

# THE BIOLOGY AND ECOLOGY OF NORTH AMERICAN CAVE CRICKETS

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**Abstract** Cave and camel crickets are widely distributed in caves throughout the world, and in North America they make up the bulk of the biomass in many caves. Most caves do not have large populations of bats, so the guano, eggs, and carcasses of these cavernicolous crickets are dependable sources of fixed energy for troglobites (Mohr and Poulson, 1966; Barr, 1967; Barr and Kuehne, 1971; Richards, 1971; Harris, 1973). The crickets often are a true keystone species, maintaining cricket guano communities and specialized egg predators, as well as providing more dispersed energy inputs that increase overall ecosystem diversity. They are all commonly referred to as crickets, and are all in the same Order (Orthopterans) with grasshoppers, crickets, and katydids. Most cave crickets actually are grasshoppers. Cave crickets in Hawaii are true crickets (Gryllids). Because cave crickets are relatively large and abundant, they have received more study as a group than most other cavernicolous invertebrates, but there are still a lot of things we don't know about cave crickets and some continuing mysteries.

## CLASSIFICATION AND GENETICS

Early researchers were fascinated by the bizarre life forms frequently encountered in caves, and spent a lot of effort looking for confirmation of their evolutionary ideas. In his 1888 *The Cave Fauna of North America*, Packard was surprised to find that cave crickets collected from deep inside a cave showed the same eye morphology as those collected near an entrance. He invoked a complicated explanation of acceleration and retardation to explain differences in ovipositor length instead of attributing differences to a range of sizes and ages in crickets.

Cavernicolous members of the tribe *Ceuthophilini* are widely distributed throughout the United States and into Mexico, while cavernicolous members of the tribe *Hadenocini* are restricted to the American southeast. The taxonomic relations and geographical distributions of the tribe *Ceuthophilini* have been reported by Hubbell (1936) and tribe *Hadenocini* by Hubbell and Norton (1978). In May of 2006, Northern Arizona University announced the discovery of a new genus of cave cricket and two new species of cavernicolous *Ceuthophilus*. These new crickets were found as part of a survey of 24 caves in the Grand Canyon-Parashant National Monument in Arizona ([www.onlinepressroom.net/nau/](http://www.onlinepressroom.net/nau/)).

Rhaphidiphorids are wingless, with long antennae. They have robust hind legs for jumping, and are sometimes called camel crickets because the back is humped up with the head bent down. Both males and females have two cerci at the end of the abdomen that are rich in sensory receptors. Adult female crickets have an ovipositor between the two sensory cerci. Cavernicolous crickets show a range of adaptations (trogomorphy) to the cave environment. Some species, such as *Ceuthophilus stygius* camel crickets in Kentucky, use the cave only as a refuge during the day. They forage and lay eggs outside in the

forest. The young crickets hatch, and many over-winter just inside cave entrances. They are clearly troglonexes. *Hadenocinus subterraneus* cave crickets in Mammoth Cave and *Ceuthophilus conicaudus* in Carlsbad Cavern leave the cave only to feed, and all other aspects of their life cycle occur in caves, so they are habitual troglonexes or troglophiles. Some species, such as *Caecanemobius varius* found in the lava tube Kaumana Cave in Hawaii, feed and reproduce in caves without ever leaving, and are true troglobites.

In Carlsbad Cavern there are three different species of *Ceuthophilus* crickets that represent a range of troglomorphic adaptations (Fig. 1). The least cave-adapted species is the robust *C. carlsbadensis* that is common in areas with bat guano. The most cave adapted species, *C. longipes*, lives in remote areas of Carlsbad where food is very limited. The intermediate species, *C. conicaudus*, is widely distributed in smaller caves throughout the Park.

