

Life History of the Northern Mole Cricket, *Neocurtilla hexadactyla* (Orthoptera: Gryllotalpidae), Utilizing Carolina-bay Habitats

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ABSTRACT Life history of the northern mole cricket, *Neocurtilla hexadactyla* (Perty), was elucidated from a sample of 432 individuals collected from Carolina-bay habitats. Terrestrial drift fences with pitfall traps were an effective sampling technique. Juveniles emerged from subterranean nests in June and July and overwintered in an immature stage. They matured the following summer and presumably mated in the autumn at 16-18 months of age. Females were larger in body size than males but relative forewing length was the same. Females underwent vitellogenesis in spring and oviposition presumably occurred in May and June. Eggs deposited in laboratory containers were found in a single underground chamber and were attended by the female. Sex ratio of the sample was skewed 3:1 in favor of females. Adults and juveniles were found during all months of the year. The life cycle of *N. hexadactyla* was semivoltine in South Carolina.

MOLE CRICKETS of the family Gryllotalpidae occur throughout the eastern and midwestern United States. They are fossorial and have large forelegs and dactyls (or claws) that are greatly modified for digging. At least two species (*Scapteriscus acletus* Rehn and Hebard, *Scapteriscus vicinus* Scudder) are considered pests of turf and agricultural crops in the Southeast (Short and Driggers 1973, Walker and Nickle 1981, Walker and Ngo 1982). They can damage grass and crops by feeding on the roots and leaves as well as by their burrowing behavior that mechanically disturbs the root systems (Short and Driggers 1973, Taylor 1979, Matheny 1981). Because of their economic importance these latter two species have been well studied (Ulagaraj 1975, 1976, Kleyla and Dodson 1978, Forrest 1980, Buegnon 1981, Walker and Nickle 1981, Walker and Nation 1982, Forrest 1983, Walker and Fritz 1983, Walker et al. 1983, Nickle and Castner 1984).

The northern mole cricket, *Neocurtilla hexadactyla* (Perty), is less well studied. In part, this is probably due to this species not being an agricultural pest, it being restricted to mesic and hydric habitats, and the ineffectiveness of collecting this species in light traps (Cantrall 1943, Hayslip 1943, Ulagaraj 1975, DeWitt 1978). However, *N. hexadactyla* is readily collected in pitfall traps with terrestrial drift fences that have been effectively utilized for many other invertebrates and vertebrates (Mitchell 1963, Greenslade 1964, Gibbons and Semlitsch 1982).

The purpose of this study was to examine some of the basic aspects of the life history and ecology

of *N. hexadactyla* in a natural population. This information can be used to compare adaptations of allied species and to help elucidate the origin of alternative life histories (Alexander 1968). These data may be applied to the development of an effective integrated pest control program for mole crickets that considers life-history stages, traits, or aspects of their ecology that renders them particularly susceptible to management.

Materials and Methods

Study Areas. All study areas were located on the U.S. Department of Energy's Savannah River Plant in Aiken and Barnwell counties, South Carolina. The study areas are natural depressions of unknown geological origin called "Carolina bays" (Sharitz and Gibbons 1982) on the Atlantic Coastal Plain of the United States. Carolina bays are a major freshwater lentic habitat on the coastal plain and serve as major breeding sites for aquatic insects and amphibians (Schalles 1979, Sharitz and Gibbons 1982). There is a well-defined mesic ecotone around the periphery of each Carolina bay relative to the xeric, sandy upland habitats that surround them.

The primary study area, Rainbow Bay, is ca. 1 ha in area, has a maximum water depth of 1.0 m, and dries each summer. Herbaceous plants common to the bay are bulrush (*Scirpus cyperinus*), rush (*Juncus repens* Michaux), cattail (*Typha latifolia* L.), and spike-rush (*Eleocharis* sp.). The bay is surrounded by slash (*Pinus elliotii* Engelm.) and loblolly (*P. taeda* L.) pine plantations of various ages with sweetgum (*Liquidambar styraciflua* L.), black gum (*Nyssa biflora* (Walter) Sargent), water oak (*Quercus nigra* L.), Blackber-

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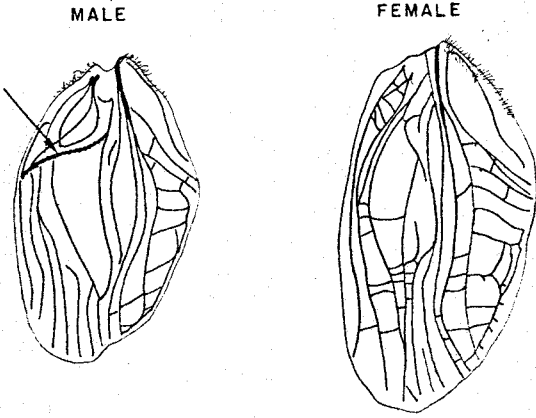


Fig. 1. Wing structure of male and female *N. hexadactyla*. Arrow points to the stridulating organ used in sound production in males.

ry (*Rubus* sp.), and wax myrtle (*Myrica cerifera* L.) along the water's edge.

