrying, feeding, and oviposition behaviors. The figures in color can be found in supplementary material online in Florida Entomologist 96(4) (2013) at <http://purl.fcla.edu/fcla/entomologist/browse>.

Materials and Methods

Adults and nymphs of *M. crenatus* were collected only in one locality in Mexico on 4 different occasions between 2009 and 2011. The study site is located in the state of Veracruz, near the municipality of Tlaltetela, 5 km NE of Tlaltetela, Ejido Monte Blanco, situated at N 19° 18' 44" W 96° 50' 53", 828 m. It is an area of dry oak forest mixed with dry forest, pasture grasslands, sugarcane, and lime plantations. In the study site *R. scabra* was restricted to the lime plantation and to areas from which cattle were excluded.

On 19-II-2009, 4 females and several nymphs were collected in 3 nests in a grassland area near the border with a dry forest. We define "nests" as

a small space beneath a rock in which aggregated nymphs, adults or eggs were found.

At the same locality on 24-IV-2010, 14 females and 7 males not in nests and several fifth instar nymphs in one nest were collected. On VI-2010 3 females and 12 nymphs ranging from third to fifth instar were collected in one nest. On 12-IV-2011, bugs were collected on a plantation where the host plant *R. scabra* was growing underneath lime trees (*Citrus × aurantiifolia* [Christm.] Swingle [pro sp.] [*medica* × sp.], Sapindales: Rutaceae); only 4 females and 10 males, were found under rocks or beneath the host plant. On all occasions the bugs were only found in small patches of the host plant, where cattle could not graze on them and where the humidity conditions allowed the development of the plant.

Bugs were transferred to the laboratory in plastic containers (10 × 8 × 8 cm), with a small quantity of soil, seeds from the host plant, and a moist cotton ball. Once in the laboratory the bugs were transferred to glass Petri dishes (10 cm diam × 2 cm) containing a layer (~7 mm deep) of moist soil (sieved from the study site) and a cotton ball. Individuals were kept under laboratory conditions at 20 °C, 70% RH and 12:12 h L:D. Because we did not know if the females had mated, adults were kept in pairs and 3 seeds of the host plant were added in the center of the Petri dish every 3rd day; old seeds were removed to avoid fungal growth. On one occasion a flower head was set in the middle of one of the petri dishes. Measurements in descriptions of bugs are expressed in mm ± SE. Between 3 and 10 individuals were measured. Drawings were made using a drawing tube adaptor, and are based on field collected specimens.