A very interesting and diverse group of true gryllid crickets live in lava-tube caves of the Hawaiian archipelago (Fig. 2). Howarth (personal communication) states that there are more different kinds of cave crickets in Hawaii than in all of continental North America. There are at least two *Caecanemobius* species that live in Kaumana Cave on the big island of Hawaii and another species in small interstitial spaces on the lava flow. Both the cave crickets and the lava flow cricket are presumably evolved from a large, dark, eyed species that lives in the wave-splash zone of rocky beaches. The lava flow cricket retains its eyes and shows a slight reduction in pigmentation and a great

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**Figure 1.** Comparison of the three Carlsbad *Ceuthophilus* crickets, left to right, *C. carlsbadensis*, *C. conicaudus*, and *C. longipes*. Adult males.

reduction in size. The highly-cave adapted species is very small, blind, and has lost nearly all of its pigment. What is particularly noteworthy is that this divergence from a common ancestor must have happened between 700,000 and 1,000,000 years ago, which is the maximum age of the big island of Hawaii (Howarth, 1983, 1987; Otte, 1994).

The genetics of nine species of cave crickets from sites in Pennsylvania through Alabama were analyzed by Caccone

and Sbordoni (1987) and Caccone and Powell (1987). The results show that populations of cave crickets in areas where the limestone is continuous, but highly fractured, are genetically more variable than populations from regions where the limestone distribution is more disjointed. This pattern suggests that cricket movement between populations through subsurface conduits is important in maintaining genetic variability. A lack of genetic differentiation among populations of the trogloneic camel cricket, *Ceuthophilus gracilipes*, was reported by Cockley et al. (1977) over a 1,000 km<sup>2</sup> (386 mi<sup>2</sup>) area in the eastern United States. This species is found in caves and in the forest under logs and loose bark. Their findings suggest that the forest populations may serve as a genetic bridge among cave populations.

Genome size is an important taxonomic factor because it influences cell size and how long it takes a cell to divide. Genome size in orthopteran averages 8.2 pg  $\pm$  0.5 for haploid DNA. The smallest known orthopteran genome size is 1.55 pg in *H. subterraneus* (Gregory, 2001).

#### LIFE HISTORY

The life history of *Hadenoecus subterraneus* begins when a female cricket inserts her ovipositor into sandy soil, and inserts an egg below the surface. The egg, about the size and shape of a grain of long rice, stays buried for about



**Figure 2.** Undescribed underground tree cricket (*Thaumotogryllus* sp) from caves on Maui. Adult female.



12 weeks before the nymph hatches. The nymph is not completely developed; it has yolk where its digestive tract will be, but the longer the egg stays in the sand, the more likely it will be eaten by a specialized egg predator, the sand beetle *Neaphaenops tellkampfi*. Once it hatches, the nymph works its way out of the soil and moves to the walls and ceiling of the passage where it has less chance of being eaten. Crickets at this stage completely lack pigment, and are called whities.

Many measures of cricket size have been used by field biologists, including head width and leg lengths. For *Hadenoeus subterraneus*, we have reliably measured the length of the drumstick (i.e., the femur of the hindmost pair of legs, or Hind Femur Length [HFL]). Whities have HFL of slightly less than 5 mm. As crickets molt they go through many stages or instars. They first begin to develop secondary sexual characteristics at around 10 mm HFL and reach a gangly teen-age stage at around 15 mm HFL and are grayish-brown in color. They make their final molt to adults at HFL usually greater than 20 mm HFL. We rarely (0.5–3.8%) find a sexually mature adult cave cricket with a HFL less than 20 mm. Most adults have a HFL of around 23 mm; we have never measured a *Hadenoeus* cave cricket larger than 26 mm HFL. Sexually mature adult crickets are darker brown than sub-adults due to hardening and tanning (sclerotization) of legs and ovipositors. We hypothesize that the crickets take up to three to four years to reach adult size that is probably influenced by their success in finding food. Crickets may live another three to four years (or longer) as a sexually mature adult. One of the best lines of evidence we have for this extreme longevity is the frequency of observed molting crickets. *C. stygius*, which lives for a year, routinely has 2–6% of the population molting, compared to *H. subterraneus*, where the rates are 0.1–0.01% (based on one molting cricket of 512 observed, one of 969, and one of 1,024 on different census dates, and many thousands of crickets observed with no molts).

