Am. Midl. Nat. 154:97–114

Foraging Range and Habitat Use of Ceuthophilus secretus (Orthoptera: Rhaphidophoridae), a Key Trogloxene in Central Texas Cave Communities

STEVEN J. TAYLOR[1]
Center for Biodiversity, Illinois Natural History Survey, 607 E. Peabody Drive, Champaign 61820

JEAN K. KREJCA
Zara Environmental LCC, 118 W Goforth Road, Buda, Texas 78610

AND

MICHAEL L. DENIGHT
Engineer Research and Development Center, CERL,
2902 Newmark Drive, Champaign, Illinois 61822

ABSTRACT.—Cave invertebrate communities are dependent upon exogenous energy sources because their environment generally lacks primary producers. In small caves of central Texas, endemic terrestrial cave invertebrates often rely in part on the energy brought into caves by cave crickets (*Ceuthophilus* spp.), which forage above ground at night and roost in caves during the daytime. Knowledge of cave cricket foraging range is needed to effectively protect invertebrate communities that include federally endangered species. We marked approximately 2000 *C. secretus* emerging from Big Red Cave (Coryell County, Texas) with UV bright paint and located 291 previously marked crickets over 17 nights. Crickets foraged up to 105 m from the cave entrance and were present in relatively uniform densities out to 80 m. While 51.1% of the crickets were found within 40 m, 8.1% were found at 80 m or beyond. Relocated crickets were predominantly found in grasses (30.7%), leaf litter (22.4%) and herbaceous vegetation (20.4%) and were found close to ground level (mean = 0.49 cm). Our results show that *C. secretus* can forage at much greater distances than previously reported. The new data from our study should assist in the development of effective preserve design and management strategies for caves with endangered species in central Texas.

INTRODUCTION

With few exceptions (*e.g.*, Sarbu *et al.*, 1996; Hose *et al.*, 2000), most caves contain relatively low-energy ecosystems without primary producers (Poulson and White, 1969; Culver, 1982; Gers, 1998; Simon *et al.*, 2003). Energy, in the form of plant and animal material, enters the caves by falling or washing in, but also is brought into caves by animals, such as bats and cave crickets. Though some terrestrial cave communities in central Texas are supported largely by the guano of large colonies of bats (*e.g.*, Bracken Bat Cave, Comal County), many of the caves in this area are much smaller and lack bat colonies. In these smaller caves, cave crickets (Orthoptera: Rhaphidophoridae: *Ceuthophilus* spp.) are important in transporting energy into caves by foraging on the surface at night and roosting in caves in the daytime, depositing feces, eggs and their dead bodies in the caves (USFWS, 2003). Even relatively small caves may harbor thousands of cave crickets and the feces they produce can form layers of energy-rich substrate. In such caves, springtails are abundant on the cricket guano and their predators, troglobitic *Cicurina* spp. spiders

[1] Corresponding author: Telephone: (217) 333-5702; FAX: (217) 333-4949; e-mail: sjtaylor@uiuc.edu

(Araneae: Dictynidae), can be found (Cokendolpher, 2004a). The cave crickets deposit their eggs in the caves, and some of the eggs are depredated by cave-adapted *Rhadine* spp. beetles (Coleoptera: Carabidae) (*e.g.*, Taylor, 2003). Other relationships among taxa are less well understood, but it is clear that the cave crickets play an important role in providing energy for the cave system. There are few published studies on the role of cave crickets in central Texas cave invertebrate communities (e.g., Mitchel and Reddell, 1971), and while the in-cave biology of other rhaphidophorids has been examined in detail at Mammoth Cave National Park (Kentucky) (*Hadenoecus subterraneus* and *Ceuthophilus stygius*) and Carlsbad Caverns National Park, (New Mexico) (*Ceuthophilus conicaudus*, *C. carlsbadensis* and *C. longipes*) – *see* literature reviews in Poulson (1992) and Studier *et al.* (2002) – surface foraging activities of cave crickets have received little scrutiny (Levy, 1976; Helf, 2003).

In the vicinity of Austin and San Antonio, sixteen of the terrestrial, cave-limited invertebrates have been listed as endangered by the U.S. Fish and Wildlife Service (USFWS, 1988, 1993, 2000). These taxa include several troglobitic *Rhadine* and *Cicurina* species which appear to be dependent, at least in part, on the energy brought into caves by cave crickets (USFWS, 2003). Consequently, it follows that maintaining healthy cave cricket populations may be important in facilitating the recovery of the endangered taxa. Three species of cave crickets, *Ceuthophilus secretus*, *C. cunnicularis* and an undescribed *Ceuthophilus* species co-occur with the federally endangered invertebrates. Two of these crickets, *C. secretus* and the undescribed *Ceuthophilus* species, regularly exit the caves to forage above ground at night during the warmer months and typically roost inside the caves during the day (USFWS, 1994, 2003), thus transporting vital nutrients into the caves. This paper examines the foraging range of *C. secretus* at Big Red Cave, Fort Hood, Coryell County, Texas, a species that is widespread in caves across central Texas [Dallas and Bexar counties west to Kinney and Terrell counties (Scudder, 1894; James Reddell, Texas Memorial Museum, Austin TX, pers. comm.)].

Fort Hood is located on the southern border of the Lampasas Cut Plain Region, the northernmost extension of the Edwards Plateau (Atkinson and Smith, 2001), a karst area extending across much of central Texas. Years of study at Fort Hood, led by James Reddell, have produced a list of fifteen cave inhabiting terrestrial invertebrate species of concern for the area: the spiders *Cicurina caliga*, *C. coryelli*, *C. hoodensis*, *C. mixmaster*, *C. troglobia*, *Neoleptoneta* n. sp., *N. paraconcinna* (Cokendolpher, 2004b; Cokendolpher and Reddell, 2001; Paquin and Hedin, 2004), the pseudoscorpion *Tartarocreagris hoodensis* (Muchmore, 2001), the ground beetle *Rhadine reyesi* (Reddell and Cokendolpher, 2001a), the antlike litter beetles *Batrisodes* n. sp., *B. feminiclypeus*, *B. gravesi* and *B. wartoni* (Chandler and Reddell, 2001) a cave/epigean harvestman, *Texella fendi* (Ubick and Briggs, 2004), the cave milliped *Speodesmus castellanus* (Elliott, 2004) and an undescribed bristletail (*Texoreddellia* n. sp.). Thirteen of these species are congeners (*Cicurina*, *Neoleptoneta*, *Tartarocreagris*, *Rhadine*, *Batrisodes*) of the federally endangered cave invertebrates of Bexar, Travis and Williamson counties.

Ceuthophilus spp. are thought to be opportunistic scavengers (Thomas l. Poulson, Jupiter FL, pers. comm.) or omnivores. In New Mexico caves, Campbell (1976) noted both animal and plant material in the stomachs of *C. conicaudus* and Cokendolpher *et al.* (2001) collected both *C. carlsbadensis* and *C. longipes* at a variety of bait types (jelly, tuna and rancid liver), with bait preferences varying seasonally. Unpublished studies by W. R. Elliott (USFWS, 2003) also indicate that *Ceuthophilus* spp. (*C. secretus* and the undescribed *Ceuthophilus* species) are attracted to a variety of baits (American cheese, pet food, oatmeal, wheat germ, peanut butter, molasses and various fruits) and feed naturally on fungi, ripe native persimmons and dead insects (including fire ants). Although Elliot observed *Ceuthophilus* spp. on dead leaves, grass and other organic material, they were not observed feeding on these materials. Cokendolpher (2001) maintained *C. carlsbadensis* in aquaria, where they fed upon oatmeal flakes, insects, arachnids, fruit and bread. Finally, Northup (1988) reported that *Ceuthophilus* spp. (including all or some of: *C. carlsbadensis, C. conicaudus* and *C. longipes*) at Carlsbad Cavern, New Mexico feed on bat and ringtail cat carcasses, human feces, guano moths (*C. carlsbadensis*) and food dropped by humans. Gut content analyses of these *Ceuthophilus* spp. (Northup, 1988) revealed that the crickets feed on Lepidoptera, *Ceuthophilus* spp. and eggs of other insects. She did not identify any plant material in the *Ceuthophilus* spp. guts.