RESULTS

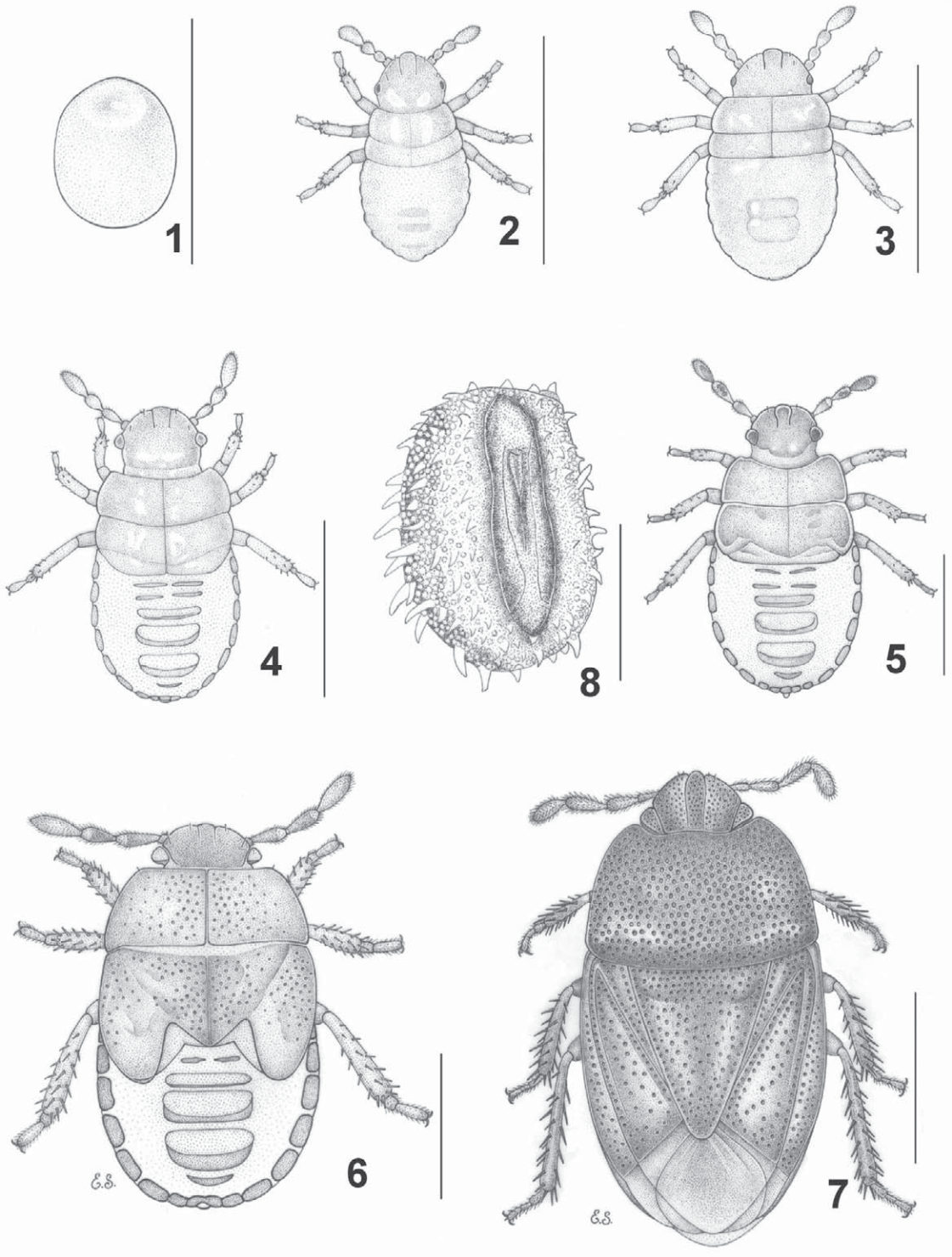
Melanaethus crenatus (Signoret) (Figs. 1-7)

Description

Adult (Fig. 7): The adult was described in detail by Froeschner (1960), and within the genus, this species can be recognized by the large terminal lobe on the peritreme and by the distinctly alutaceous coria.

Egg: (Fig. 1) Length 0.54 ± 0.4 ; width 0.34 ± 0.05 . Egg oval, yellowish in color; chorion smooth.

First instar (Fig. 2): Body length 0.9 ± 0.05 . Ovoid, with dorsal surface convex, maximum width through abdominal segment II; dorsal punctures absent. Head, pro-, mesonotum, and abdomen white; eyes reddish. Rostrum reaching abdominal sternite II; antennae, rostrum, legs, and scent gland openings of segments III-IV- and IV-V pale brown. Measurements ($n = 10$). Head length 0.21 ± 0.03 ; width through eyes 0.30 ± 0.01 ; interocular distance 0.28 ± 0.03 ; antennal



Figs. 1-8. *Melanaethus crenatus*. 1. Egg. 2. First Instar. 3. Second Instar. 4. Third Instar. 5. Fourth Instar. 6. Fifth Instar. 7. Adult. 8. Seed of *Richardia scabra*. (Scale bars = 1 mm).



Fig. 9. *Richardia scabra*, host plant of *Melanaethus crenatus*.

segments: I 0.06 ± 0.01 , II 0.08 ± 0.01 , III 0.07 ± 0.01 , IV 0.1 ± 0.02 ; rostral segments : I 0.08 ± 0.01 , II 0.08 ± 0.01 , III 0.11 ± 0.01 , IV 0.11 ± 0.01 ; pronotum length 0.12 ± 0.01 ; width across anterior margin 0.34 ± 0.02 ; width across humeral angles 0.5 ± 0.02 ; length fore femur 0.15 ± 0.02 ; length fore tibia 0.16 ± 0.01 ; length fore tarsi I 0.04 ± 0.01 , II 0.06 ± 0.01 .