Two other study areas, Sun Bay and Ellenton Bay, were sampled periodically during the study. Sun Bay is ca. 1 ha in area and dries each year. Vegetation of Sun Bay is similar to that of Rainbow Bay. Ellenton Bay is ca. 10 ha in area and has a maximum water depth calculated at 2.0 m. Ellenton Bay is nearly permanent, drying only twice in the last 15 years. It is surrounded by an old-field community undergoing secondary succession with sweetgum (*L. styraciflua* L.), willow (*Salix* sp.), blackberry (*Rubus* sp.), and wax myrtle (*M. cerifera* L.) around the periphery.

Sampling Techniques. Rainbow Bay was completely encircled by a terrestrial drift fence (440 m) constructed of aluminum flashing (50 cm high). Paired pitfall traps (40-liter buckets) were placed on opposite sides of the fence at 10-m intervals (see Gibbons and Semlitsch 1982). The fence was

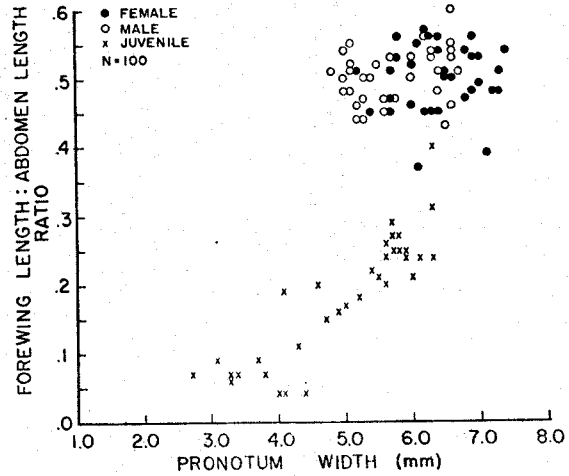


Fig. 3. Relationship between the forewing length to abdomen length ratio and pronotum width in adult and juvenile *N. hexadactyla*.

buried 10–15 cm in the soil and well packed to prevent individuals from easily crawling under the fence although some probably did. Pitfall traps were checked daily for other purposes since construction of the drift fence on 21 September 1978 continuously through 1 September 1984. Crickets were collected at irregular intervals during that time period. Upon collection, individuals were preserved in 10% formalin for 10 days and then stored in 80% ethanol.

Precipitation at ground level was measured at Rainbow Bay by a rain gauge and recorded daily. Maximum and minimum air temperature (ca. 1.5 m aboveground) was measured and recorded daily. Water depth was measured on a permanently fixed depth gauge in the deepest portion of the bay and recorded weekly. Date of complete drying

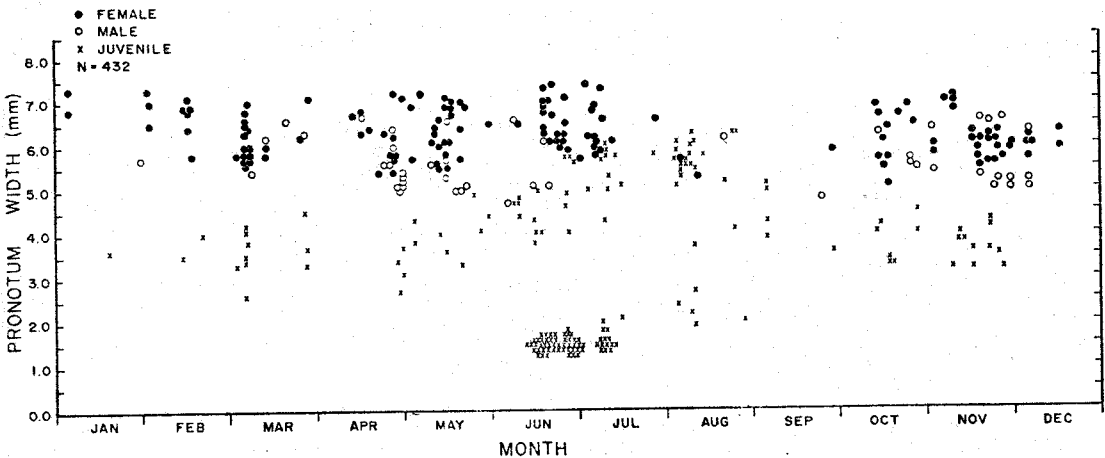


Fig. 2. Seasonal distribution of pronotum widths of *N. hexadactyla* adults and juveniles collected periodically in South Carolina from September 1978 to September 1984.

