ANNUAL MIGRATIONS AND SPAWNING OF *COENOBITA CLYPEATUS* (HERBST) ON MONA ISLAND (PUERTO RICO) AND NOTES ON INLAND CRUSTACEANS

BY

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ABSTRACT

Annual migrations and spawning for the common land hermit crab, *Coenobita clypeatus* in Playa Sardinera and possibly in Uvero, Mona Island, occur in August or early September. Spawning corresponds to the crescent moon in the lunar cycle.

RESUMEN

Las migraciones anuales y desove del cangrejo ermitaño terrestre común, *Coenobita clypeatus* en Playa Sardinera y posiblemente en Uvero, Isla de Mona, ocurren en agosto o principios de septiembre. El desove corresponde al cuarto creciente en el ciclo lunar.

INTRODUCTION

The soldier crab or common land hermit crab, *Coenobita clypeatus* (Herbst, 1791) (Decapoda, Coenobitidae) is widely distributed in the xeric habitats of Mona Island (Puerto Rico), but it is mostly concentrated in the more humid habitats of the island, for example, in the coastal plain forest, in the caves, and in "bajuras" (natural depressions similar to sinkholes). *Coenobita clypeatus* is active during the day and night hours, except during the periods of drought when it typically remains hidden in holes, cracks, or accumulated debris. The diet of *C. clypeatus* of Mona Island consists mostly of the feces of the Mona Island ground iguana, *Cyclura stejnegeri* Barbour & Noble, 1916 (or *Cyclura cornuta stejnegeri* Barbour

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& Noble, 1916) (Schwartz & Carey, 1977; Wiewandt, 1977). Grubb (1971) and Alexander (1979) found that the tawny hermit crab, *Coenobita rugosus* H. Milne Edwards, 1837 depends for food on the droppings of the giant tortoise of Aldabra, *Dipsochelys dussumieri* (Gray, 1831). The reason why these feces are so attractive to *Coenobita* spp. is because they are already partially degraded and have a high caloric content (Wiewandt, 1975, 1977). Also, *C. clypeatus* have been observed climbing trees (vertical migration) to a height of 3 m in order to obtain tender pieces of plant cortex, bark, and branches, similar to the observations by Glynn (1964) for *C. clypeatus* on the Puerto Rico mainland and Barnes (1997) for the land hermit crab *Coenobita cavipes* Stimpson, 1858 and *C. rugosus* of Quirimba Island, Mozambique. Similarly, Dansforth (1926) reported to have seen hermit crabs climbing southern cattail *Typha domingensis* Persoon, 1807 with the same purpose, to obtain food or to escape predators, at Cartagena Lagoon in Lajas, southwestern Puerto Rico.

During the last year (1995) of a mycological study for his master's degree in Mona Island, one of us (ÁMNR) became interested in the geographical distribution and diverse ecological aspects of the terrestrial decapods of this island. Early studies and surveys of the terrestrial decapods of Puerto Rico with special reference to *C. clypeatus* were performed by Stahl (1883), Gundlach (1887), Schmitt (1935), Chace (1954), Glynn (1964), Chace & Hobbs (1969), Erdman (1973), Vélez (1967), and Wiewandt (1975). The annual migrations of *C. clypeatus* are of particular scientific and social interest, and are known in Spanish by the local fishermen as the "cobada". Seemingly, these migrations occur in limited areas and periods of time during the summer in connection with lunar phases.

Provenzano (1962) studied the larval development of *C. clypeatus* by spawning several females in aquariums in August 1960-61 during the new moon. He raised larvae to juvenile crabs in 57 days. In Mona Island, however, Wiewandt (1975) found that the females of *C. clypeatus* actually spawned their embryos in August by the crescent moon on the following dates: 14 August 1964; 1 August 1971, and 15-17 August 1972 (table I). A great migration of about 10,000 *C. clypeatus* was reported by Wiewandt (1975) just north of the concrete jetty of Playa Sardinera during 16-17 August 1972; another migration was observed in Uvero on 15 August 1972. By the night of 16 August 1972, a total of 2,200 *C. clypeatus* were marked with a brilliant red paint to track their migrations (Wiewandt, 1975). The next day, the animals dispersed and three days later Wiewandt counted about 40 marked individuals along the cliff between the 'Jail' of Sardinera and the Portugués Well. The same day, the botanist Dr. Roy O. Woodbury sighted a few marked *C. clypeatus* on the plateau along the sidewalk of Los Caobos, the most distant about 150 m to the north of the radio towers (Wiewandt, 1975). Continuing with the census between the Portugués Well and the Jail (9 September 1972), Wiewandt