Perhaps the most critical management problems facing the rare and endangered endemic cave fauna of central Texas are tied to the threats that have arisen with the invasion of the red imported fire ant, *Solenopsis invicta* (hereafter 'fire ants'). These ants are aggressive and opportunistic omnivores that are able to capitalize on localized resources (Wilson and Oliver, 1969; Taber, 2000; Wojcik *et al.*, 2001), and Elliott (1992) indicated that prey in caves includes "young cave crickets, millipeds, pseudoscorpions, earthworms and other fauna." Because both fire ants and *Ceuthophilus secretus* actively forage at night, and *C. secretus* is thought to be important in providing nutrients for cave-limited taxa, controlling fire ant populations within the foraging range of *C. secretus* becomes an important concern for land managers interested in protecting rare and endangered cave invertebrates. Unpublished studies by W. R. Elliott (USFWS, 2003) indicated that cave crickets mostly foraged from 5 to 10 m from cave entrances, with large adults being found up to 50 m from cave entrances. Elliott notes that large adults probably travel well beyond 60 m. However, no quantitative studies of foraging range of any *Ceuthophilus* species have been published to date, and *C. secretus* can be found during the day in non-cave habitats [*e.g.*, under large stones (pers. obs. James Reddell, Texas Memorial Museum, Austin TX, pers. comm.)] and in areas where no caves are present. The type locality for *C. secretus* is Dallas, Texas (Scudder, 1894) – an area with only one known cave (Atkinson, 2003).

A reasonable management strategy for the protection of endangered cave invertebrates is to exclude *Solenopsis invicta* from an area around a cave entrance (Elliott, 1992), or cave footprint, by defining an exclusion area based on a radius at least equal to the known foraging range of this ant (USFWS, 2003), plus an exclusion area based on the foraging range of cave crickets. Fire ants can construct foraging tunnels that may extend up to 30 m from their mound (Taber, 2000). More typical home ranges for *S. invicta* colonies are about 10–15 m in diameter or less (Wilson *et al.*, 1971; Markin *et al.*, 1975) and maximum territory area for a colony is around 100 m^2 (Tschinkel *et al.*, 1995; Korzukhin *et al.*, 2001). Clearly, fire ant foraging range data need to be supplemented with well-defined cave cricket foraging range data and hydrogeological data (Veni, 1999) to determine how much land area needs to be protected around a central Texas cave in order to protect the cave fauna (USFWS, 2003).

Here we report on a study of the surface foraging range of *Ceuthophilus secretus* in the vicinity of Big Red Cave (Fort Hood, Coryell County, Texas), a cave in which fire ants are present, *C. secretus* are relatively abundant, and in an area (Fort Hood) where several endemic terrestrial troglobites congeneric with endangered species are known to occur.

METHODS

Ceuthophilus secretus emerging from Big Red Cave at dusk were marked with yellow fluorescent, or UV bright, paint (Crayola® water-based paint) (Fig. 1) just outside the cave entrance (pink paint was used on one night). The paint was applied with a fine-tipped brush to the thoracic nota with a paint brush, creating a 1–4 mm diameter mark. Although cricket handling time was less than 10 s per individual, approximately 5% of the individuals shed a single rear leg during handling. By utilizing an experienced researcher to handle crickets, leg loss was almost completely eliminated. Larger individuals were painted first because they

FIG. 1.—Painting the thorax of *Ceuthophilus secretus* with fluorescent (UV bright) paint at Big Red Cave, Coryell County, Texas

were easier to handle and paint without damaging the crickets, and would be more likely to provide data on the maximum foraging range of *C. secretus.* After painting, the crickets were immediately released within 1 m of the cave entrance and most (>95%) moved out away from the cave entrance, the rest returning immediately into the cave. As crickets emerged from the cave, we also estimated the number of emerging crickets and number of marked crickets emerging. Cricket marking stopped when about 50 to 250 crickets had been marked, or until few crickets were exiting the cave. Each evening we recorded the duration of searches and starting and ending air temperature and relative humidity.

Within 1 h after each marking session, two researchers began searching for crickets with a portable, battery powered black light. A 100 m diameter circle around the cave entrance was divided into northern and southern halves, with one person examining each half. We attempted to examine all open and wooded habitats with equal effort, but some densely wooded areas probably were under-sampled because the high density of woody vegetation made access difficult. Occasionally, searches extended beyond 100 m, and we include data out to 110 m in our analyses. During searching, a WAAS-enabled Garmin Etrex® series GPS receiver (GPSr) was carried with tracking enabled, recording latitude/longitude values at the most frequent interval setting available on this model–every 8 to 15 s when walking or up to 1.5 min when moving very slowly. In addition to coordinate data, the track log included a time stamp, allowing us to obtain distances and time intervals between track points. The display of the GPSr showed the completed search track, facilitating allocation of search effort fairly uniformly across the study area (Fig. 2). When a cricket was found during the search, its location was recorded in the GPSr and marked with a wire flag. For each cricket encounter,

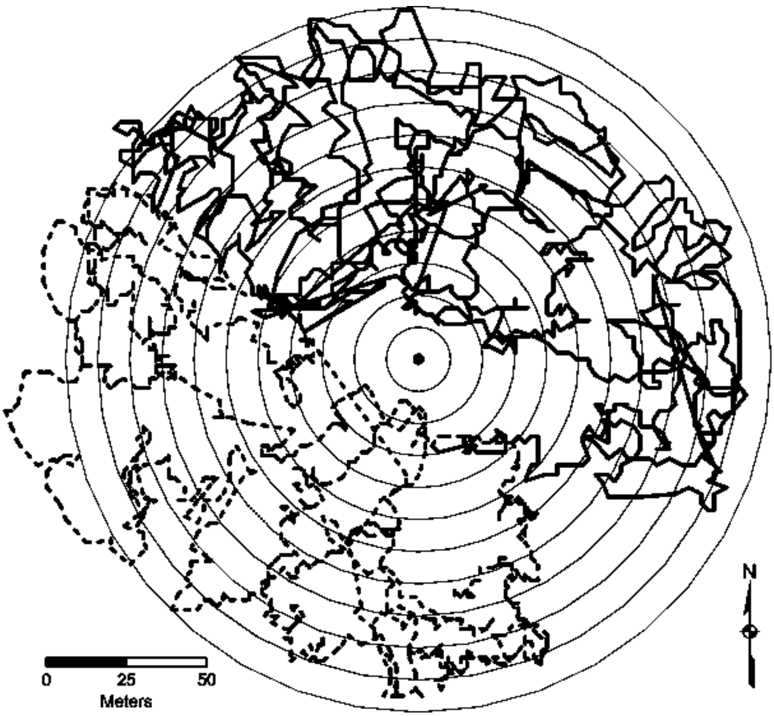


FIG. 2.—The GPSr track of two searches on 25 June 2003 around Big Red Cave, Coryell County, Texas. One person generally searched the northern half of the study area (solid line), the other the southern half (dashed line). Concentric rings are 10 m wide distance intervals, cave entrance at center. Using ArcGIS, search tracks are clipped such that the summation of the search times associated with the track segments is a measure of the search effort on this night for each distance interval

we recorded life stage (adult/nymph), gender, general behavior, substrate and elevation of the cricket above the ground surface. We also recorded the time at which the cricket was found. The field work was conducted during Daylight Saving Time, and all times were converted from Central Daylight Time to Central Standard Time (CST) by subtracting 1 h.

The following day, we used a compass and fiberglass measuring tape to survey from the flagged cricket locations to the cave entrance. Survey data were processed using a surveying program (Walls 2.0 B6,© Dave McKenzie) to convert distance and azimuth data to latitude/longitude values. Locations based on the survey provided a measure of foraging distance that was independent of the location obtained using a GPSr, allowing error checking and comparison of localities. Estimated position errors of the GPSr readings ranged from 3 to 8 m.

Later, GPSr track data were converted to shape files in ArcGIS® (Environmental Systems Research Institute, Inc., Redlands, California). Obvious spikes corresponding to loss of satellite coverage were evident by examining the speed of the track legs, and obviously erroneous readings were removed from the analysis. The GPSr track data, as shape files, were used to quantify search effort in concentric rings at 10 m distance intervals from the cave entrance to obtain a distribution of crickets at various distances per unit search effort. Thus, the amount of time spent searching for crickets in each concentric ring (Fig. 2) was calculated using GPSr track data (line segment lengths and speed). By clipping line segments within ArcGIS® and summing the total search time of line segments or portions of line segments within a given ring (*e.g.*, 80 m to <90 m, Fig. 2), we were able to determine the amount of time spent searching at that distance. We then converted the number of crickets found at each distance into number of crickets per unit effort (time). Finally, we adjusted the crickets per minute data to account for the differing areas (m^2) of the concentric 10 m-wide distance intervals by dividing crickets per minute at each interval by the area (m^2) of the interval (*i.e.*, number of crickets/min/m^2).

The day after cave cricket locations were marked, we used a digital camera to take low resolution (640 × 480 pixels) photographs of ground cover within a 0.5 m^2 (0.701 × 0.701 m) quadrat. A canopy cover photograph was also taken at low resolution and with the camera on its wide-angle setting and held at chest height. Photographs were later analyzed in Adobe Photoshop® by overlaying them with a 10 × 10 array of points and scoring the substrate or canopy under each point, to produce an estimate of percent ground cover in various cover classes (grass, leaf litter, herbaceous vegetation, bare rock, bare soil, woody vegetation and cactus) and percent canopy cover. We also measured the maximum height of the ground cover and the maximum height of vegetation, recording each of these within 10 cm of the flagged point where each cave cricket had been found.