Reproductive studies on cave crickets have concentrated on the presence and size of mature gonads, egg-laying rates, and reproductive behaviors. Seasonal dissections of crickets for spermatophores in males and ova in females suggest that *H. subterraneus* are capable of reproduction in all months with the possible exception of July. (Cyr et al., 1991). These data support the observed seasonality in reproduction reported by Hubbell and Norton (1978) and Griffith and Poulson (1993).

Measurable ova were found in *Ceuthophilus stygius* only in August, September, and October samples, indicating marked seasonality in reproduction in this annual species (Cyr et al., 1991). Parasitism by hairworms markedly affects number and size of ova formed in *C. stygius* (Studier et al., 1991). Six non-parasitized *C. stygius* contained  $25.5 \pm 4.2$  ova/female while nine parasitized

females collected at the same time contained an average of 2.2 ova. Seven parasitized females had no ova at all.

Northup and Crawford (1992) studied two of the *Ceuthophilus* species in three passages in Carlsbad Cavern. Some seasonality in reproduction and frequency of adults of *C. carlsbadensis* was noted, but the pattern is not as strong for the more cave-adapted *C. longipes*. *C. carlsbadensis* females (n=745) contained 0–60 eggs, with a mean of 6.34 (+/-1.09) eggs per female. *C. longipes* (n= 43) had a range of 0–4 eggs per female, with an average of 0.67 eggs (+/-0.17). Seventy-two percent of adult female *C. carlsbadensis* had eggs compared to only 37% of adult *C. longipes*. *C. longipes* produces significantly fewer and larger eggs, as expected of a more cave-adapted animal. Patterns of distribution of immature and adolescent crickets were highly variable in both time and location. The authors suggest that both species of camel crickets are able to reproduce throughout the year.

Total annual egg production by *H. subterraneus* was estimated by Cyr et al. (1991). During winter, 20–30 eggs were laid by individually caged female crickets in a 2–3 day period of rapid egg laying, while in early summer, the rate was 1–3 eggs laid every eight days. If average eggs laid per year is based on maximum egg-laying rates for each period of observation, then the annual egg production is 96 to 371 eggs laid per year per female. It is unlikely that crickets maintain measured maximum egg-laying over extended time periods. Three pairs of caged cave crickets, collected *in copulo*, however, laid an average of 0.46 eggs/day over a 154 day interval from March to August, which corresponds to an annual egg-laying rate of 167 eggs/year. The time span studied was not the peak time for egg production, and the 154 day interval is also longer than the estimated 12 weeks needed for eggs to hatch, so this rate estimate is probably low. Compared to other Orthopterans, the estimated range is somewhat low. In a year, the common house cricket lays 728 eggs, German cockroaches lay 218–267 eggs, and American cockroaches lay 200–1000 eggs (Altman and Dittmer 1972).

Individually-caged adult female *H. subterraneus* showed seasonal differences in the amount of egg-laying in Mammoth Cave (Cyr et al., 1991). At a deep cave site in Sophy's Avenue, many more eggs were laid in two day intervals from October to February (4.3 ova/day) than in April and July (0.6 ova/day). Egg-laying at the Frozen Niagara Entrance site averaged 0.1–0.8 ova/day in spring through fall. The influence of seasonal environmental conditions is shown in the winter data, where the greatest number of eggs were laid in Sophy's Avenue, and no eggs were laid in Frozen Niagara. At that study time the entrance door to Frozen Niagara was damaged, which allowed cold, dry air to enter and extend approximately 75 m into the cave where the females were caged. Half of the caged females died, and none of the survivors laid any eggs or even made any ovipositor holes.

## POPULATION SIZE

The size of individual *H. subterraneus*, and the side passages and alcoves we can't access, make complete direct population counts extremely difficult and of limited reliability. And except in small caves, exactly where is the end of the cave for purposes of a census? Only a few attempts at population studies have been made and only for large cave crickets. In general, results are more consistent in very small caves, such as Little Beauty Cave and White Cave in Mammoth Cave National Park.