TABLE I

Observations on the phenology of the hermit crab, *Coenobita clypeatus* (Herbst, 1791) on Mona Island[1])

Dates	Remarks, references	Locality
14 Aug 1964	State of embryonic development indicates crabs would spawn soon (Erdman, 1973)	Unspecified (Playa Sardinera?)
1 Aug 1971	Migratory season (Erdman, 1973)	Unspecified (Playa Sardinera?)
15-17 Aug 1972	Migratory season (Wiewandt, 1975)	Sardinera; 0.65 m SE of Playa Uvero
6 Aug 1973	Conspicuous migration toward the coast forming notable aggregates (Wiewandt, 1975)	At the base in Sardinera and surroundings Cuesta Geña (= Doña Geña Hill, Uvero)
12 Aug 1973	Formation of aggregates (Wiewandt, 1975)	At the base of the slope in Sardinera
1-3 Sep 1973[2])	Migration (smaller aggregates than in 1972) (Wiewandt, 1975)	Playa Sardinera
2 Sep 1973	Emerging of thousands of hermit crabs in primary adult stages (Wiewandt, 1975)	Playa Sardinera
3-4 Sep 1973	Migration moving away from spawning sites (Wiewandt, 1975)	At the base of the slope in Sardinera
7 Aug 1974	Conspicuous movement of *C. clypeatus* adults down the hill (Wiewandt, 1975)	Cuesta Geña
Aug-Sep 1974	Aggregates are not comparable to those observed in 1972 and 1973 (Wiewandt, 1975)	SW of the coastal plain
14-16 Aug 1991	Migratory season and aggregates (Nieves-Rivera, unpubl. data)	Playa Sardinera
3 Aug 1992	Migratory season and aggregates (Nieves-Rivera, unpubl. data)	Playa Sardinera
18-20 Aug 1993	Migratory season and aggregates recorded in video (Álvarez, 1993; Hopgood, 1994)	Playa Sardinera
28-30 Aug 1995	Migration and occurrence of spawning at 06:00 h; by 07:00 h A.S.T. crabs started to move away from the spawning sites; the sand where spawning took place turned into an olive-green color because of high quantity of eggs in substrate (Nieves-Rivera, unpubl. data)	Playa Sardinera, two places of migration: (1) close to dock and (2) at the base of the slope, next to public restrooms to the beach; Cuesta Geña

[1])Modified from Wiewandt (1975).

[2])Güell et al. (1975) filmed the annual migration of *C. clypeatus* on video for the first time.

only found two *C. clypeatus* marked among 175 adults. By 11 October 1972, two visitors reported to Wiewandt a painted *C. clypeatus* in Las Carmelitas, 2.8 km north of Sardinera; by October 16th, a visitor sighted another marked *C. clypeatus* crossing the road to Uvero, 5 km southeast of Sardinera (Erdman, 1973; Wiewandt, 1975).

A year later, 13 August 1973, near the cliff next to Playa Sardinera, Wiewandt counted 19 marked shells of the thousands of *C. clypeatus* aggregated in this place. It was impossible to tell if they were the same crabs or other individuals who took marked shells. Of the thousands of crabs that he observed in Uvero by 3-4 September 1973, only one shell had the mark. Based on Wiewandt's (1975) observation, he was able to calculate the movement rate of the dispersed *C. clypeatus*, which was 170 to 300 m/day. On two subsequent occasions, several visitors informed Wiewandt of marked *C. clypeatus* in the Bajura de los Cerezos (at the center of the island). From his calculations, Wiewandt suggested that *C. clypeatus* would take about one or two months traveling from the Bajura de los Cerezos to Playa Sardinera. In 1995, two mature *C. clypeatus* with reddish marks on their shells were observed in Sardinera, and a third, abandoned shell was collected near the PRDNER (Puerto Rico Department of Natural and Environmental Resources) kitchen (Nieves-Rivera, unpubl. data). The present study documents observations on the migrations and spawning of *C. clypeatus* on Mona Island, Puerto Rico.