Statistical analyses (correlations, means, paired *t*-tests, etc.) were carried out using SAS® procedures (SAS Institute, 2001). Level of significance for statistical tests was set *a priori* at $\alpha = 0.05$. Summary statistics are reported as $\bar{x} \pm$ SE (range, n) unless otherwise indicated. Voucher specimens have been deposited in the Illinois Natural History Survey Insect Collection.

RESULTS

During evenings in late spring and summer 2003 (8–9 May, 15–19 June, 23–26 June, 30 June–10 July) we estimated that we marked more than 2000 emerging crickets out of a total of more than 15,000 cricket emergences at the cave entrance over the 17 nights. Two instances of depredation of emerging *Ceuthophilus secretus* at the cave entrance by mice (*Peromyscus* sp.), also emerging from the cave, were observed on 26 June.

On 17 June, 122 crickets were marked with pink paint (all other nights yellow paint was used), on subsequent evenings pink-painted crickets were observed emerging from the cave (18 June, 14 crickets; 25 June, 5 crickets; 26 June, 11 crickets; 2 July, 3 crickets; and 7 July, 1 cricket). During timed searches, 314 crickets – 291 of which had paint marks – were relocated at night on the surface around Big Red Cave (Tables 1, 2; Fig. 3). Although one unmarked *Ceuthophilus secretus* was found at 136 m from the cave entrance, the unmarked crickets are excluded from our analyses because we could not verify that they had emerged from Big Red Cave. Of the marked *C. secretus*, 193 were adults, 94 were nymphs and the developmental stage of 4 individuals was not reported because they moved away before stage could be determined. The larger number of adults reflects, at least in part, our bias towards marking larger individuals. One *C. secretus* was found on 30 June at 20.56 h CST with a still-living Broad-headed Bug (Hemiptera: *Alydidae*, *Alydus* sp.) in its mandibles.

Distance from entrance as measured by GPSr [38.2 ± 1.3 m (2.3–105.8 m, 281)] and by compass and tape survey [38.0 ± 1.4 m (2.2–108.1 m, 284)] were positively correlated ($r^2 = 0.9751$, $P < 0.0001$) and were not significantly different ($t = -1.89$, df = 273, $P = 0.0593$). We here report distances based on the GPSr data, except for 10 crickets for which only survey distance data were available.

On average, adults [41.74 ± 1.69 m (2.3–105.8 m, 193)] were found farther from the cave entrance than nymphs [30.73 ± 1.90 m (7.6–90.4 m, 94)] of *Ceuthophilus secretus* (df = 229, $t = 4.33$, $P < 0.0001$) (Table 1). Adult males [43.92 ± 2.94 m (3.4–105.8 m, 73)] and females [40.13 ± 2.10 m (2.3–94.9 m, 110)] did not differ in distance from entrance (df = 140,

TABLE 1.—Distance from the entrance of Big Red Cave, Coryell County, Texas, to the location of marked crickets foraging above ground at night. Based on 17 nights (8 May–10 July, 2003) of data collection

Distance interval (m)	Adults	Nymphs	Undetermined	Total
0 to <10	7	7	0	14
10 to <20	33	26	0	59
20 to <30	32	23	1	56
30 to <40	30	15	1	46
40 to <50	27	9	0	36
50 to <60	12	7	0	19
60 to <70	21	3	0	24
70 to <80	20	2	1	23
80 to <90	6	1	1	8
90 to <100	4	1	0	5
100 to <110	1	0	0	1
Total	193	94	4	291

$t = 1.05$, $P = 0.2954$). Crickets were active from about 8 pm to at least 2 am CST (the latest that the field crew stayed out searching), the average cave cricket was found shortly before 23 h CST [22.88 ± 0.06 h CST (20.85–01.57 h CST, 288)] and adult males [23.72 ± 0.10 h CST (21.9–25.6 h CST, 73)] and females [23.89 ± 0.11 h CST (22.0–26.6 h CST, 110)] did not differ in average time of night found (df = 178, $t = -1.14$, $P = 0.2552$). Over the 17 nights of searching, humidity and temperature during searches ranged from 57 to 100% and 19.9 to 29.4 C, respectively. Total person-hours of searching effort (Fig. 4) was 45.5 [per 10 m distance interval: 9.09 ± 1.18 h (0.55–13.16 h,11)], with over 4 to nearly 6 h spent searching in each 10 m interval between 30 and 100 m, somewhat less closer to the cave and beyond 100 m.

TABLE 2.—Numbers of crickets found in each concentric 10 m distance interval adjusted for the proportion of time spent searching in that distance interval and to the total area at each distance interval. Based on 17 nights (8 May–10 July, 2003) of data collection around Big Red Cave, Coryell County, Texas

Distance interval (m)	Number of crickets	Total search min	Crickets per min	m^2 area at distance interval	Crickets per min per m^2	Proportion of crickets per min per m^2	Cumulative proportion of crickets per min per m^2
0 to <10	14	15.0	0.933	314.2	293.07	0.098	0.098
10 to <20	59	141.7	0.416	942.5	392.51	0.132	0.230
20 to <30	56	195.5	0.287	1570.8	450.06	0.151	0.382
30 to <40	46	261.8	0.176	2199.1	386.48	0.130	0.511
40 to <50	36	321.1	0.112	2827.4	317.00	0.106	0.618
50 to <60	19	246.7	0.077	3455.8	266.21	0.089	0.707
60 to <70	24	312.2	0.077	4084.1	313.94	0.105	0.813
70 to <80	23	342.7	0.067	4712.4	316.27	0.106	0.919
80 to <90	8	348.4	0.023	5340.7	122.63	0.041	0.960
90 to <100	5	359.2	0.014	5969.0	83.10	0.028	0.988
100 to <110	1	186.0	0.005	6597.4	35.47	0.012	1.000
Total	291	2730.1	2.187	38,013.3	2976.73	1.0	

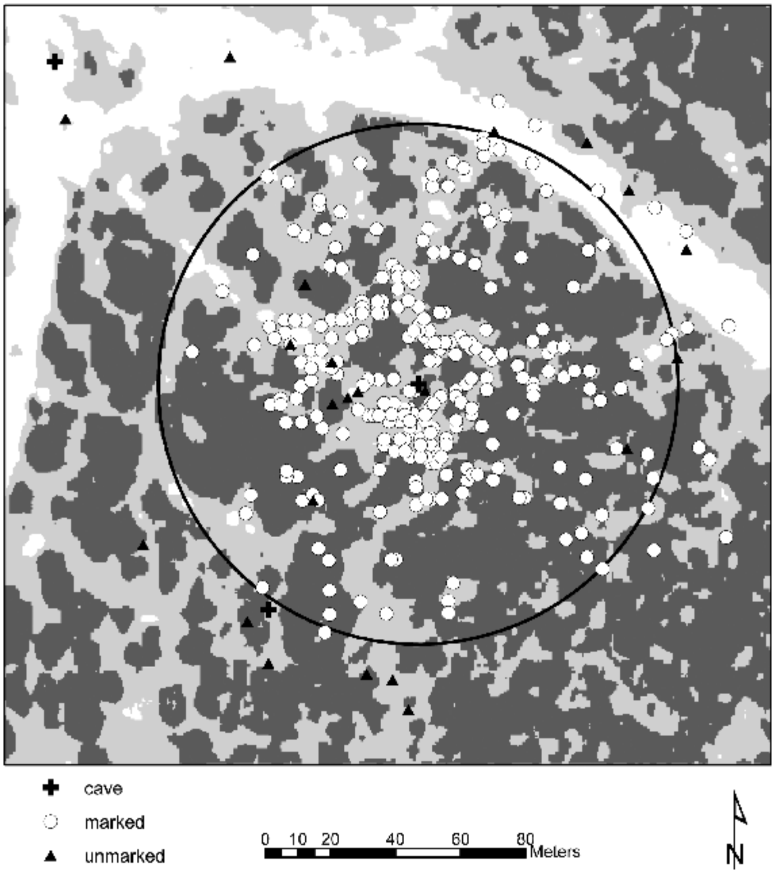


FIG. 3.—Locations [based on GPSr data, except when only surveyed location data were available (10 crickets)] of 291 marked crickets (open circles) located in the field around Big Red Cave (Coryell County, Texas). Filled triangles indicate the locations of 23 additional unmarked crickets found during nighttime searches. The entrance to Big Red Cave is indicated by a '+' at the center of the study area, another cave entrance is located in the northwestern corner, and a sinkhole is located about 85 m southwest of Big Red Cave. General vegetation types, derived from aerial photography, are: white–bare ground, light gray–grassland, dark gray–forested/shrub. The large ring marks a distance of 80 m from the entrance of Big Red Cave. Based on 17 nights (8 May–10 July, 2003) of data collection

Marked crickets were present at similar densities for each distance interval from 10 to 80 m (Table 2, Fig. 5a). Proportionally, about half (51.1%) of the crickets were foraging less than 40 m from the cave, 70.7% less than 60 m from the cave, 81.3% less than 70 m from the cave, 91.9% less than 80 m from the cave, and 96.0% less than 90 m from the cave entrance (Table 2; Figs. 5a, b). The trend of our data (Fig. 5a) suggests that some individuals may forage even farther from the cave than the maximum of 105 m observed in our study.