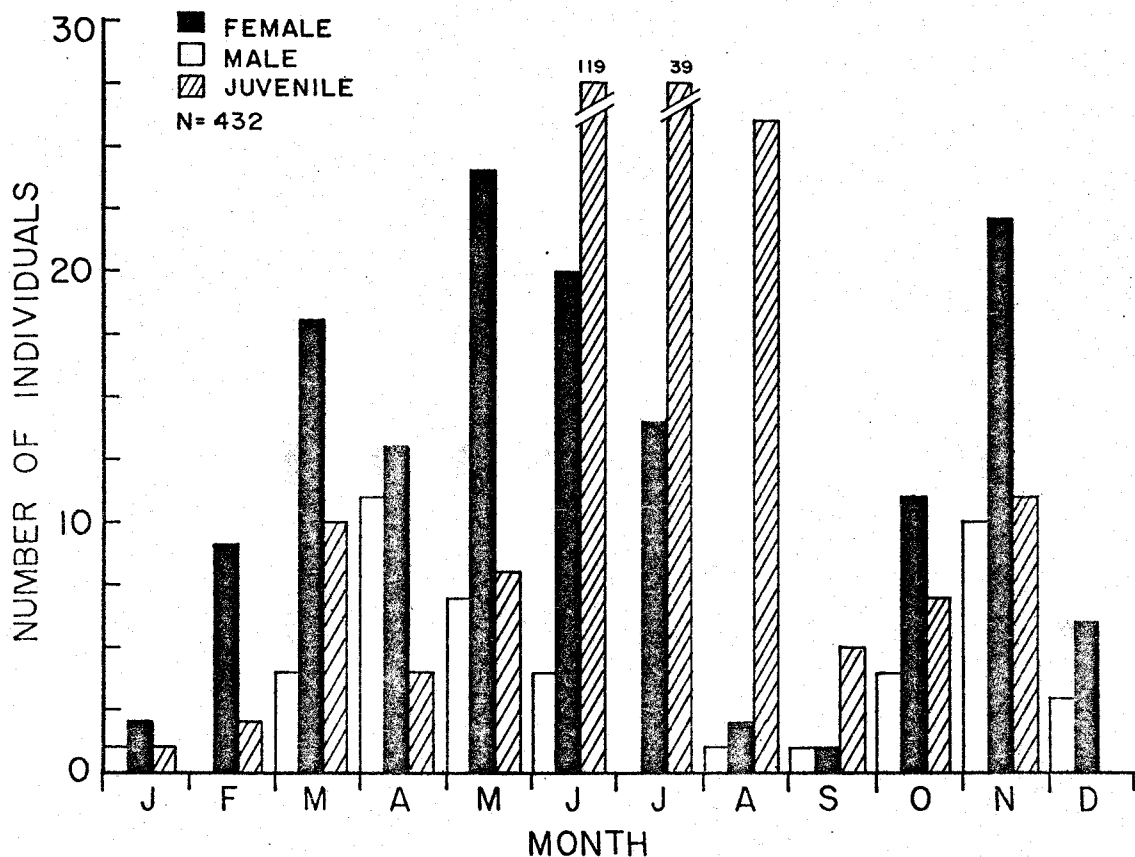


Fig. 4. Seasonal distribution of the number of adult and juvenile *N. hexadactyla* collected periodically in pitfall traps in South Carolina from September 1978 to September 1984.

and date that filling was initiated was recorded each year.

Dissections. The presence of the stridulating organ and veination pattern on the forewing (Fig. 1) was used to distinguish the sexes. Males and females were dissected to determine reproductive condition (immature, mature, oocyte development). Sexual maturity was determined by the presence of enlarged testes in males and the presence of enlarged eggs or enlarged ovaries in the females. The diameter of 10 eggs (across the short axis) was measured in each female to determine the pattern of vitellogenesis. Pronotum width, abdomen length, and forewing length were used as measures of body size and measured with an ocular micrometer or calipers to the nearest 0.1 mm.