MATERIALS AND METHODS

The study areas (fig. 1A) are located on the beaches known as Playa Sardinera (18°05′18″N 67°56′20″W; fig. 1B) and Uvero (18°03′37″N 67°54′22″W; fig. 1C), which are narrow coastal lands, enlarged to a maximum width of 1 km to the west and southwest of Mona Island, protected by coral reefs and sand banks. A detailed description of the coastal geomorphology of Mona Island appears in Kaye (1959), Hernández-Ávila (1970), Briggs & Seiders (1972), Taggart (1992), and González et al. (1997), the flora of the coastal plain was reported on by Woodbury et al. (1977), and this vegetation was studied ecologically by Cintrón & Rogers (1991). The methodology used for this study follows Wiewandt (1975), and basically consisted in the observation and registration by means of photography and videos of the migration of *C. clypeatus*. Behavior of migrating females inland was observed by using flashlights. Also, the literature and the previous audiovisual records were used as an alternating source and ÁMNR observations per se as a direct source during the migrations of 1991, 1992, and 1995.

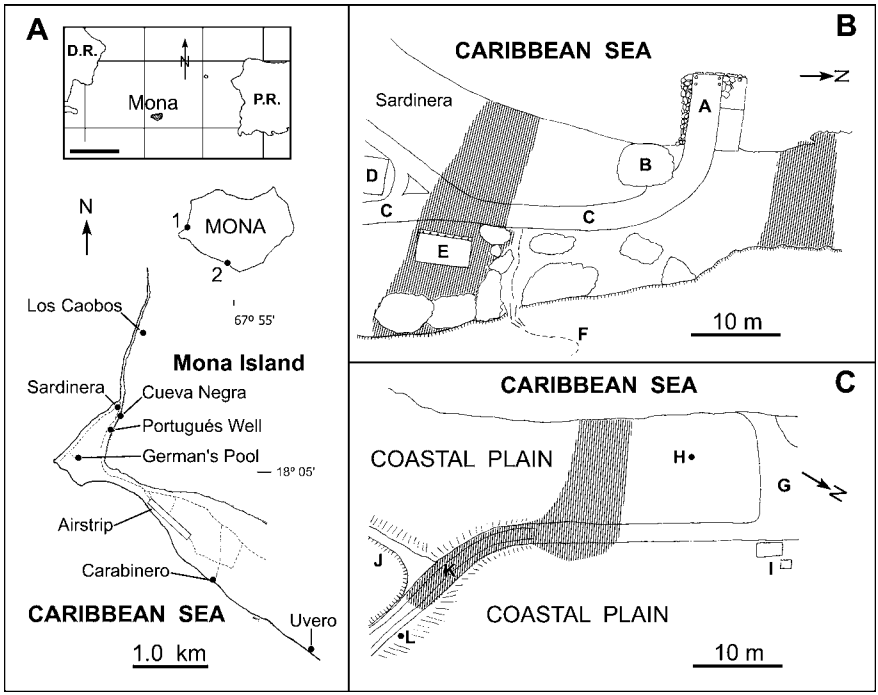

Fig. 1. A, Map of the study areas, including: B, Playa Sardinera; and C, Uvero beach, Mona Island, where the annual migrations of *Coenobita clypeatus* (Herbst, 1791) occurred (1991, 1992, and 1995). Shadowed areas are the place where most *C. clypeatus* aggregated during annual migrations and spawning. Insert in A is the general location of Mona Island (1, Playa Sardinera; 2, Uvero); D.R., Dominican Republic; P.R., Puerto Rico; scale bar = 45 km. In smaller font: A, Sardinera's dock; B, El Peñón; C, Camino Sardinera; D, Ranger's Headquarter (PRDNER); E, public bathrooms; F, Los Caobos trail; G, Uvero; H, tomb of Tomás Andújar Rodríguez; I, Uvero's well; J, Geña's Cave; K, Geña's Slope; L, tomb of Sgt. José A. Caraballo.

RESULTS AND DISCUSSION

The following field notes (Nieves-Rivera, unpubl. data) are based on observations of the annual migration of *Coenobita clypeatus* by ÁMNR in August 1995:

"Land Hermit Crabs [*C. clypeatus*] took three consecutive days for completing the "washing of eggs" [spawning], interrupted by the daylight hours, during August 28-30, 1995. However, I suspect that these migrations take about three to four days to complete. The hours of the migrations were similar in previous observations, near the midnight (23:00-24:00 h A.S.T. = Atlantic Standard Time). During this season (1995), I observed that at 03:00 h, the hermit crabs had not reached the coast area. While they descended to the bank, they formed what I called a "tongue". By "tongue" I mean the silhouette formed by the hermit crabs. It was 04:30-05:00 h when the hermit crabs reached the seawater [figs. 2A-B]. The crabs entered to the water to a maximum depth of 60 cm, maybe swept by the surf. At 06:00 h, massive spawning ("washing of eggs") took place. The eggs were liberated quickly once in contact with the seawater. The concentration of eggs in the local area, caused a much reduced portion (or a small patch) of the sand turned to a very pale olive-greenish color. Half hour later, the crabs began to retreat from the 'washing of eggs' areas."