Time of night at which crickets were discovered was positively correlated with distance from the cave entrance ($R^2 = 0.0262$, $P = 0.0059$), indicating that the later in the night we searched, the further out from the cave entrance crickets were likely to be found (Fig. 6). Adults [22.85 ± 0.07 h CST (20.85–1.57 h CST, 193)] and nymphs [22.96 ± 0.10 h CST

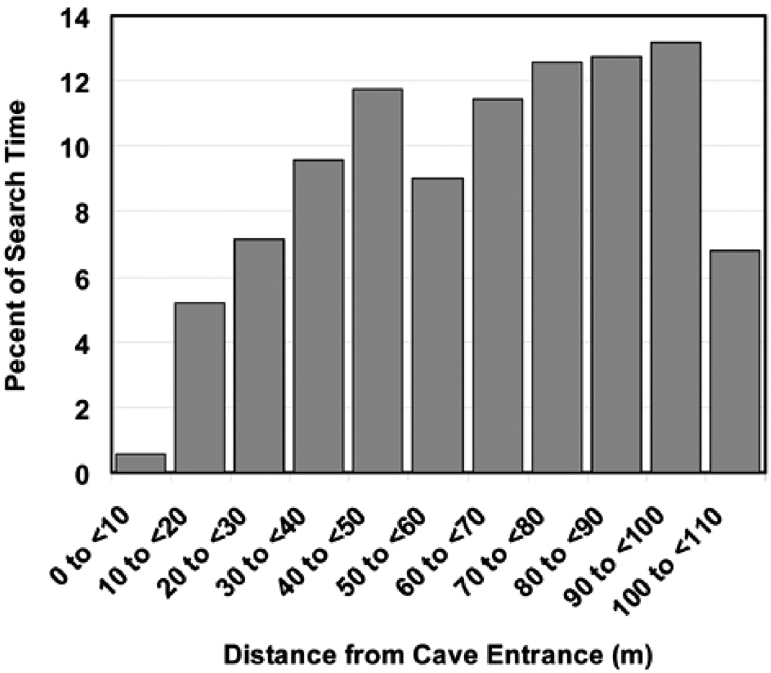
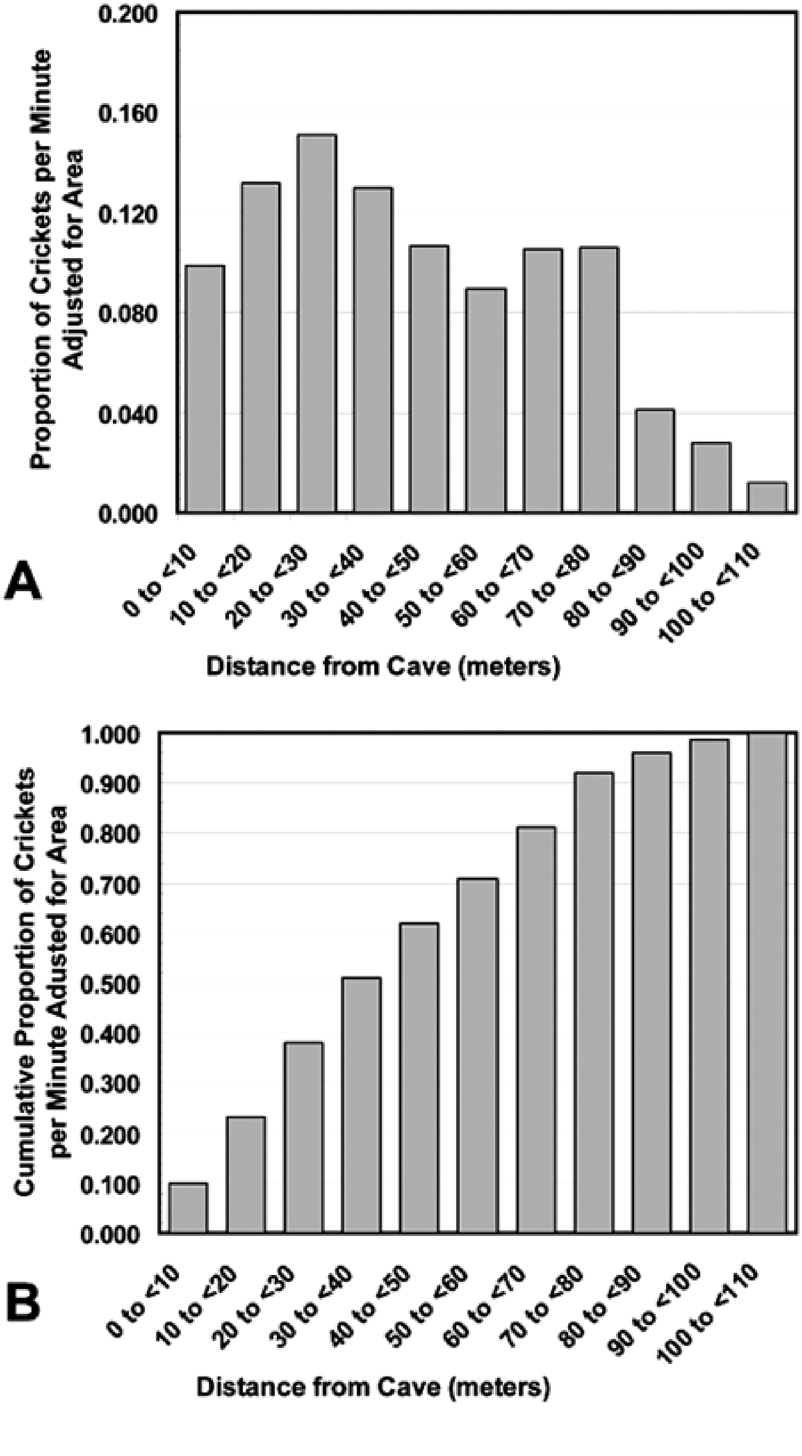


FIG. 4.—Effort, as a percentage of total search time (45.5 h) over 17 nights (8 May–10 July, 2003), spent searching for foraging *Ceuthophilus secretus* around Big Red Cave, Coryell County, Texas, within 10 m wide concentric distance intervals

(21.17–1.07 h CST, 94)] did not differ in time of night at which they were encountered (df = 189, $t = -0.86$, P = 0.3903).

Ground cover height [26.7 ± 1.0 cm (0–102 cm, 256)] was significantly greater (df = 247, $t =$ 24.72, P < 0.0001) than the height at which *Ceuthophilus secretus* were found [0.49 ± 0.13 cm (0–25 cm, 282)], and ground cover height and cricket height were not significantly correlated ($R^2 = 0.0001$, P = 0.9123, n = 248). These data suggest that *C. secretus* forages primarily at ground level. Ground cover type data were available for 276 marked crickets, and relative percentages of cover types [grass 30.8 ± 1.7% (0–100%), leaf litter 22.4 ± 1.4% (0–97%), herbaceous vegetation 20.4 ± 1.1% (0–86%), bare rock 14.5 ± 1.3% (0–100%), bare soil 5.9 ± 0.7% (0–78%), woody vegetation 5.1 ± 0.8% (0–83%) and cactus 1.0 ± 0.3% (0–34%)] indicate that the crickets occurred primarily among grasses, leaf litter and herbaceous vegetation (collectively about 73.5% of the ground cover at cricket localities). Maximum height of vegetation was variable [0.90 ± 0.74 m (0–6 m, 273)] and canopy cover data available for 280 marked *C. secretus* [open 85.94 ± 1.50% (7–100%); canopy 14.03 ± 1.50% (0–93%)] indicated that most crickets were found in open areas. Percentage canopy cover was unrelated to distance from cave entrance ($R^2 < 0.0001$, P = 0.9223, n = 280), and of the ground cover type categories, only percentage bare soil was significantly correlated with distance from cave entrance ($R^2 = 0.0225$, P = 0.0126, n = 276), perhaps because a primitive dirt road intersects the study area at 95 to 110 m (Fig. 3). Significant correlations between percentage canopy cover and ground cover type categories were positive correlations for leaf litter ($R^2 = 0.1720$, P < 0.0001, n = 274) and for woody vegetation ($R^2 = 0.2333$,


Proportion of Crickets per Minute Adjusted for Area
0.200
0.160
0.120
0.080
0.040
0.000
A
0 to <10
10 to <20
20 to <30
30 to <40
40 to <50
50 to <60
60 to <70
70 to <80
80 to <90
90 to <100
100 to <110
Distance from Cave (meters)
Cumulative Proportion of Crickets per Minute Adusted for Area
1.000
0.900
0.800
0.700
0.600
0.500
0.400
0.300
0.200
0.100
0.000
B
0 to <10
10 to <20
20 to <30
30 to <40
40 to <50
50 to <60
60 to <70
70 to <80
80 to <90
90 to <100
100 to <110
Distance from Cave (meters)