One technique used to estimate total population size is known as mark-recapture. All individuals (marked and unmarked) are counted and marked with a different color on days 1 and 2 and counted again on day 3. Crickets can be marked successfully with dots of different colored office correction fluid or paint on their backs, by gluing on numbered bee tags, or using UV bright paint. Total numbers of marked and unmarked crickets on each day are used to calculate a statistical estimate of total population size. Attempts to do mark-recapture studies of cave cricket populations are often complicated by the large turnover of animals from accessible staging areas where we can see and mark them, to roost areas that are inaccessible to humans. Problems with mark-recapture studies are a continuing mystery.

A mark-recapture study by Hellman (1989) from fall to winter for the Frozen Niagara Entrance of Mammoth Cave estimated that there were 976.8 ( $\pm$  209.4) adult crickets in October 1987, but only 70.6 ( $\pm$  35.9) crickets in February 1988. The differences are not due to a huge population crash, but reflect the reduced movement of crickets in the winter months. Hobbs and Lawyer (2002) marked 769 adult *Hadenocetus cumberlandicus* cave crickets from a parthenogenic population (all females) in Coon-in-the Crack Cave in Kentucky. Based on the mark-recapture rate, they estimate the total adult population size in this cave as 5,508 individuals.

During a long-term biomonitoring project at Mammoth Cave National Park, Poulson et al. (1998) found some interesting differences among *H. subterraneus* populations at nine monitored entrances. They collected census data by dividing crickets into four size classes, 1–4, with size one being the smallest juveniles, and size four being sexually mature adults as estimated by size and degree of tanning of ovipositors and legs. Instead of existing as one metapopulation with roughly equal interactions among subpopulations, there are source and sink populations. In a source population there is a greater number of smaller size classes relative to larger size classes, which suggests a population that is increasing, although small crickets never outnumber large adults. A sink population is greatly skewed to the larger adult and sub-adult size classes, with low levels of local reproduction. The sink populations are maintained by immigration of crickets from source populations. There were source populations at three of

nine entrances, and sinks at the remaining six. There is no relationship between total population size and whether an entrance is a source or a sink. In general, source populations are located in entrances that have ceiling pockets that provide a refuge above the influx of surface air and are close to suitable reproductive areas. Most of the source entrances are located in sinkholes or in mature forests that offer good foraging opportunities and a protected microclimate. Both types of populations should be protected since emigration of adults from a sink can repopulate a source population should it be wiped out.

## INTRACAVE DISTRIBUTION

In many caves, crickets are difficult to find, but in other caves you can easily see hundreds of individuals in a relatively small area. These numbers may change drastically with time of day and season. Cave crickets gather around entrances as roosts and in staging areas where they can evaluate surface conditions before leaving the cave to forage. They are also found in stable deep cave areas away from human-sized entrances, but close to cricket-sized entrances.

Cathedral Cave, a small cave in a limestone bluff overlooking the Green River in Mammoth Cave National Park, was the site for a three year study of the migration patterns of *H. subterraneus* by Brother Nicholas and his students (Nicholas, 1962). Crickets were the only important source of food input into the cave. The small cave was divided into 12 3.1 m (10 ft) long transects. A different color paint was assigned to each transect, and all large crickets in each transect were marked, a total of 3,750 individuals. Ninety-seven percent of marked individuals were found in their original 3.1 m (10 ft) quadrant each day (Nicholas, 1962). Daily observation showed that about 1/3 of the crickets emerged each night to forage under optimal environmental conditions. This regular exiting of 1/3 of the population is not consistent with more recent metabolic studies, as discussed below. We also observe great reductions in the numbers of marked crickets over longer periods of time.

Neilsen (1989) took advantage of the very flat ceiling in Floyd Collins Crystal Cave, Mammoth Cave National Park, for a study of *H. subterraneus* distribution over six days. He mounted a light on a tripod with a grid over the end to project a pattern of one meter squares on the ceiling in the first 28 meters of the cave. Every six hours, every other day for three census days, he and a team mapped the location of every individual cricket. They found that the distribution of total crickets was very uneven (Fig. 3), with some areas having large numbers of individuals of all sizes, and other areas consistently having none. The distribution is probably related to local microclimate differences with less wind flow or higher moisture for the crickets.