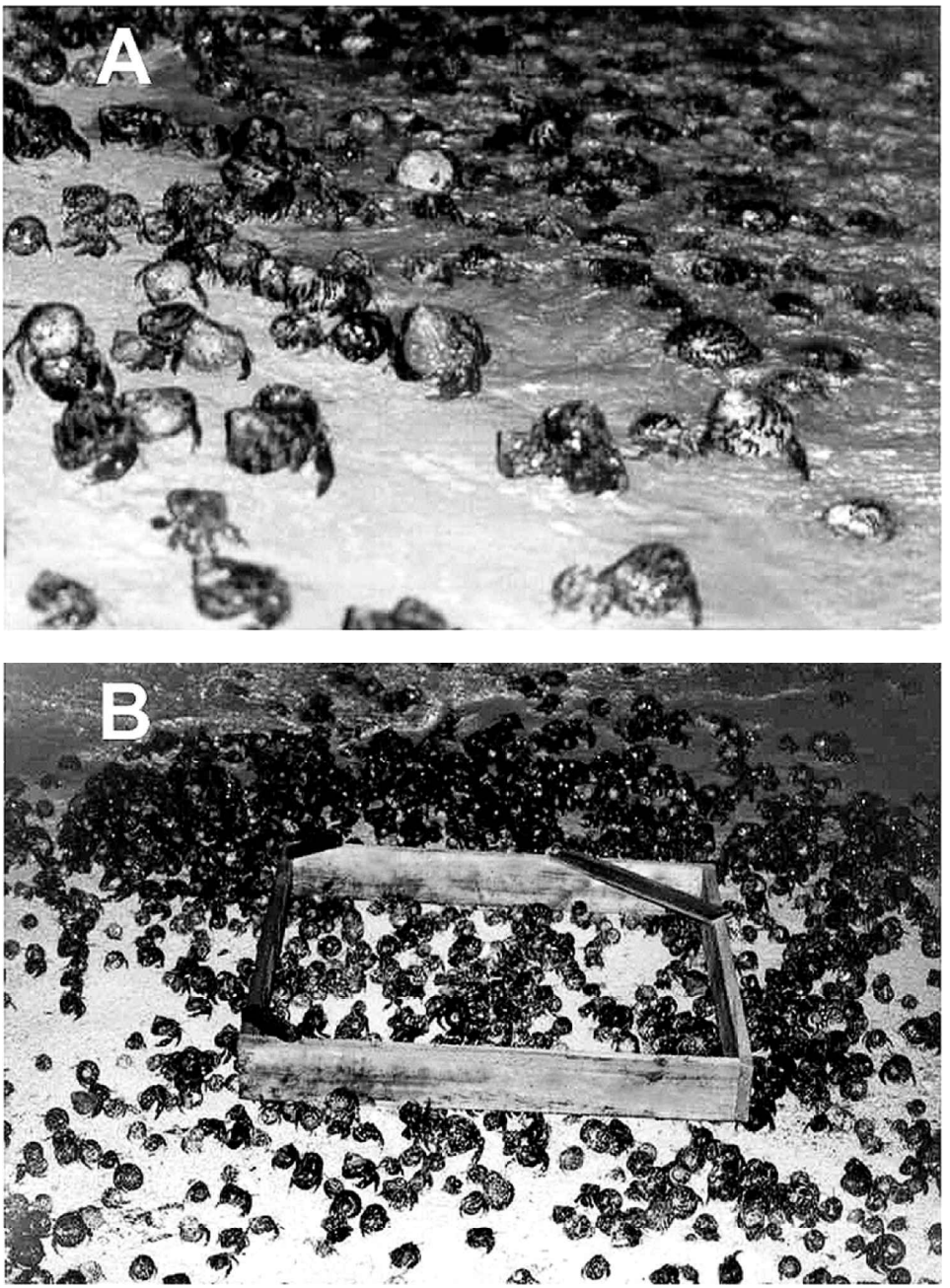

Fig. 2. A-B, Annual migration or "cobada" of *Coenobita clypeatus* (Herbst, 1791) in August 1991, next to the dock of Playa Sardinera, Mona Island, Puerto Rico. (Photos by Miguel A. Nieves, PRDNER).