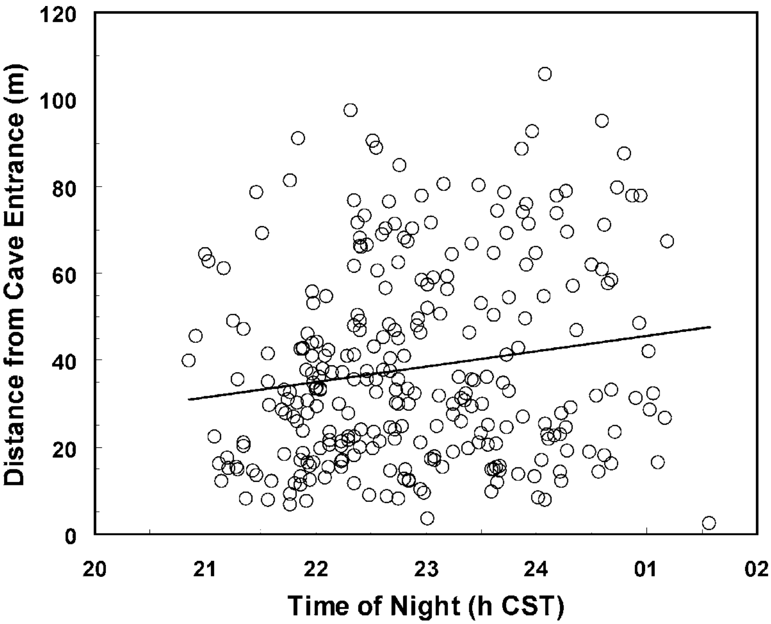


FIG. 6.—Time of night (h CST) at which *C. secretus* was encountered and the GPSr distance (m) from Big Red Cave (Coryell County, Texas) are positively correlated ($R^2 = 0.0262$, $P = 0.0059$). Best fit line is Distance = 3.5545 * Time − 43.199. Based on 17 nights (8 May–10 July, 2003) of data collection

$P < 0.0001$, $n = 274$) and negative for grasses ($R^2 = 0.1041$, $P < 0.0001$, $n = 274$) and for bare soil ($R^2 = 0.0386$, $P = 0.0011$, $n = 274$). The elevation of foraging crickets was positively correlated with the percentage of cactus ($R^2 = 0.0845$, $P < 0.0001$, $n = 267$), but was not significantly correlated with any other ground cover type.

Temperatures dropped [start, 25.48 ± 0.65 C (21.2–29.4 C, 17); end, 23.45 ± 0.74 C (19.9–28.9 C, 15)] and relative humidity rose [start, 80.0 ± 3.0% (57–96%, 15); end, 87.8 ± 2.7% (66–100%, 14)] during the course of the evening searches. The average distance from Big Red Cave at which *Ceuthophilus secretus* was found each night was not significantly correlated with start temperature ($R^2 = 0.0807$, $P = 0.2692$, $n = 17$) or humidity ($R^2 = 0.2062$, $P = 0.0891$, $n = 15$), but was positively correlated with ending temperature ($R^2 = 0.2748$, $P = 0.0449$, $n = 15$) and negatively correlated with ending humidity ($R^2 = 0.4416$, $P = 0.0095$, $n = 14$).

DISCUSSION

While the painting of and searching for crickets might alter their behavior and foraging pattern, preliminary trials did not demonstrate any obvious behavioral differences between painted and unpainted *Ceuthophilus secretus*. Crickets marked with pink paint on 17 June were observed exiting the cave in numbers on several subsequent nights, and continued to be observed as long as 20 d following marking, indicating that at least some foraging

←

FIG. 5.—Proportion (A) and cumulative proportion (B) of the total crickets per minute and adjusted for the total area at each concentric 10 m wide distance interval from the entrance of Big Red Cave, Coryell County, Texas. Based on 17 nights (8 May–10 July, 2003) of data collection

C. secretus returned to the same cave and emerged multiple times over the course of the study and that paint marks are retained for a period of time suitable for our study. These observations also indicate that the paint marks are probably not harmful to the crickets. Further, because crickets return to the cave and emerge again on other nights, many individuals have been counted more than once in the estimates of emerging crickets (above). While it is possible that crickets may alter their behavior due to handling or painting, several aspects of our study design makes it more likely that observed foraging distances are natural: (a) only crickets emerging to forage were marked; (b) a high proportion of emerging crickets could be marked by an experienced and skilled researcher; (c) the cave was subjected to less disturbance than if researchers had entered the cave to mark crickets; (d) no technical caving gear (ropes, etc.) were needed, so the effort expended to mark each cricket was considerably less than in-cave marking; (e) the emergence location of all foragers was known; and (f) we avoided the shortfalls of bait stations, as used in some of W. R. Elliott's unpublished studies (USFWS, 2003) and by Cokendolpher *et al.* (2001) in a cave in New Mexico, which could bias the distribution and movements of crickets by attracting them to energy-rich locations.

Earlier observations by W. R. Elliott indicated that most crickets forage within 30 to 50 m of cave entrances, and that distances of 60 m or more are possible for large adults (USFWS, 1994, 2003; Reddell and Cokendolpher, 2001b). Our results provide a quantitative measure of cave cricket foraging range, and indicate that *Ceuthophilus secretus* routinely forages out to 80 m or more from the cave entrance, and is relatively uniform in density out to this distance (Fig. 5a). The high percentage (85.9%) of crickets found in open areas, where grasses and bare ground are the dominant cover types, may result from the difficulty of searching the forested areas, where vegetation was typically too dense to examine fully (Fig. 3).

Ceuthophilus secretus is important in central Texas cave communities because it brings significant energy, acquired by foraging above ground at night, into the caves (Reddell and Cokendolpher, 2001b). Also, actively foraging above ground is *Solenopsis invicta*, an important introduced predator that can dominate invertebrate communities and alter their structure (Porter and Savignano, 1990; Vinson, 1991, 1994; Wojcik *et al.*, 2001; but *see* Morrison, 2002, Morrison and Porter, 2003). We have attracted night-foraging *C. secretus* with tuna and with Vienna sausage, and unpublished work by W. R. Elliott reported this species at cheese baits, suggesting proteins are a component of their diet. We observed one *C. secretus* with an insect, *Alydus* sp. (Hemiptera: Alydidae), in its mandibles, and have seen another individual feeding on *Triatoma* sp. (Hemiptera: Reduviidae), supporting W. R. Elliott's unpublished observation (USFWS, 2003) that cave crickets feed on dead insects. Collectively, these observations indicate that insects, along with ripe fruits and perhaps fungi, are important components of the diet of *C. secretus.* Fire ants are omnivorous, but prefer arthropods (Taber, 2000) and, thus, possible interactions – competition for key food resources and/or predation – between *C. secretus* and fire ants could have significant negative impacts on cave communities. The two instances of depredation of *C. secretus* by *Peromyscus* sp. observed during this study corroborate Baily's (1928) report of *Peromyscus* as a predator of *Ceuthophilus* and Viele and Studier's (1990) finding of *P. leucopus* foraging around a cave entrance. Because the presence of fire ants may alter foraging behavior of *Peromyscus* (Holtcamp *et al.*, 1997), it is possible that fire ants could influence the rates of predation of *Ceuthophilus* by *Peromyscus.* Collectively, the above observations indicate that the foraging range of the cricket is important for land managers who may wish to control fire ant populations around caves that contain federally endangered terrestrial cave invertebrates.

Cave communities typically include cave-limited (troglobitic) species exhibiting adaptations to a low-energy environment (Poulson and White, 1969). Among these adaptations are reduced metabolic rates, longer life spans and the production of fewer offspring (Culver, 1982; Howarth, 1983). The cave organisms depend on scarce resources obtained from epigean habitats (*e.g.*, Wilkens *et al.*, 2000). Cave-limited terrestrial invertebrates of central Texas depend upon a natural influx of nutrients in the form of organic material–fecal material from major trogloxenes (*e.g.*, cave crickets), leaf litter and animals (both dead and alive). *Ceuthophilus secretus* is a key species (Davic, 2003) in caves where it is abundant (*e.g.*, the present study), a view held by Reddell and Cokendolpher (2001b) who indicated the primary threat posed to cave communities by fire ants is the impact of these ants on cave cricket populations. We have documented large numbers of the crickets emerging from a cave and foraging up to at least 105 m from the cave entrance. When we account for search effort (time) and adjust for available area at each distance interval, we found that 50% of the crickets are foraging within 40 m of the cave entrance. Even so, our calculations also indicate that more than 18% of the crickets are foraging beyond 70 m from the cave entrance. Our study focused on a single cave and, thus, there is a need for comparative work at other caves in central Texas to assess the generality of our findings.