Second instar (Fig. 3): Body length 1.15 ± 0.04 . Ovoid dorsally, convex with maximum width through second abdominal segment. Head, pro-, meso-, metanotum, antennal segments, rostral segments, legs, scent gland openings of segments II-III, III-IV, and IV-V, and lateral margins of abdominal segments whitish-yellow; eyes deep red; abdomen white, rostrum reaching abdominal sternite II. Measurements ($n = 4$). Head length 0.25 ± 0.04 ; width through eyes 0.36 ± 0.01 ; interocular distance 0.3 ± 0.01 ; antennal segments: I 0.08 ± 0.01 , II 0.07 ± 0.01 , III 0.07 ± 0.02 , IV 0.23 ± 0.05 ; rostral segments : I 0.12 ± 0.02 , II 0.12 ± 0.01 , III 0.1 ± 0.01 , IV 0.15 ± 0.01 ; pronotum length 0.17 ± 0.02 ; width across anterior margin 0.43 ± 0.02 ; width across humeral angles 0.62 ± 0.01 ; length fore femur 0.18 ± 0.01 ; length

fore tibia 0.22 ± 0.01 ; length fore tarsi I 0.05 ± 0.01 , II 0.08 ± 0.01 .

Third instar (Fig. 4): Body length 1.38 ± 0.07 . Very similar to second instar. Head, antennae, rostrum, pronotum, scent gland openings, and legs slightly darker and sclerotized. Rostrum reaching apex of mesosternum; lateral margins of abdomen with darker markings. Measurements ($n = 5$). Head length 0.31 ± 0.02 ; width through eyes 0.44 ± 0.01 ; interocular distance 0.37 ± 0.01 ; antennal segments: I 0.08 ± 0.01 , II 0.11 ± 0.01 , III 0.11 ± 0.01 , IV 0.18 ± 0.02 ; rostral segments : I 0.15 ± 0.01 , II 0.16 ± 0.01 , III 0.16 ± 0.01 , IV 0.16 ± 0.01 ; pronotum length 0.25 ± 0.01 ; width across anterior margin 0.5 ± 0.02 ; width across humeral angles 0.76 ± 0.02 ; length fore femur 0.26 ± 0.02 ; length fore tibia 0.31 ± 0.01 ; length fore tarsi I 0.05 ± 0.01 , II 0.06 ± 0.01 .

Fourth instar (Fig. 5): Body length 2.11 ± 0.04 . Pyriform, dorsally convex, and maximum width through abdominal segment III. Head, antennal segments I and II, rostral segments, pronotum, lateral plates, scent gland plates of abdominal segments III-IV, IV-V, V-VI, VI-VII, femora, tibiae, and tarsi pale brown; antennal segments

III, IV; abdomen, and mesial line of pro-, meso-, and metanotum whitish-yellow; eyes red-brown. Rostrum reaching base of abdominal sternite II; scent gland openings of segments III-IV, and IV-V dark brown. Mesothoracic wing pads reaching base of abdominal segment I. Measurements ($n = 3$). Head length 0.3 ± 0.02 ; width through eyes 0.56 ± 0.01 ; interocular distance 0.48 ± 0.04 ; antennal segments: I 0.11 ± 0.01 , II 0.14 ± 0.02 , III 0.15 ± 0.01 , IV 0.23 ; rostral segments: I 0.21 , II 0.22 ± 0.01 , III 0.22 ± 0.01 , IV 0.24 ± 0.01 ; pronotum length 0.35 ± 0.01 ; width across anterior margin 0.63 ± 0.01 ; width across humeral angles 1.08 ± 0.02 ; length fore femur 0.34 ± 0.02 ; length fore tibia 0.41 ± 0.02 ; length fore tarsi I 0.08 ± 0.01 , II 0.1 ± 0.01 .