At Christmas Island, in the Indian Ocean, a similar migration of the red land crab *Gecarcoidea natalis* (Pocock, 1888) occurs. *Gecarcoidea natalis* is one of the most abundant species of terrestrial crabs on this island. During the 18 days that the migration lasts before the spawning, Hicks (1985) estimated the *G. natalis* traveled inland at the rate of 200 m/h. Likewise, Hicks (1985) estimated the total biomass for these crustaceans at 8.0×10^{-1} metric tons per hectare.

In synchrony with the lunar cycle and tides, *C. clypeatus* travels many meters to spawn in the sea, a similar procedure as practiced by *G. natalis*. The season of migration and spawning of *C. clypeatus* in Playas Sardinera (fig. 1B) and Uvero (fig. 1C), corresponds to August or early September. This happens when the moon phase is close to crescent moon (lunar cycle). The results of this study agree with the previous observations of Provenzano (1962), Erdman (1973), and Wiewandt (1975), in which the migrations occur in August or early September in connection with the lunar cycle and the tides. However, Provenzano reported that the spawning occurred during the new moon, while Erdman and Wiewandt considered that it usually occurred during the crescent moon. Most recorded spawnings of *C. clypeatus* on Mona Island occurred during the crescent moon.

Along Mona's northern periphery, the existence of vertical cliffs and the absence of beaches impede the possibilities for *C. clypeatus* to spawn. Obviously, the routes taken by *C. clypeatus* reflect the pattern of the topography of the island. *Coenobita clypeatus* reach the southwestern plateau and descend to the sand bank, and they go to the northwest or southeast toward the points where the cliff unites with the ocean. In these sites, the animals congregate in aggregates of thousands of individuals and later they spawn "en masse" during a period of three or four days. The southeast and the south-central coastal areas of Mona are topographically broken into fragments and the migratory patterns on the beaches have not yet been examined. Spawning occurs in narrow areas on the beach and it requires less than five minutes per individual. *Coenobita clypeatus* are shy and usually retreat off the water when disturbed (Wiewandt, 1975).

Two obvious reasons for *C. clypeatus* to prefer the night or morning hours to migrate and spawn are (1) avoiding the intense heat of the day and (2) avoiding egg predators. This preference was confirmed by the daily retreat to shady areas until the night or dawn, when the spawning continues. The orientation mechanisms involved in the extensive migrations of crustaceans have not yet been studied in detail. Some researchers have suggested potential mechanisms to explain this phenomenon, for instance, magnetism, polarized light, brightness of the horizon on the sea, tide cycles, aeolian conditions including celestial events, or a combination of some or all of these factors (Wolcott, 1988).

After hatching, young *C. clypeatus* must find a refuge, usually an empty shell, for protection. *Coenobita clypeatus* pick up shells at sea when juvenile and on

land when adult. Although there are a wide variety of gastropod shells that may serve as protection, the most commonly used shells on Mona are those of the Mona Island cerion (*Cerion monaense* Clench, 1950; cf. Clench, 1950), the West Indian top-shell (*Cittarium pica* Linnaeus, 1758), the nerite (*Nerita* spp., usually the tessellated nerite, *N. tessellata* Gmelin, 1791), and the beaded periwinkle *Tectarius muricatus* (Linnaeus, 1758) (cf. Wiewandt, 1975). *Coenobita clypeatus* is the species most responsible for dragging the shells of marine gastropods inland, with the exception of humans. Also, when *C. clypeatus* abandon shells, these can be filled with rainwater, if being left in a favorable position, thus providing a drinking trough for some animals and a place for reproduction to others, examples of the latter are mosquitoes and other dipterans of which the larvae need fresh water to thrive.

Although *C. clypeatus* is apparently abundant on Mona Island, this organism has been overexploited. Many mature *C. clypeatus* have been removed off Mona Island and were sold as pets in Puerto Rico. They are also used as fishing bait. This has caused a drastic reduction of the population as exemplified by the almost extinguished population of *C. clypeatus* of Desecheo Island. Individuals of *C. clypeatus* no longer attain the normal or large adult size on the main island of Puerto Rico. This seems primarily due to the lack of large mollusk shells (e.g., *Cittarium pica*), but is also caused by humans removing adult *C. clypeatus* specimens as well as large mollusk shells.