Elliott's unpublished data (USFWS, 2003), coupled with knowledge of fire ant foraging ranges, have been used as the basis for carrying out fire ant treatments around caves in the San Antonio (USFWS, 2003) and Austin (Elliott, 1992) areas and have influenced the size of preserves needed to protect federally endangered cave faunas (USFWS, 2003). Our data suggest that a relatively large area may need protection. Based on the foraging range data we provide here for *Ceuthophilus secretus*, cave resource managers may wish to create buffers around the footprint of a cave–not just the entrance, as there may be other, cricket-sized openings that may have been overlooked in spite of intensive searches in the vicinity of Big Red Cave during and prior to this study. It may not be feasible to encompass the entire cave cricket foraging range. Instead, it may be reasonable to choose some percentage (*i.e.*, Fig. 5b) of the known foraging range and manage that area. Further, it may be appropriate to extend another buffer beyond the cricket foraging range to account for the foraging range of fire ants, thus avoiding interactions, and perhaps another buffer around that, within which one could attempt to maintain natural vegetation, avoiding edge effects that favor fire ants. The concept of buffers around a cave footprint previously has been discussed by Veni (1999) and discussed and implemented by USFWS (2003).

Our data also suggest that *Ceuthophilus secretus* can and will cross at least primitive dirt roads. Critical habitat boundaries for seven federally endangered cave invertebrates were designated at 22 urban sites in Bexar County, Texas (USFWS, 2003). Numerous studies have examined mortality impacts of roadways on vertebrates (Forman and Alexander, 1998; Spellerberg, 1998), and a few studies have examined effects of roads on invertebrates (*e.g.*, Bhattacharya *et al.*, 2003; Haskell, 2000; Mader *et al.*, 1990). For vertebrate taxa, underpasses for roads have been used with mixed success to reduce mortality (*e.g.*, Jackson and Tyning, 1989; Yanes *et al.*, 1995; Clevenger and Waltho, 2000; Cain *et al.*, 2003; Dodd *et al.*, 2004; Ng *et al.*, 2004). Because surface-foraging *C. secretus* are largely ground dwelling, they may be subject to significant mortality when cave entrances are adjacent to urban roads. Furthermore, roads could have more subtle effects on *C. secretus* by altering site fidelity, as has been reported for bumblebees (Bhattacharya *et al.*, 2003), or by avoidance of roadways, as has been reported for other terrestrial ground dwelling invertebrates (Mader *et al.*, 1990). The sites where critical habitat was designated by USFWS (2003) in San Antonio average 19.45 ha (range 5-37 ha) in size, and more than half (12 of 22) of these encompass roads. It may be that *C. secretus* mortality in such settings, especially in high traffic areas, could be reduced by the construction of underpasses such as those that have been used for salamanders (*e.g.*, Jackson and Tyning, 1989) or by other means such as slightly elevating roadways (*e.g.*, Clevenger *et al.*, 2003). Our study was conducted in a rural setting, and there is still a need for further study of habitat use by *Ceuthophilus* spp. in the vicinity of caves harboring endangered species in more urban settings in Travis, Williamson (USFWS, 1994), and Bexar (USFWS, 2003) counties to elucidate the nature of the interactions between the relatively large foraging range of the crickets and an urban environment.

In a broader perspective, our study underscores the importance of linking cave invertebrate conservation to surface foraging invertebrate trogloxenes (*e.g.*, Orthoptera and Opiliones) and suggests that development of cave preserves should consider corridors for movement and gene flow (Samways, 1993) that take into account the foraging range of these trogloxenes, especially where large colonies of cave-roosting bats or other energy sources are limited. Patterns of genetic divergence among trogloxenic invertebrate populations (*e.g.*, Allegrucci *et al.*, 1997; Ketmaier *et al.*, 2000; Bernardini and Ketmaier, 2002) may be partially explained by the dispersal capacities of the species.

Rhaphidophorid crickets inhabit caves of temperate and tropical regions of the world, and at least half of the approximately 300 known species of Rhaphidophoridae are cavernicoles (Sbordoni and Cobolli, 2004). Of these, various species, including *Spelaeiacris tabula* in South Africa (Carchini *et al.*, 1991; Sharratt *et al.*, 2000), *Dolichopoda geniculata* in Italy (Carchini *et al.*, 1995), *Gymnoplectron waitomoensis* and *Pallidoplectron turneri* in New Zealand (Richards, 1961, 1965), *Pallidotettix nullarborensis* in Australia (Richards, 1970, 1971) *Troglophilus cavicola* and *T. neglectus* in Slovenia (Novack and Kustor, 1983; Pehani *et al.*, 1997), *Heteromallus cavicola* in Chili (Di Russo *et al.*, 1996), *Ceuthophilus conicaudus* in New Mexico (Campbell, 1976) and *Hadenoecus subterraneus* in Kentucky (Hubbell and Norton, 1978; Nichols, 1962; Park and Reichle, 1963; Reichle *et al.*, 1965; Levy, 1976; Helf, 2003), forage in epigean habitats at night during the warmer months, returning to roost in caves and other sheltered habitats in large numbers during the daytime. A similar pattern has been observed in some harvestmen, notably *Goniosoma spelaeum* (Arachnida: Opiliones: Gonyleptidae) in caves of southeastern Brazil (Gnaspini, 1996; Hoenen and Gnaspini, 1999). Cave crickets contribute quantities of guano to the cave environment, and concentrations of this guano can represent resource-rich areas where other cavernicoles accumulate (Benoit *et al.*, 2004; Hubble and Norton, 1978; Peck, 1976; Poulson and Culver, 1969; Poulson, 1992; Poulson and Kane, 1981; Poulson *et al.*, 1995). In addition, cave crickets may function as a transport mechanism allowing other organisms to move into or out of caves, as suggested by Benoit *et al.* (2004) for fungi. Our data, therefore, have broader implications for understanding the role of invertebrate trogloxenes in providing energy to caves and in defining the ecotone between cave and surface environments (Culver, 2004).

Acknowledgments.—We thank Frank Hutto, Nick Dolce, Luke Garver, Stacey Clementz, Erin Raboin and Jennifer E. Smith for laboratory assistance; and Denise Prendergast, Chris Krejca, Vivian Loftin and Andy Gluesenkamp for their help with field work. Research funds were provided through the Engineer Research and Development Center and the Department of the Army under DACA88-99-D-0002-14. Information contained in this manuscript does not necessarily reflect the position or policy of the U.S. government. We are grateful to the Natural Resources Branch of Fort Hood and to the Texas Nature Conservancy (Fort Hood TX) for cooperation and assistance, especially John D. Cornelius, B. R. Jones, Charles E. Pekins, and Paul M. Cavanagh. We thank James Reddell (Texas Memorial Museum, Austin TX), JoAnn Jacoby (University of Illinois, Champaign IL), Thomas L. Poulson (Jupiter FL), Kurt L. Helf (Mammoth Cave National Park, Mammoth Cave KY), two anonymous reviewers and the associate editor of this journal for their comments on an earlier draft of this paper.

LITERATURE CITED

ALLEGRUCCI, G., M.-G. MINASI AND V. SBORDONI. 1997. Patterns of gene flow and genetic structure in cave-dwelling crickets of the Tuscan endemic, *Dolichopoda schiavazzii* (Orthoptera, Rhaphidophoridae). *Heredity,* **78**:665–673.

ATKINSON, G. L. 2003. The caves and pseudokarst of east Texas. Bulletin 4. Texas Speloeol. Surv., Austin, Texas. 25 p.

——— AND A. R. SMITH. 2001. Geology of the Lampsas Cut Plain, p. 4–8. *In:* J. R. Reddell (ed.). The caves of the Lampasas Cut Plain. Texas Spelol. Surv., Austin, Texas. 64 p.

BAILY, V. 1928. Animal life of the Carlsbad Cavern. (Monographs of the American Society of Mammalogists, no. 3). Williams and Wilkins Company, Baltimore, Maryland, USA. 195 p.

BENOIT, J. B., J. A. YODER, L. W. ZETTLER AND H. H. HOBBS, III. 2004. Mycoflora of a trogloxenic cave cricket, *Hadenoecus cumberlandicus* (Orthoptera: Rhaphidophoridae), from two small caves in northeastern Kentucky. *Ann. Entomol. Soc. Amer.,* **97**:989–993.

BERNARDINI, C. AND V. KETMAIER. 2002. Isolation and characterization of five microsatellite loci in *Dolichopoda* cave crickets (Orthoptera Rhaphidophoridae). *Mol. Ecol. Notes,* **2**:501–503.

BHATTACHARYA, M., R. B. PRIMACK AND J. GERWEIN. 2003. Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biol. Conserv.,* **109**:37–45.

CAIN, A. T., V. R. TUOVILA, D. G. HEWITT AND M. E. TEWES. 2003. Effects of a highway and mitigation projects on bobcats in southern Texas. *Biol. Conserv.,* **114**:189–197.