Distributions of body size were compared using nonparametric Wilcoxon rank sum tests (Hollander and Wolfe 1973). Sex ratios were tested against a 1:1 expected ratio with a χ^2 test.

Results

Emergence of Juveniles. The earliest that young juveniles were collected in pitfall traps was 15 June (Fig. 2). Large numbers of these juveniles were collected throughout the rest of June and early

July. They were small in body size ($\bar{x} = 1.5 \pm 0.01$ mm [\pm SE] pronotum width, $n = 117$) and were presumed to be newly emerged young of the year. Juveniles of this size were found at no other time of year (Fig. 2).

Growth and Maturity. Juveniles emerged in June at an average body size of 1.5 mm pronotum width (Fig. 2). By November, individuals averaged 3.8 ± 0.13 mm (\pm SE) in pronotum width. They overwintered as immatures and continued growing the following spring. In June, at 13 months of age, juveniles averaged 4.7 ± 0.17 mm in pronotum width. During the summer (June–August), presumably after their final molt, individuals began showing signs of sexual maturity and had adult wing length and body size. Testes and ovaries were enlarged as the forewing length to abdomen length ratio approached 40% and pronotum width was >5.0 mm (Fig. 3). Presumably, individuals were capable of mating in autumn at ca. 16–18 months of age.

Adult females had significantly wider pronotums ($\bar{x} = 6.3 \pm 0.05$ mm) than males ($\bar{x} = 5.6 \pm 0.09$ mm; Wilcoxon rank sum test, $Z = 5.92$, $n_1 = 140$, $n_2 = 47$, $P < 0.0001$). Females ($\bar{x} = 19.2 \pm 1.2$ mm) also had significantly longer abdomens than males ($\bar{x} = 16.3 \pm 1.1$ mm; Wilcoxon rank

Table 1. Summary of the life histories of three species of mole crickets from the southeastern United States

Life history traits	<i>N. hexadactyla</i> (This study)	<i>S. acletus</i> (Hayslip 1943)	<i>S. vicinus</i> (Hayslip 1943)
Study area	South Carolina	North Florida	North Florida
Time of oviposition	May-June	April-July	April-June
Juvenile emergence	June-July	May-July	May-July
Age at maturity (months)	16-18 ^a	9 ^a	10 ^a
Age at first reproduction (months)	24-25	133 days ^b	135 days ^b
\bar{x} fecundity (eggs)	48	12-13	12-13
\bar{x} egg size (mm)	1.7 by 2.7	106 ^c	68 ^c
Incubation period (days)	16 ^d	—	—
Life cycle	Semivoltine	Univoltine	Univoltine

^a Adult transforming in spring.

^b Adult transforming in autumn.

^c Total eggs laid in multiple "cells" or multiple clutches.

^d Fulton (1951).

sum test, $Z = 3.66$, $n_1 = 140$, $n_2 = 47$, $P < 0.0003$). However, forewing length was proportionally the same in females (forewing to abdomen ratio $\bar{x} = 0.51 \pm 0.01$) as in males ($\bar{x} = 0.51 \pm 0.01$).

Reproduction. In autumn, at the time of maturity, intense male calling (personal observation), and presumably first mating, the eggs of females are small (0.1-0.2 mm diam) and undeveloped. Vitellogenesis did not begin until March or April the following spring when eggs enlarged to 0.4-0.6 mm in diameter. Eggs continued to develop to a maximum diameter of 1.7 mm in May. All adult females in the May samples had enlarged eggs. No females had enlarged eggs after June. Oviposition was presumably annual and occurred in late May and June at individual ages of 24-25 months.

Eggs were not found in the field. However, two females deposited eggs in the laboratory. One female collected on 30 May from Rainbow Bay deposited 58 eggs in a plastic container filled with damp sand a few days later. Another female collected on 25 June from Rainbow Bay deposited 37 eggs. Eggs of both females were found in small chambers or "cells" (15 by 37 mm and 16 by 40 mm) off of a main burrow. Females were attending the eggs when excavated. Eggs were light gray-brown and elliptical averaging 2.7 by 1.7 mm across the long and short axis, respectively. There was no evidence that females laid more than a single clutch of eggs per season.