NOTES ON INLAND CRUSTACEANS OF MONA ISLAND

Terrestrial crustaceans. — Mona Island sustains a population of five terrestrial crustaceans (including *C. clypeatus*), which are observed mostly in the coastal plain forest, on the sandy beaches, and in the 'bajuras' and caves: the great land crab, *Cardisoma guanhumi* Latreille, 1825, the Cariba, Mona, or black land crab, *Gecarcinus lateralis* (Fréminville, 1835), the mountain or red crab, *Gecarcinus ruricola* (Linnaeus, 1758), and the ghost crab *Ocypode quadrata* (Fabricius, 1787) (cf. Wiewandt, 1975; Smith & Wier, 1999). Of these, *G. ruricola* is also present on Monito Island (Wiewandt, 1975; Nieves-Rivera, unpubl. data). *Gecarcinus lateralis* and *G. ruricola* serve as a main food source for the yellow-crowned night-heron, *Nycticorax violaceus* (Linnaeus, 1758) (cf. Wiewandt, 1975), which can ingest about 10 *G. lateralis* per day (Wolcott, 1988). *Cardisoma guanhumi* commonly inhabits holes located on land next to the margin of the swamp community and reaches places at considerable distances inland. Feliciano (1962) and Rojas (1978, 1981) studied the biology and the importance of *C. guanhumi* as a nutritious source of human food in Puerto Rico in further detail.

Aquatic crustaceans. — The microcrustacean fauna of Mona Island has been well studied in fresh water (Van Name, 1936; Hobbs et al., 1977; Peck & Kukalova-Peck, 1981; Peck, 1994; Smith & Wier, 1999; Santos-Flores, 2001) and poorly studied in marine habitats (Nieves-Rivera et al., 2003). Recent collections (Nieves-Rivera & Santos-Flores, unpubl. data) have produced a few new records for Mona Island. We have collected the anostracan *Streptocephalus antillensis* Mattox, 1950 (cf. Mattox, 1950) and the Platyhelminthes *Mesostoma* cf. *georgianum* Darlington, 1959 and *M. tubiseminalis* Smith, 1998 (cf. Smith, 1998) in rainwater pools at Corral de los Indios (close to the lighthouse) and Caigo o no caigo (Nieves-Rivera & Santos-Flores, unpubl. data). A few specimens of the notostracan *Triops*, probably *Triops* cf. *longicaudatus* (LeConte, 1846) have been seen in rainwater ponds formed on the plateau on the way to Cueva Espinar (Cabo Barrionuevo) (Nieves-Rivera, unpubl. data). A limited limnofauna such as the cladocerans *Biapertura* (*Alonella*) *karua* (King, 1853), *Ceriodaphnia rigaudi* Richard, 1894, *C. cornuta* G. O. Sars, 1885 s. str., *Paralona pigra* (G. O. Sars, 1862), and *Chydorus* sp. (cf. Santos-Flores, 2001), have been detected in Charca de las Tilapias, a small brackish pond dominated by a small grove of red mangrove, *Rhizophora mangle* Linnaeus, 1753, white mangrove *Laguncularia racemosa* (Linnaeus) Gaertn., 1805, and by manchioneel or "manzanillo" *Hippomane mancinella* Linnaeus, 1753, next to Playa Mujeres, in the coastal plain forest. A few cyclopoid copepods have been isolated from bromeliads (a habitat termed phytotelmata) in the plateau on the way to the lighthouse (Santos-Flores, pers. comm.). Other invertebrates that share their habitat with aquatic crustaceans in Charca de las Tilapias include rotifers *Colurella* sp., *Lecane* sp., and *Philodina* sp., ciliates *Balladyna* sp., *Metopus* sp., *Tetrahymena* sp., *Uronema* sp., and *Vorticella* sp., euglenoids *Anisonema* sp., *Euglena* sp., and *Phacus* sp., a gastrotrich *Ichthydium* sp., and an annelid *Dero* sp. Neither the decapod malacostracan *Typhlatya monae* Chace, 1954 (cf. Chace, 1954), the subterranean shrimp *Macrobrachium faustinum* (De Saussure, 1857) var. (cf. Smith & Wier, 1999), nor the branchiopod *Eulimnadia* sp. (*E.* cf. *texana* (Packard, 1852)) (Smith & Wier, 1999), all reported earlier according to the authorities cited, were found by the authors of this survey.

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REFERENCES

ALEXANDER, H. G. L., 1979. A preliminary assessment of the role of the terrestrial decapod crustaceans in the Aldabran ecosystem. Phil. Trans. Roy. Soc., London, (B) **286**: 247-254.

ÁLVAREZ, R., 1993. La cobada. Centro de Diseño y Producción de Recursos Institucionales (CEDPRI), Universidad de Puerto Rico, Humacao, Puerto Rico. (VHS-video, color, approx. 13 min.).