CAMPBELL, G. D. 1976. Activity rhythm of the cave cricket, *Ceuthophilus conicaudus* Hubbell. *Am. Midl. Nat.,* **96**:350–366.

CARCHINI, G., C. DI RUSSO AND M. RAMPINI. 1991. Observations on the biology of *Spelaeiacris tabulae* Peringuey (Orthoptera, Rhaphidophoridae), from the Wynberg cave (Capetown, South Africa). *Internat. J. Speleol.,* **20**:47–55.

———, M. RAMPINI AND V. SBORDONI. 1995. Life cycle and population ecology of the cave cricket *Dolichopoda geniculata* (Costa) from Valmarino cave (Central Italy). *Internat. J. Speleol.,* **23**: 203–218.

CHANDLER, D. S. AND J. R. REDDELL. 2001. A review of the ant-like litter beetles found in Texas caves (Coleoptera: Staphylinidae: Pselaphinae). *Texas Mem. Mus., Speleol. Monogr.,* **5**:115–128.

CLEVENGER, A. P. AND N. WALTHO. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conserv. Biol.,* **14**:47–56.

———, B. CHRUSZEZ AND K. E. GUNSON. 2003. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biol. Conserv.,* **109**:15–26.

COKENDOLPHER, J. C. 2001. Reproductive behavior of *Ceuthophilus carlsbadensis,* a cave inhabiting camel cricket. *Texas Mem. Mus., Speleol. Monogr.,* **5**:95–104.

———. 2004a. *Cicurina* spiders from caves in Bexar County, Texas (Araneae: Dictynidae) from Fort Hood, Texas, with description of another new species. *Texas Mem. Mus., Speleol. Monogr.,* **6**: 13–58.

———. 2004b. Notes on troglobitic *Cicurina* (Araneae: Dictynidae) from Fort Hood, Texas, with description of another new species. *Texas Mem. Mus., Speleol. Monogr.,* **6**:58–62.

——— AND J. R. REDDELL. 2001. Cave spiders (Araneae) of Fort Hood, Texas, with descriptions of new species of *Cicurina* (Dictynidae) and *Neoleptoneta* (Leptonetidae). *Texas Mem. Mus., Speleol. Monogr.,* **5**:35–55.

———, R. K. LAWRENCE AND V. J. POLYAK. 2001. Seasonal and site-specific bait preferences of crickets and diplurans in Hidden Cave, New Mexico. *Texas Mem. Mus., Speleol. Monogr.,* **5**:95–104.

CULVER, D. C. 1982. Cave life: evolution and ecology. Harvard University Press, Cambridge, Massachusetts. 189 p.

———. 2004 [2005]. Ecotones, p. 207–208. *In:* D. C. Culver and W. B. White (eds.). Encylopedia of Caves. Elsevier Academic Press, Amsterdam. 654 p.

DAVIC, R. D. 2003. Linking keystone species and functional groups: a new operational definition of the keystone species concept. *Conserv. Ecol.,* **7**:r11. [online] URL: http://www.consecol.org/vol7/iss1/

DI RUSSO, C., L. DE PASQUALE AND M. RAMPINI. 1996. Observations on the biology of two Patagonian Rhaphidophoridae (Orthoptera): *Heteromallus cavicola* and *Udenus w-nigrum. An. Inst. Patagonia Ser. Cien. Nat.,* **24**:105–116.

DODD, C. K., JR., W. J. BARICHIVICH AND L. L. SMITH. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. *Biol. Conserv.,* **118**:619–631.

ELLIOTT, W. R. 1992. The imported red fire ant in Texas caves. *NSS Bull.,* **54**:83–84.

———. 2004. *Speodesmus* cave millipedes. Four new species from central Texas (Diplopoda: Polydesmida: Polydesmidae). *Texas Mem. Mus., Speleol. Monogr.,* **6**:163–174.

FORMAN, R. T. T. AND L. E. ALEXANDER. 1998. Roads and their major ecological effects. *Ann. Rev. Ecol. Syst.,* **29**:207–231.

GERS, C. 1998. Diversity of energy fluxes and interactions between arthropod communities: from soil to cave. *Acta Oecologica,* **19**:205–213.

GNASPINI, P. 1996. Population ecology of *Goniosoma spelaeum*, a cavernicolous harvestman from south-eastern Brazil (Arachnida: Opiliones: Gonyleptidae). *J. Zool. (London),* **239**:417–435.

HASKELL, D. G. 2000. Effects of roads on macroinvertebrate soil fauna of the southern Appalachian Mountains. *Conserv. Biol.,* **14**:57–63.

HELF, K.L. 2003. Foraging ecology of the cave cricket *Hadenoecus subterraneus*: effects of climate, ontogeny, and predation. Ph.D. Dissertation, University of Illinois at Chicago. xvii + 170 p.

HOENEN, S. AND P. GNASPINI. 1999. Actitvity rhythms and behavioral characterization of two epigean and one cavernicolous harvestman (Arachnida, Opiliones, Gonyleptidae). *J. Arachnol.,* **27**:159–167.

HOLTCAMP, W. N., W. E. GRANT AND S. B. VINSON. 1997. Patch use under predation hazard: effect of the red imported fire ant on deer mouse foraging behavior. *Ecology,* **78**:308–317.

HOSE, L. D., A. N. PALMER, M. V. PLANER, D. E. NORTHUP, P. J. BOSTON AND H. R. DUCHENE. 2000. Microbiology and geochemistry in a hydrogen-sulphide-rich karst environment. *Chem. Geol.,* **169**:399–423.

HOWARTH, F. G. 1983. Ecology of cave arthropods. *Ann. Rev. Entomol.,* **28**:365–389.

HUBBELL, T. H. AND R. M. NORTON. 1978. The systematics and biology of the cave-crickets of the North American Tribe Hadenoecini (Orthoptera Saltatoria: Ensifera: Rhaphidophoridae: Dolichlpodinae). *Misc. Publ. Mus. Zool.,* **156**:1–124.

JACKSON, S. D. AND T. F. TYNING. 1989. Effectiveness of drift fences and tunnels for moving spotted salamanders *Ambystoma maculatum* under roads, p. 93–99. *In:* T. E. S. Langton (ed.). Amphibians and roads. ACO Polymer Products, Ltd., Shefford, UK.

KETMAIER, V., M. COBOLLI, E. DE MATTHAEIS AND M. RAMPINI. 2000. Biochemical systematics and patterns of genetic divergence between the *Troglophilus* species of Crete and Rhodos (Orthoptera, Rhaphidophoridae). *Belgian J. Zool.,* **130**(Suppl.):51–55.

KORSUKHIN, M. D., S. D. PORTER, L. C. THOMPSON AND S. WILEY. 2001. Modeling temperature-dependent range limits for the Fire Ant *Solenopsis invicta* (Hymenoptera, Formicidae) in the United States. *Environ. Entomol.,* **30**:645–655.

LEVY, E. S. 1976. Aspects of the biology of *Hadenoecus subterraneus* with special reference to foraging behavior. M.Sc. Thesis, University of Illinois at Chicago Circle. xii + 266 p.

MADER, H. J., C. SCHELL AND P. KORNACKER. 1990. Linear barriers to arthropod movements in the landscape. *Biol. Conserv.,* **54**:209–222.

MARKIN, G. P., J. O'NEAL AND J. H. DILLIER. 1975. Foraging tunnels of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc.,* **48**:83–89.

MITCHELL, R.W. AND J.R. REDDELL. 1971. The invertebrate fauna of Texas caves, p 35–90. *In:* E.L. Lundelius and R.H. Slaughter (eds.). Natural History of Texas caves. Gulf Nat. Hist., Dallas, Texas. 174 p.

MORRISON, L. W. 2002. Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis invicta. Ecology,* **83**:2337–2345.

——— AND S. D. PORTER. 2003. Positive association between densities of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), and generalized ant and arthropod diversity. *Environ. Entomol.,* **32**:548–554.

MUCHMORE, W. B. 2001. Review of the genus *Tartarocreagris* with descriptions of new species (Pseudoscorpionida: Neobisiidae). *Texas Mem. Mus., Speleol. Monogr.,* **5**:57–72.

NG, S. J., J. W. DOLE, R. M. SAUVAJOT, S. P. D. RILEY AND T. J. VALONE. 2004. Use of highway undercrossings by wildlife in southern California. *Biol. Conserv.,* **115**:499–507.

NICHOLS, G. 1962. Nocturnal migration of *Hadenoecus subterraneus*. *NSS News,* **20**:102.

NORTHUP, D. E. 1988. Community structure of the arthropods of Carlsbad Cavern emphasizing Rhaphidophoridae of the genus *Ceuthophilus*. M.Sc. Thesis, University of New Mexico. viii + 53 p.