Total counts of roosting *H. subterraneus* show a cyclical pattern with respect to day and time of collection. Highest

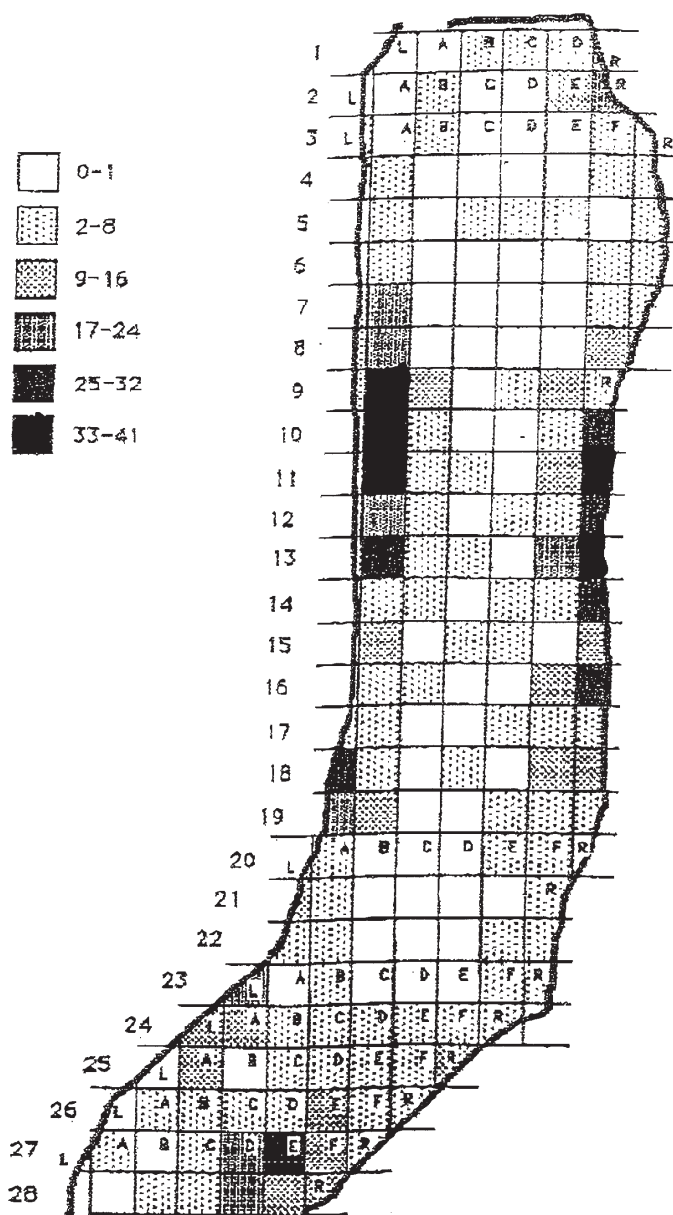


Figure 3. Cave cricket distribution summed over all census counts in Floyd Collins Crystal Cave (Neilson 1989).

population counts in the entire census area are in the evening at 1800 hours (367 individuals) while the lowest count is in the early morning at 0600 hours (255 individuals). Emergence of more crickets into the study area during the 1800 hour count is consistent with crickets sampling entrance conditions in the evening to see if epigeal climate is appropriate for foraging (Studier et al., 1986). Numbers also fluctuate with time as crickets retreat to and emerge from sites that are inaccessible to humans. Crickets were observed at distances into the cave greater than the 28 meters sampled in this study. Where the crickets go when they leave the accessible sites is one of the mysteries of the cave.

Patchy distributions of female *Hadenoeus cumberlandicus* cave crickets in sheltered locations were reported by Hobbs and Lawyer (2002). Yoder et al. (2002) report that aggregation behaviors in these cave crickets serve to protect them from dehydration. Increasing cricket group size (1, 5, 10, and 20) caused lower water loss rates in caged crickets. The protective group effect was eliminated when they used dry flowing air. They proposed that the protection from clustering is from increased local relative humidity.