BARNES, D. K. A., 1997. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: vertical migrations (tree climbing). Mar. Ecol. Progr. Ser., **158**: 233-240.

BRIGGS, R. P. & V. M. SEIDERS, 1972. Geologic map of the Isla de Mona quadrangle, Puerto Rico. Miscellaneous Geological Investigations, U.S. Geological Survey, Map **I-718**.

CHACE, F. A., JR., 1954. Two new subterranean shrimps (Decapoda: Caridea) from Florida and the West Indies, with a revised key to the American species. Journ. Washington Acad. Sci., **44**: 318-324.

CHACE, F. A., JR. & H. H. HOBBS, JR., 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. U.S. natl. Mus. Bull., **292**: 1-258.

CINTRÓN, B. & J. L. ROGERS, 1991. Plant communities of Mona Island. Acta Científica, **5**: 10-64.

CLENCH, W. J., 1950. Land shells of Mona Island, Puerto Rico. Journ. Conchol., **90**: 269-276, 1 pl.

DANSFORTH, S. T., 1926. An ecological study of Cartagena Lagoon, Porto Rico, with special reference to the birds. Journ. Dept. Agric. Puerto Rico, **10**: 1-135.

ERDMAN, D. S., 1973. Mona Island terrestrial crustaceans. In: JUNTA DE CALIDAD AMBIENTAL (ed.), Mona and Monito Islands: an assessment of their natural and historical resources, **2**, (Appendix H): 1-2. (Office of the Governor, San Juan, Puerto Rico).

FELICIANO, C., 1962. Notes on the biology and economic importance of the land crab *Cardisoma guanhumi* Latreille of Puerto Rico: 1-29, figs. 1-12. (Special Contribution, Institute of Marine Biology, University of Puerto Rico, Mayagüez, Puerto Rico).

GLYNN, P. W., 1964. Common marine invertebrate animals of the shallow waters of Puerto Rico: 1-53. (Special Contribution, Institute of Marine Biology, University of Puerto Rico, Mayagüez, Puerto Rico).

GONZÁLEZ, L. A., H. M. RUIZ, B. E. TAGGART, A. F. BUDD & V. MONELL, 1997. Geology of Isla de Mona, Puerto Rico. In: H. L. VACHER & T. M. QUINN (eds.), Geology and hydrology of carbonate islands, **54**: 327-358. (Developments on Sedimentology, Elsevier, Amsterdam).

GRUBB, P., 1971. Ecology of terrestrial decapod crustaceans on Aldabra. Phil. Trans. Roy. Soc., London, (B) **260**: 411-416.

GÜELL, F. B., F. CABRERAS ROJAS & M. DÍAZ SIERRA, 1975. Amoná. (Producción de Francisco Güell & Associates, San Juan, Puerto Rico). (VHS-video, color, approx. 50 min.).

GUNDLACH, D. J., 1887. Apuntes para la fauna puertorriqueña (IV). Crustáceos. Anal. Soc. Española Hist. nat., **16**: 115-133.

HERNÁNDEZ-ÁVILA, M. L., 1970. Beach studies at Isla Mona: 1-171. (M.Sc. Thesis, University of Puerto Rico, Mayagüez, Puerto Rico).

HICKS, J. W., 1985. The breeding behavior and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). Australian Journ. Zool., **33**: 127-142.

HOBBS, H. H., JR., H. H. HOBBS, III & M. A. DANIEL, 1977. A review of the troglobitic decapod crustaceans of the Americas. Smithson. Contrib. Zool., **244**: 1-183.

HOPGOOD, N. M., 1994. Cobos de Isla de Mona. (Audio Visuales del Caribe, Inc., San Juan, Puerto Rico). (VHS-video, color, approx. 16 min.).

KAYE, C. A., 1959. Geology of Isla Mona, Puerto Rico and notes on age of Mona Passage. U.S. Geol. Surv. prof. Pap., **317-C**: 1-178, 1 map.

MATTOX, N., 1950. A new species of phyllopod of the genus *Streptocephalus* from Mona Island, Puerto Rico. Journ. Washington Acad. Sci., **40**: 12.

NIEVES-RIVERA, Á. M., C. J. SANTOS-FLORES & J. R. GARCÍA, 2003. Preliminary taxonomic composition of epipelagic zooplankton from two localities near Mona Island, Puerto Rico: 1-19. (Report to Sea Grant College Program, University of Puerto Rico, Mayagüez, Puerto Rico).