NOVAK, T. AND V. KUSTOR. 1983. On *Troglophilus*. (Rhaphidophoridae, Saltatoria) from north Slovenia (YU). *Mém. Biospéol.,* **10**:127–137.

PAQUIN, P. AND M. HEDIN. 2004. The power and perils of 'molecular taxonomy': a case study of eyeless and endangered *Cicurina* (Araneae: Dictynidae) from Texas caves. *Mol. Ecol.,* **13**:3239–3255.

PARK, O. AND D. REICHLE. 1963. Observations on the ecology and behavior of the cave cricket *Hadenoecus subterraneus*. *Bull. Ecol. Soc. Amer.,* **44**:126–127.

PECK, S. B. 1976. The effect of cave entrances on the distribution of cave-inhabiting terrestrial arthropods. *Internat. J. Speleol.,* **8**:309–321.

PEHANI, Š., M. VIRANT-DOBERLET AND S. JERAM. 1997. The life cycle of the cave cricket *Troglophilus neglectus* Krauss with a note on *T. cavicola* Kollar (Orthoptera: Rhaphidophoridae). *Entomol.,* **116**:224–238.

PORTER, S. D. AND D. A. SAVIGNANO. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology,* **71**:2095–2106.

POULSON, T. L. 1992. The Mammoth Cave ecosystem, p. 569–611. *In*: A. Camacho (ed.). The Natural History of Biospeleology. Monogr. Museo Nac. Cien. Nat., Madrid, Spain. 680 p.

——— AND D. C. CULVER. 1969. Diversity in terrestrial cave communities. *Ecology,* **50**:153–158.

——— AND T. C. KANE. 1981. How food type determines community organization in caves. *Proc. 8th Int. Congr. Speleol.,* **1**:56–59.

———, K. LAVOIE AND K. L. HELF. 1995. Long-term effects of weather on the cricket (*Hadenoecus subterraneus*, Orthoptera, Rhaphidophoridae) guano community in Mammoth Cave National Park. *Am. Midl. Nat.,* **134**:226–236.

——— AND W. B. WHITE. 1969. The cave environment. *Science,* **165**:971–981.

REICHLE, D. E., J. D. PALMER AND O. PARK. 1965. Persistent rhythmic locomotor activity in the cave cricket, *Hadenoecus subterraneus*, and its ecological significance. *Amer. Midl. Nat.,* **74**:57–66.

RICHARDS, A. M. 1961. The life history of some species of Rhaphidophoridae (Orthoptera). *Trans. R. Soc. N. Z. (Zool.),* **1**:121–137.

———. The effect of weather on Rhaphidophoriae (Orthoptera) in New Zealand and Australia. *Ann. Spéléol.,* **20**:391–400.

———. 1969. Observations on the biology of *Palidotettix nullarborensis* Richards (Rhaphidophoridae: Orthoptera) from the Nullarbor Plain. *Proc. Linnean Soc. New South Wales,* **94**:195–206.

———. 1971. An ecological study of the cavernicolous fauna of the Nullarbor Plain, Southern Australia. *J. Zool. (London),* **164**:1–60.

REDDELL, J. R. AND J. C. COKENDOLPHER. 2001*a*. A new species of troglobitic *Rhadine* (Coleoptera: Carabidae) from Texas. *Texas Mem. Mus., Speleol. Monogr.,* **5**:109–114.

——— AND ———. 2001*b*. Ants (Hymenoptera: Formicidae) from the caves of Belize, Mexico, and California and Texas (U. S.A.). *Texas Mem. Mus., Speleol. Monogr.,* **5**:129–154.

SARBU, S. M., T. C. KANE AND B. K. KINKLE. 1996. Chemoautotrophically based cave ecosystem. *Science,* **272**:1953–1955.

SAMWAYS, M. J. 1993. Insects in biodiversity conservation: some perspectives and directives. *Biodiv. Conserv.,* **2**:258–282.

SAS INSTITUTE. 2001. The SAS system for Windows, release 8.2. SAS Institute, Inc., Cray, North Carolina.

SCUDDER, S. H. 1894. The North American Ceuthophili. *Proc. Amer. Acad. Arts Sci.,* **30**:17–111.

SBORDONI, V. AND M. COBOLLI. 2004. Insecta: pterygota, p. 451–453. *In:* G. W. Gunn (ed.). Encyclopedia of Caves and Karst Science. Fitzroy Dearborn, New York. 902 pp.

SHARRATT, N. J., M. D. PICKER AND M. J. SAMWAYS. 2000. The invertebrate fauna of the sandstone caves of the Cape Peninsula (South Africa): patterns of endemism and conservation priorities. *Biodiv. Conserv.,* **9**:107–143.

SIMON, K. S., E. F. BENFIELD AND S. A. MACKO. 2003. Food web structure and the role of epilithic biofilms in cave streams. *Ecology,* **84**:2395–2406.

SPELLERBERG, I. F. 1998. Ecological effects of roads and traffic: a literature review. *Global Ecol. Biogeog. Lett.,* **7**:317–333.

STUDIER, E. H., K. H. LAVOIE AND F. G. HOWARTH. 2002. Leg attenuation and seasonal femur length: mass relationships in cavernicolous crickets (Orthoptera: Gryllidae and Rhaphidophoridae). *J. Cave Karst Stud.,* **64**:126–131.

TABER, S. W. 2000. Fire Ants. Texas A&M University Press, College Station, Texas. 308 p.

TAYLOR, S. J. 2003. America, North: biospeleology, p. 45–49. *In:* G. W. Gunn (ed.). Encyclopedia of Caves and Karst Science. Fitzroy Dearborn, New York. 902 p.

TSCHINKEL, W. R., E. S. ADAMS AND T. MACON. 1995. Territory area and colony size in the fire ant *Solenopsis invicta. J. Anim. Ecol.,* **64**:473–480.

UBICK, D. AND T. S. BRIGGS. 2004. The harvestman family Phalangodidae. 5. New records and species of *Texella* Goddnight and Goodnight (Opiliones: Laniatores). *Texas Mem. Mus., Speleol. Monogr.,* **6**:101–141.

U.S. FISH AND WILDLIFE SERVICE, DEPARTMENT OF THE INTERIOR (USFWS). 1988. Endangered and threatened wildlife and plants: final rule to determine five Texas cave invertebrates to be endangered species. *Fed. Reg.,* **53**:36029–36033.

———. 1993. Endangered and threatened wildlife and plants: coffin Cave mold beetle (*Batrisodes texanus*) and the Bone Cave harvestman (*Texella reyesi*) determined to be endangered. *Fed. Reg.,* **58**:43818–43820.

———. 1994. Recovery plan for endangered karst invertebrates in Travis and Williamson counties, Texas. Albuquerque, New Mexico. 154 p.

———. 2000. Endangered and threatened wildlife and plants; Final rule to list nine Bexar County, Texas invertebrate species as endangered. *Fed. Reg.,* **65**:81419–81433.

———. 2003. Endangered and threatened wildlife and plants; Designation of critical habitat for seven Bexar County, TX, invertebrates species. *Fed. Reg.,* **68**:17156–17231.

VENI, G. 1999. A geomorphological strategy for conducting environmental impact assessments in karst areas. *Geomorphol.,* **31**:151–180.

VIELE, D. P. AND E. H. STUDIER, 1990. Use of a localized food source by *Peromyscus leucopus*, determined with an hexagonal grid system. *NSS Bull.,* **52**:52–53.

VINSON, S. B. 1991. Effect of the red imported fire ant (Hymenoptera: Formicidae) on a small plant-decomposing arthropod community. *Environ. Entomol.,* **20**:98–103.

———. 1994. Impact of the invasion of *Solenopsis invicta* (Buren) on native food webs, p. 240–258. *In:* D. F. Williams (ed.). Exotic ants. Biology, impact, and control of introduced species. Westview Press, Boulder, Colorado. 322 p.

WILKENS, H., D. C. CULVER AND W. F. HUMPHREYS (eds.). 2000. Subterranean ecosystems. Ecosystems of the World, 30. Elsevier, Amsterdam. 791 p.

WILSON, N. L., J. H. DILLIER AND G. P. MARKIN. 1971. Foraging territories of imported fire ants. *Ann. Entomol. Soc. Amer.,* **64**:660–665.

——— AND A. D. OLIVER. 1969. Food habits of the imported fire ant in pasture and pine forest areas in southeastern Louisiana. *J. Econ. Entomol.,* **62**:1268–1271.

WOJCIK, D. P., C. R. ALLEN, R. J. BRENNER, E. A. FORYS, D. P. JOUVENAZ AND R. S. LUTZ. 2001. Red imported fire ants: impact on biodiversity. *Amer. Entomol.,* **47**:16–23.

YANES, M., J. M. VELASCO AND F. SUAREZ. 1995. Permeability of roads and railways to vertebrates: the importance of culverts. *Biol. Conserv.,* **71**:217–222.

SUBMITTED 04 AUGUST 2004 ACCEPTED 10 DECEMBER 2004