Fifth instar (Fig. 6): Ovoid, very similar to fourth instar, with dorsum slightly convex, mesothoracic wing pads reaching middle area of abdominal segment III. Head with 4 setigerous punctures, located one in front each eye, and one on each jugum. Rostrum reaching metasternum. Measurements ($n = 3$). Body length 2.22 ± 0.07 ; head length 0.33 ± 0.05 ; width through eyes 0.67 ± 0.02 ; interocular distance 0.51 antennal segments: I 0.13 ± 0.03 , II 0.25 ± 0.02 , III 0.23 ± 0.02 , IV 0.27 ± 0.05 ; rostral segments: I 0.31 ± 0.04 , II 0.34 ± 0.04 , III 0.26 ± 0.06 , IV 0.22 ± 0.01 ; pronotum length 0.53 ± 0.04 ; width across anterior margin 0.77 ± 0.04 ; width across humeral angles 0.84 ± 0.01 ; length fore femur 0.58 ; length fore tibia 0.64 ± 0.04 ; length fore tarsi I 0.09 ± 0.02 , II 0.16 ± 0.02 .

Distribution

USA: Arizona, Texas; Mexico: Distrito Federal, Guerrero, Hidalgo, Jalisco, Puebla, Veracruz.

Material Examined

MEXICO: Veracruz, Tlaltetela, 5 Km. NE Tlaltetela, Ejido Monte Blanco, 828 m, 19-II-2009, N $19^{\circ} 18' 44''$ W $96^{\circ} 50' 53''$, L. Cervantes, under rocks, 9 first instar nymphs, 4 second instar, 5 third instar, 3 fourth instar, 3 fifth instar, and 4 ♀. Same locality, but: 24-IV-2010, M. López, 7 ♂ and 14 ♀. Same locality, but: VI-2010, L. Cervantes, M. Lopez, 3 ♀. Same locality, but: 12-IV-2011, L. Cervantes, M. Lopez 4 ♀, 10 ♂ (from the adults collected on this date, we obtained the following from the laboratory colony: 16 first instar nymphs, 7 second instars, 10 fifth instars, 16 adults (7 ♀, and 9 ♂).

Behavior in the Field

During 2009, 3 nests were found under small flat rocks. In one nest one female and several third, fourth and fifth instar nymphs were found

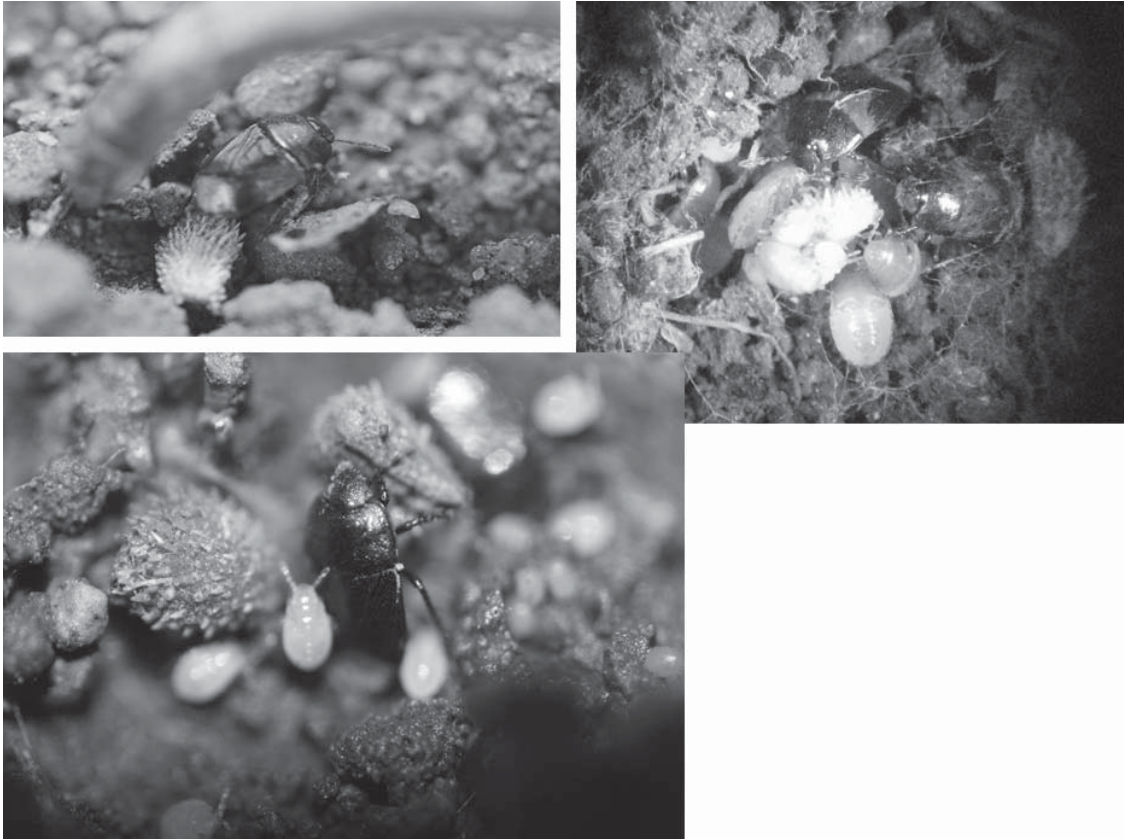
with around 16 seeds of *R. scabra* (Fig. 8). In another nest 2 females with 5 seeds were located, and in the last nest one female and 6 singly-laid eggs were found. In Apr 2010, 14 females and 7 males were collected individually; they were only collected under rocks but no nests were found. In Jun 2010, 3 females and 12 nymphs of third and fifth instar were collected under a rock with a few seeds of *R. scabra*. In Apr 2011, 4 females and 10 males were collected scattered in the area, none formed a nest.