Few studies examine the intracave movement and dispersal of cave crickets. Hobbs and Lawyer (2002) marked 2,378 adult female and juvenile *Hadenoeus cumberlandicus* cave crickets from Coon-in-the-Crack Cave in Kentucky. Based on tagged individuals, the majority of crickets moved an average of 10–15 m d<sup>-1</sup>, with a mean of 41 m. Downing and Hellman (1989) also examined in-cave movement of *H. subterraneus* from White Cave, Mammoth Cave National Park. They used different colors of typewriter correction fluid to mark adult cave crickets near the entrance (10–15 m from the entrance) and those found deeper in the cave (35–40 m from the entrance). The distribution of the marked adult crickets was monitored daily for a week by 5 m transects from the entrance to 50 m into the cave. Within 24 hours there was a general movement of crickets from the front of the cave towards the rear, including one individual that moved 25 m. Crickets marked from deeper in the cave tended to move around less. On the morning of day 4, after the one warm night during the study period, there was movement of crickets from the back to the front of the cave. A similar rhythmic movement pattern was observed by Campbell (1976) with *C. conicaudus* in Spider Cave in New Mexico.

#### SEASONAL DISTRIBUTION AND ABUNDANCE

In some cave entrances in central Kentucky, *H. subterraneus* co-exist in very large numbers with much smaller numbers of *C. stygius*. Large numbers of crickets were collected in their roosting caves during all four seasons from White Cave, Walnut Hill Cave, the Frozen Niagara Entrance to Mammoth Cave, and Floyd Collins Crystal Cave (Studier, et al., 1988). Crickets were collected by hand, sexed when large enough, and hind femur lengths (HFL) measured to the nearest 0.1 mm. Considerable care was taken in searching for and collecting all sizes of crickets since smaller crickets are easily overlooked because they roost in small crevices and stay away from open spaces.

The distribution of crickets by HFL for all caves studied for each season is presented in Fig. 4. *H. subterraneus* of all sizes are present in all seasons, and adults (HFL > 19.9 mm) make up the greatest fraction of each population in all seasons. There is no apparent seasonal difference in distribution by size, and no traceable peaks for the smaller