PECK, S. B., 1994. A synopsis of the invertebrate cave fauna of Puerto Rico, Mona Island and the Virgin Islands. In: C. JUBERTHIE & V. DECU (eds.), Encyclopaedia Biospeologica, **43**: 505-512. (Moulis-Bucarest).

PECK, S. B. & J. KUKALOVA-PECK, 1981. The subterranean fauna and conservation of Mona Island: a Caribbean karst environment. Natl. Speleol. Soc. Bull., **43**: 59-68.

PROVENZANO, A. J., 1962. The larval development of the tropical land hermit *Coenobita clypeatus* (Herbst) in the laboratory. Crustaceana, **4**: 207-228.

ROJAS, H. M., 1978. El cangrejo terrestre (*Cardisoma guanhumi* Latreille) y su aparente disminución poblacional en Puerto Rico. In: DEPARTAMENTO DE RECURSOS NATURALES DE PUERTO RICO (ed.), Quinto Simposio de Recursos Naturales: 120-127. (Departamento de Recursos Naturales de Puerto Rico, San Juan, Puerto Rico).

— —, 1981. Estudio sobre el cangrejo de tierra en Guanajibo, Mayagüez y Guayanilla; su tamaño, relación de peso a tamaño y resultados preliminares de su cultivo. In: C. A. ABRAHAMSON, J. VIVALDI, D. FOLCH & B. CINTRÓN (eds.), Octavo Simposio de Recursos Naturales: 100-105. (Departamento de Recursos Naturales de Puerto Rico, San Juan, Puerto Rico).

SANTOS-FLORES, C. J., 2001. The taxonomy and distribution of the freshwater micro-crustaceans and "green algae" of Puerto Rico, with a synopsis on West Indian limnology and three contributions to American cladocerology: 1-1421. (Ph.D. Dissertation, University of Wisconsin-Madison, Madison, Wisconsin).

SCHMITT, W. L., 1935. Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands. Scientific Survey of Porto Rico and the Virgin Islands, New York Acad. Sci., **15**: 125-227, 4 pls.

SCHWARTZ, A. & M. CAREY, 1977. Systematics and evolution in the West Indian iguanid genus *Cyclura*. Stud. Fauna Curaçao Caribb. Islands, **173**: 15-97.

SMITH, D. G., 1998. *Mesostoma* (Platyhelminthes: Rhabdocoela, Typhloplanidae) of Mona Island, Puerto Rico. Invert. Biology, **117**: 101-108.

SMITH, D. G. & A. M. WIER, 1999. On some inland Crustacea and their habitats of Mona Island in the northern Caribbean region. Crustaceana, **72**: 635-646.

STAHL, A., 1883. Fauna de Puerto Rico — Clasificación sistemática de los animales que corresponden a esta fauna. Catálogo del Gabinete Zoológico del Dr. Agustín Stahl. (Boletín Mercantil, San Juan, Puerto Rico).

TAGGART, B. E., 1992. Tectonic and eustatic correlations of radiometrically dated Late Quaternary marine terraces on northwestern Puerto Rico and Isla de Mona, Puerto Rico: 1-252. (Ph.D. Dissertation, University of Puerto Rico, Mayagüez, Puerto Rico).

VAN NAME, W. G., 1936. The American land and fresh-water isopod Crustacea. Bull. American Mus. nat. Hist., **71**: 1-535.

VÉLEZ, M. J., 1967. Checklist of the terrestrial and freshwater Decapoda of Puerto Rico. Caribb. Journ. Sci., **7**: 41-44.

WIEWANDT, T. A., 1975. Management of Mona Island land crabs. In: J. L. ROGERS (ed.), Unit plan for the management of the Mona Island Forest Reserve, **1** (Appendix K): 1-17, 1 table. (Unpubl. Report, Forestry Task Force, Puerto Rico Department of Natural Resources, San Juan, Puerto Rico).

— —, 1977. Ecology, behavior, and management of the Mona Island ground iguana, *Cyclura stejnegeri*: 1-338. (Ph.D. Thesis, Cornell University, Ithaca, New York).

WOLCOTT, T. G., 1988. Ecology. In: W. W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 55-96. (Cambridge University Press, Cambridge, Massachusetts).

WOODBURY, R. O., L. F. MARTORELL & J. G. GARCÍA-TUDURÍ, 1977. The flora of Mona and Monito Islands, Puerto Rico (West Indies). Univ. Puerto Rico agric. exp. Stn. Bull., **252**: 1-60.

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