The fact that only females were located in nests in the field suggests that the males do not play a role in the seed-carrying behavior. The bugs always were found less than 50 cm from a patch of their host plant, and they rarely were seen above ground. Nests always were found in a small hole under a flat rock at sites with good drainage but not very dry. Bugs only were found between Feb and Jun, depending on the presence of the host plant. The area has a very long dry season between Oct and Apr and not many bugs have been found during this dry period. However, lime (*Citrus × latifolia* Tanaka; Rutaceae) plantations have been introduced recently to the area and special irrigation systems allow the host plant to be present yr round, so it is probable that the bugs will also be present yr round. Ants were abundant on most of the sites, and bugs were located only where there were no ants.

Behavior in the Laboratory

Insects collected in 2009 did not mate or lay eggs. However, the bugs from 2010 and 2011 started to produce eggs a few days after collection. Eggs were laid in small holes dug out by the bugs, usually situated near the walls of the Petri dishes (Fig. 11). Eggs were laid individually, not in a mass, but usually very close together and between 10 and 30 eggs per hole. Only females were observed, usually at night, relocating the 3 seeds (Fig. 10) we had placed in the Petri dish from the center of the Petri dish to the holes. Around 6 days after the eggs were laid, first instar nymphs hatched. Then the mother started to move more seeds to the hole and the nymphs started to feed immediately; there were usually 2 to 4 seeds at one time in each hole (Fig. 11). Old seeds were not removed by the authors from the Petri dishes, unless they had fungi, but sometimes the bugs moved to new holes and females provided the nymphs with fresh seeds (Fig. 12). On 2 occasions more eggs were deposited while nymphs were in the third instar, 2 on one occasion and 3 on the other. These were considered to be non-viable eggs because they did not develop.

From the nymphs reared in the laboratory, first instar nymphs molted to the second instar in 4 or 5 days; second instar lasted 7 days; third instars 5 days; fourth instars 4 or 5 days, and fifth



Figs. 10-12. Adults and nymphs of *Melanaethus crenatus*. 10. Female moving seed of *R. scabra* in the field. 11. Bug nest in the laboratory. 12. Adults and nymphs feeding on scattered seeds in the laboratory.

instars molt to the adult stage after 5 days. So the life cycle was completed in 23 to 25 days. Not all the nymphs from the same clutch developed at the same time, so there were nymphs of several different instars feeding on the seeds, sometimes covering the whole seed and forming a mass of nymphs with the seed in the center. Male and female parents were usually in the hole with the nymphs or nearby. When Petri dishes were opened the adults and nymphs start to move immediately and disperse away from the seeds.

Males sometimes hid under the moist cotton ball or also dug out small holes, but sometimes also were found in the same hole with the nymphs. No males were observed moving seeds to the nests.