Sex Ratios. There were 47 males and 140 females in the pooled adult sample from the three populations. Sample sizes from the secondary study areas were not large enough to warrant separate analyses. Sex ratio of the sample was skewed 3:1 in favor of females (deviation from 1:1, $\chi^2 = 46.25$, $df = 1$, $P < 0.001$). The proportion of adult males present in October and November (30%, $n = 47$) was the same as the proportion of adult males present after winter (March to May, 29%; $n = 77$; Fig. 4), indicating that the sex ratio of pitfall trap-caught adults did not change seasonally.

Seasonal Activity. Individuals were captured in pitfall traps around Carolina bays during every month of the year (Fig. 4). More individuals were

captured during June and July than during other months. This was primarily because of the large number of emerging juveniles, 81% of the 196 individuals, captured at that time (Fig. 4). There was seasonal movement of individuals into and out of Rainbow Bay that appeared to be associated with seasonal flooding and drying of the bay. As Rainbow Bay filled with water in the winter and spring, individuals were captured moving out of the bay. Likewise, as the bay dried during the summer, individuals were captured moving into the bay, presumably following the soil moisture gradient.

Discussion

N. hexadactyla is relatively abundant in the mesic and hydric habitats around the periphery of Carolina bays. Drift fences with pitfall traps placed in adjacent sandy, dry-upland habitats collected few individuals. *S. acletus* (four-dot morph) was the only other mole cricket collected in the mesic habitat around Rainbow Bay ($n = 3$). This was either because of the absence of other species in Carolina bay habitats or their ability to fly out of the pitfall traps. Clearly, the flightless behavior of *N. hexadactyla* contributed to the effectiveness of drift fences and pitfall traps along, with their apparent preference of mesic and hydric habitats (Cantrall 1943).

The presence of three stages of individuals (small emerging juveniles, large juveniles, and mature adults) in June strongly suggests that *N. hexadactyla* has a semivoltine life cycle. This appears to confirm a suggested 2-year life cycle for *N. hexadactyla* in North Carolina (Fulton 1951). However, Hayslip (1943) suggested a univoltine life cycle for *N. hexadactyla* in Florida based on the fact that most juveniles reached maturity by October or November of their first year of life. Although it was possible that some juveniles in South Carolina matured in autumn at 5-6 months of age (marked individuals were not followed directly), the majority did not. Most individuals at Rainbow Bay matured the summer following emergence and presumably mated no sooner than the presumed

autumn breeding period of their second year. Fulton (1951) defined the calling period of *N. hexadactyla* to be from late July through early November in North Carolina. My own observations for *N. hexadactyla* in South Carolina confirm the late summer/autumn calling period.

Juvenile *N. hexadactyla* emerged synchronously in early summer at Rainbow Bay. This also appeared to be the case for populations in North Carolina and Florida (Hayslip 1943, Fulton 1951). Likewise, the timing of oviposition and emergence of juveniles was similar for two other species of mole crickets in the southeastern United States, *S. acletus* and *S. vicinus* (Table 1). Geographic variation in temperature and growing season length may very well contribute to such population differences, although data are not available to test such a prediction.

The sex ratio of *N. hexadactyla* in natural populations has not been described. The sex ratio of the sample collected in pitfall traps in South Carolina was skewed 3:1 in favor of females. Our ability to trap insects of both sexes was assumed to be the same because both sexes have short wings and were presumably both flightless. The sex ratio of adult females to males (3:1) did not change from the autumn breeding period to the spring. This suggests that all adult males do not die after mating and that the sex ratio bias is not exclusively related to disproportional movements of females toward stationary calling males. It is possible that males mature at a smaller body size than females and consequently at a younger age. Thus, males present in the spring may be individuals that have only recently matured as opposed to males that overwintered after mating. Individuals must be marked and followed directly to choose between the alternatives. However, the absence of adult males and females in August and September (Fig. 2) suggests that many or most adults in the population die after summer reproduction. It is not clear what the mechanism is for the reduction of male *N. hexadactyla* in the population. Similarly skewed sex ratios have also been noted for *S. acletus* and *S. vicinus* (83% females) in Florida (Ulagaraj 1975). Walker et al. (1983) suggested that the female biased sex ratios of *S. acletus* and *S. vicinus* resulted from female movement between egg laying events (i.e., egg laying in multiple "cells") relative to stationary calling males.

In conclusion, the life histories of three species of mole crickets from the southeastern United States (Table 1) are similar except for age at maturity and age at first reproduction. This demographic difference results in *N. hexadactyla* having a semivoltine life cycle compared to the univoltine life cycle of *S. acletus* and *S. vicinus*.

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