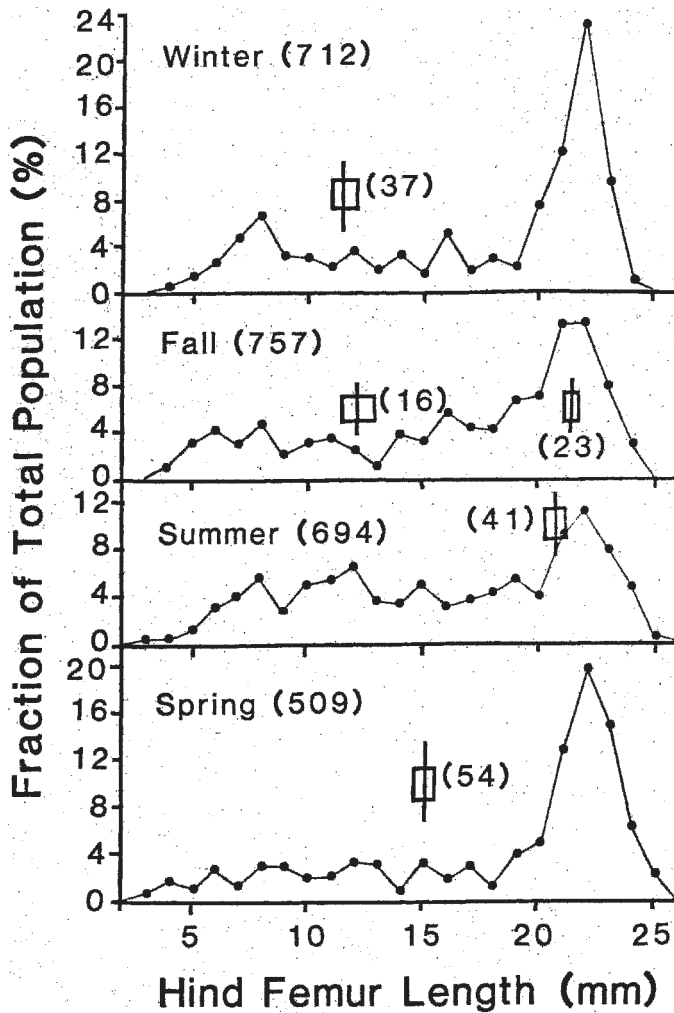


Figure 4. Seasonal distribution by hind femur length (HFL) of *H. subterraneus* (data points) and *C. stygius* (box of mean, width is 95% confidence interval) from four entrances in Kentucky (Studier, et al. 1988).

sized crickets that would indicate a seasonal period of intense reproduction within the populations, despite reported marked seasonal differences in reproductive effort in this species (Barr, 1967; Kane and Poulson, 1976; Hubbell and Norton, 1978). Differences could be because all sites sampled for this study are entrance sites in contrast to deep cave sites as discussed later in this paper.

The population structure for *H. subterraneus* shown in Figure 4 where adults predominate, is typical of a long-lived population. We know from recovery of marked, numbered, individuals that adult cave crickets can live as adults at least 17 to 24 months, considerably longer than the 7 to 11 months reported by Hubbell and Norton (1978). The preponderance of large, sexually-mature adults at all times of the year shows that cave crickets are relatively long-lived, perhaps living for four years or more.

Data for *C. stygius* are also presented in Figure 4 as discrete boxes, where the vertical line is the mean HFL of crickets measured, and the width shows 95% confidence intervals (Studier et al., 1988). Camel crickets are typically found in discrete size categories in each season due to their yearly life cycle. *C. stygius* shows a big jump in size from spring to summer with a period of rapid growth and attainment of sexual maturity. A new cohort of young appears in the fall to join the cohort of current adults. By winter, mostly small camel crickets over-winter to become the next season's cohort of adults as they emerge in the spring to feed.

The same data from Figure 4 shows that total crickets by gender among sub-adults (15.0–19.9 mm; 263 females and 231 males) have a sex ratio close to 1:1. Adult crickets by gender (713 females: 509 males) have a sex ratio that is significantly different in which females predominate. Lack of a gender bias among sub-adults and the preponderance of females among adult crickets suggests a differential mortality with greater death rates for adult male crickets. Male crickets must leave the safety of the cave to feed more frequently and they stay out longer than females, which probably results in a higher mortality rate for males (Studier, et al., 1986). Alternatively, females may simply live longer than males. Norton (personal communication) found unpredictable variations in male: female ratios of *H. subterraneus*, so this is another mystery of the cave.

#### ENTRANCE VS. DEEP CAVE SITES

Hubbell and Norton (1978) suggest that there may be differences between entrance populations of cave crickets and deep cave populations. An entrance site is a location that can be used by humans to enter the cave. A deep cave site is located away from an entrance accessible to humans and does not experience the seasonal changes in temperature and humidity at an entrance site. Because of a dome-pit arrangement at the Sophy's Avenue site and at Bubbly Pit in Great Onyx Cave, dense cold winter air flows directly past the roost site with little effect on roost temperature or relative humidity. In all cases, successful reproduction requires an area with a suitable sand-clay substrate. *H. subterraneus* cave crickets are very negatively affected by air that is not water-saturated and by temperature fluctuations (Studier et al., 1987b; Studier and Lavoie, 1990).

Our long term biomonitoring study shows that the populations from these two areas can grade into one another. Our best example comes from the New Discovery entrance, where a large population of crickets of all sizes, with adults predominating, is found in the first 20 meters from the entrance ready to exit the cave and forage. Continuing into the cave for 100 meters shows a switch to a deep cave site where the main function of the population is reproduction and there are only adults and small young crickets present.