DISCUSSION

This is the first record of a species of Cydinae in which the females carry seeds to the area where they deposited their eggs and where the nymphs are aggregated. These observations in the field and laboratory may suggest that some

of the behaviors shown by *M. crenatus* represent behaviors exhibited by the Sehirinae and Parastrachidae mentioned above and could be an evolutionary stage between the nonparental and the truly parental behaviors in the Heteroptera.

Detailed studies are needed to quantify the exact number of eggs produced by the females, the number of seeds that are carried and their frequency, as well as many other characteristics which can vary depending on the abundance of the host plant, predators, time of day, or weather conditions. However with regard to an insect species that passes much of its life below ground, it is difficult to observe and quantify activities without disturbing the eggs, nymphs and adults.

At the moment, some conclusions can be made. *Melanaethus crenatus* differs from the 5 species of burrowing bugs that have extended parental behavior in the way the eggs are laid, since all the 5 listed species deposit the eggs in masses, while *M. crenatus* deposits the eggs individually; also the *M. crenatus* female does not exactly sit on top of the eggs guarding them. *Melanaethus crenatus* females protect entire nests, which

are already somewhat protected by a rock. It is known that other species of cydnids that do not have this guarding behavior, such as *Adrisa magna* Uhler, move seeds to their shelters. In *A. magna* males and nymphs moved the seeds in addition to the females (Takeuchi & Tamura 2000). This kind of behavior is known in species of Hemiptera with aggregated behavior.

Apparently the females forage for seeds during night. As in the other species of bugs, the seeds of the host plant of *M. crenatus* are sometimes bigger than the adult female, but they still managed to move them to their nests. Distances from the host plant to the nest are usually short for *M. crenatus* (less than 50 cm). *Parastrachia japonensis* Scott is known to search for seeds that are 12 m or more away from the nest (Nomakuchi et al. 1998). Two facts suggest that the males do not play a role in the provisioning and defending of nymphs; first, only females were located in nests in the field, and in the laboratory only females were observed moving the seeds to the nests.

The species of Cydnidae and Parastrachidae that exhibit progressive provisioning feed on seeds of members of the Lamiales, Santalales, and Gentianales, all of which are related groups within the Asteranae. *Adomerus variegatus* (Signoret) feeds on Rosales, which belongs to the Rosanae, which is considered to be a sister group of Asteranae (Chase & Reveal 2009; Stuessy 2010). A close host plant relationship is common for some other groups of Hemiptera and could explain their feeding evolution.

Sehirus cinctus cinctus feeds on several species of mint (Lamiaceae), including *Monarda punctata* L., *Perilla frutescens* (L.) Britto, *Teucrium canadense* L., *Lamium amplexicaule* L., and *Lamium purpureum* L. (Labiatae) (Sites & McPherson 1982; Agrawal et al. 2004); *Adomerus triguttulus* have been collected on *Lamium album* L. and *Lamium purpureum* (Kudo et al. 2006); *Adomerus variegatus* feeds solely on *Ulmus davidiana* var. *japonica* (Rehder) Nakai (Ulmaceae) (Mukai et al. 2010); *Canthophorus niveimarginatus* feeds on *Thesium chinense* Turcz. (Santalaceae) (Filippi et al. 2009); *Parastrachia japonensis* feeds on *Schoepfia jasminodora* Siebold and Zucc. (Schoepfiaceae) (Tachikawa & Schaefer 1985); and the main species in this study, *Melanaethus crenatus* feeds on *R. scabra* (Rubiaceae).

It is probable that because most of the species of Cydnidae have an underground life style, this kind of behavior has rarely been observed. Although just a few observations have been made for *M. crenatus*, some other species of *Melanaethus* have been found aggregated underneath rocks all around Mexico, so it is probable that this kind of conduct will be more commonly reported in the group.

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REFERENCES CITED

- AGRAWAL, A. F., JEREMY, J. M., AND BRODIE, E. D. 2004. On the social structure of offspring rearing in the burrower bug *Sehirus cinctus* (Hemiptera: Cydnidae). Behav. Ecol. Sociobiol. 57: 139-148.
- AGRAWAL, A. F., COMBS, N., AND BRODIE, E. D. 2005. Insights into the cost of complex maternal care behavior in the burrower bug (*Sehirus cinctus*). Behav. Ecol. Sociobiol. 57: 566-574.
- BABA, N., HIRONAKA, M., HOSOKAWA, T., MUKAI, H., NOMAKUCHI, S., AND UENO, T. 2011. Trophic eggs compensate for poor offspring feeding capacity in a subsocial burrower bug. Biol. Letters 7: 194-196.
- CHASE, M., AND REVEAL, J. L. 2009. A phylogenetic classification of the land plants to accompany APG III. Bot. J. Linnean Soc. 161: 122-127.
- FILIPPI, L. T., NOMAKUCHI, S., AND TOJO, S. 1995a. Habitat selection, distribution, and abundance of *Parastrachia japonensis* (Hemiptera: Cydnidae) and its host tree. Ann. Entomol. Soc. America 88(4): 456-464.
- FILIPPI, L. T., NOMAKUCHI, S., KUKI, K., AND TOJO, S. 1995b. Adaptiveness of parental care in *Parastrachia japonensis* (Hemiptera: Cydnidae). Ann. Entomol. Soc. America 88(3): 374-383.
- FILIPPI, L. T., NOMAKUCHI, S., HIRONAKA, M., AND TOJO, S. 2000a. Insemination success discrepancy between long-term and short-term copulations in the provisioning shield bug, *Parastrachia japonensis* (Hemiptera: Cydnidae). J. Ethol. 18: 29-36.
- FILIPPI, L. T., HIRONAKA, M., NOMAKUCHI, V., AND TOJO, S. 2000b. Provisioned *Parastrachia japonensis* (Hemiptera: Cydnidae) nymphs gain access to food and protection from predators. Animal Behav. 60: 757-763.
- FILIPPI, L. T., HIRONAKA, M., AND NOMAKUCHI, S. 2001. A review of the ecological parameters and implications of subsociality in *Parastrachia japonensis* (Hemiptera: Cydnidae), a semelparous species that specializes on a poor resource. Popul. Ecol. 43: 41-50.
- FILIPPI, L. T., HIRONAKA, M., AND NOMAKUCHI, S. 2002. Risk-sensitive decisions during nesting may increase maternal provisioning capacity in the subsocial shield bug *Parastrachia japonensis*. Ecol. Entomol. 27: 152-162.
- FILIPPI, L. T., HIRONAKA, M., AND NOMAKUCHI, S. 2005. Kleptoparasitism and the effect of nest location in a subsocial shield bug *Parastrachia japonensis* (Hemiptera: Parastrachidae). Ann. Entomol. Soc. America 98(1): 134-142.
- FILIPPI, L. T., BABA, N., INADOMI, K., YANAGI, T., HIRONAKA, M., AND NOMAKUCHI, S. 2009. Pre- and post-hatch trophic egg production in the subsocial burrower bug, *Canthophorus niveimarginatus* (Heteroptera: Cydnidae). Naturwissenschaften 96: 201-211.

- FROESCHNER, R. C. 1960. Cydnidae of the Western Hemisphere. Proc. U.S. Natl. Mus. 111: 337-680.
- HIRONAKA, M., NOMAKUCHI, S., IWAKUMA, S., AND FILIPPI, L. 2005. Trophic egg production in a subsocial bug, *Parastrachia japonensis* (Hemiptera: Parastrachidae), and its functional value. Ethology 111: 1089-1102.
- HIRONAKA, M., TOJO, S., AND HARIYAMA, T. 2007a. Light compass in the provisioning navigation of the subsocial bug, *Parastrachia japonensis* (Heteroptera: Parastrachidae). Appl. Entomol. Zool. 42(3): 473-478.
- HIRONAKA, M., FILIPPI, L., NOMAKUCHI, S., HORIGUCHI, H., AND HARIYAMA, T. 2007b. Hierarchical use of chemical marking and path integration in the homing trip of a subsocial bug. Animal Behav. 73: 739-745.
- HIRONAKA, M., TOJO, S., NOMAKUCHI, S., FILIPPI, L., AND HARIYAMA, T. 2007c. Round-the-clock homing behavior of a subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Parastrachidae), using path integration. Zool. Sci. 24: 535-541.
- KUDO, S., AND NAKAHIRA, T. 2004. Effects of trophic-egg on offspring performance and rivalry in a sub-social bug. Oikos 107: 28-35.
- KUDO, S., AND NAKAHIRA, T. 2005. Trophic-egg production in a sub-social bug: plasticity in response to resource conditions. Oikos 111: 459-464.
- KUDO, S., NAKAHIRA, T., AND SAITO, Y. 2006. Morphology of trophic eggs and ovarian dynamics in the subsocial bug *Adomerus triguttulus* (Heteroptera: Cydnidae). Canadian J. Zool. 84: 723-728.
- MAYORGA, C. 2002. Revision generica de la familia Cydnidae (Hemiptera-Heteroptera) en México, con un listado de las especies conocidas. An. Inst. Biol. Univer. Nacional Autonoma de Mexico. Serie Zool. 73(2): 157-192.
- MUKAI, H., HIRONAKA, M., BABA, N., YANAGI, T., INADOMI, K., FILIPPI, L., AND NOMAKUCHI, S. 2010. Maternal-care behaviour in *Adomerus variegatus* (Hemiptera: Cydnidae). Canadian Entomol. 142(1): 52-56.
- NAKAHIRA, T., AND KUDO, S. 2008. Maternal care in the burrower bug *Adomerus triguttulus*: defensive behavior. J. Insect Behav. 21: 306-316.
- NOMAKUCHI, S., FILIPPI, L., AND TOJO, S. 1998. Selective foraging behavior in nest-provisioning females of *Parastrachia japonensis* (Hemiptera: Cydnidae): cues for preferred food. J. Insect Behav. 11(5): 605-619.
- RZEDOWSKI, G. C., AND RZEDOWSKI, J. 2001. Flora fanerogamica del Valle de Mexico. 2a ed. Instituto de Ecologia y Comision Nacional para el Conocimiento y Uso de la Biodiversidad. Patzcuaro, Michoacan, Mexico. 1406 pp.
- SITES, R. W., AND MCPHERSON, J. E. 1982. Life history and laboratory rearing of *Sehirus cinctus cinctus* (Hemiptera: Cydnidae), with description of immature stages. Ann. Entomol. Soc. America 75: 210-215.
- STUESSY, T. F. 2010. Paraphyly and the origin and classification of angiosperms. Taxon 59(3): 689-693.
- TACHIKAWA, S., AND SCHAEFER, C. W. 1985. Biology of *Parastrachia japonensis* (Hemiptera: Pentatomoidae: ?-idea). Ann. Entomol. Soc. America 78: 387-397.
- TAKEUCHI, M., AND TAMURA, M. 2000. Seed-carrying behavior of a stink bug, *Adrisa magna* Uhler (Hemiptera: Cydnidae). J. Ethol. 18: 141-143.
- TALLAMY, D. W., AND SCHAEFER, C. 1997. Maternal Care in the Hemiptera: ancestry, alternatives, and current adaptive value, pp. 94-115 In J. C. Choe and B. J. Crespi [eds.], The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge, UK.
- TOJO, S., NAGASE, Y., AND FILIPPI, L. 2005. Reduction of respiration rates by forming aggregations in diapausing adults of the shield bug *Parastrachia japonensis*. J. Insect Physiol. 51: 1075-1082.
- TSUKAMOTO, L., AND TOJO, S. 1992. A report of progressive provisioning in a stink bug, *Parastrachia japonensis* (Hemiptera: Cydnidae). J. Ethol. 10: 21-29.
- TSUKAMOTO, L., KUKI, K., AND TOJO, S. 1994. Mating tactics and constraints in the gregarious insect *Parastrachia japonensis* (Hemiptera: Cydnidae). Ann. Entomol. Soc. America 87(6): 962-971.
- VILLASEÑOR, R. J. L., AND ESPINOSA, F. J. G. 1998. Catalogo de malezas de Mexico. Universidad Nacional Autonoma de Mexico. Consejo Nacional Consultivo Fitosanitario. Fondo de Cultura Economica. Mexico, D.F. 449 pp.