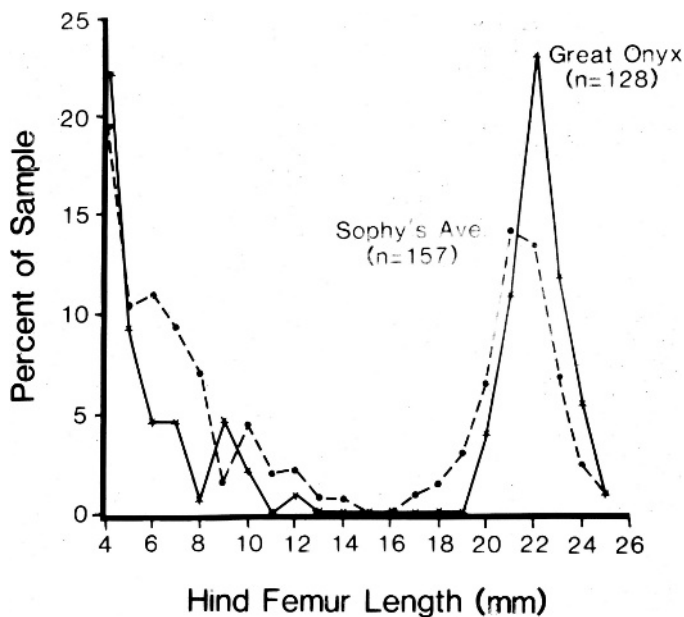


Figure 5. Distribution of *H. subterraneus* by hind femur length (HFL) at two deep cave sites in Mammoth Cave National Park. (Studier and Lavoie unpublished data.)

Seasonal averages of ova (eggs) per female *H. subterraneus* are quite consistent, but do show site-related differences. Crickets in entrance areas show consistently low levels of reproduction as evidenced by the number of eggs per female cricket (average 6.7 ova/female), while females from a deep cave site show strong seasonal differences in reproduction and egg-laying (average 18.1 ova per female) (Cyr et al., 1991). Hubbell and Norton (1978) report average numbers of large ova for females in July and January at the entrance at Great Onyx at 2.1 and 5.3, from deep in Great Onyx at 5.6 and 7.0, and from January in Parkers Cave at 3.6 in the entrance and 7.6 deeper in the cave.

Another striking difference is the size-class distribution between *H. subterraneus* in entrance sites and deep cave sites. Entrance sites (Fig. 4) show a majority of adults and a fairly even representation of crickets in other size classes. Data collected from two deep cave sites are shown in Figure 5 (Studier and Lavoie, unpublished data). There are many large adults and many small juveniles, but the intermediate size classes are nearly absent. Adults are skewed to a male sex bias, and males and females have much less food in their crops than in entrance areas. The deep cave sites serve as reproductive and nursery areas where crickets go to mate and lay eggs (Hubbell and Norton, 1978; Kane and Poulson, 1976). The eggs hatch and the young crickets go through several molts in the cave before leaving to roost around entrances where they can leave the cave to feed. Young crickets in the deep cave areas may feed mostly on other individuals of their species

(Levy, 1976). The actual number of molts to reach adult size is estimated by Hubbell and Norton (1978) as eight. They reported that caged hatchlings stayed in the non-feeding white stage for five weeks, molted to feeding second instars for ten weeks, and they were unable to raise the crickets beyond that.

#### METABOLIC RATES AND WATER BALANCES

Low metabolic rates are assumed to be a troglomorphic characteristic. Studies of the metabolism and water balance of *H. subterraneus* and *C. stygius* were made by caging adult individuals in the cave and measuring weight loss as a function of time (Studier et al., 1986, 1987a, 1987b; Viele and Studier, 1990). These were wild-caught animals, and we selected for crickets that appeared to have more crop contents. Dissected crops, carcasses, gonads, and combined wastes were analyzed in the lab for moisture content and caloric value. The metabolic rates for *H. subterraneus* are one-half that of surface insects of similar mass (Studier et al., 1986). The relationship between body mass and HFL differs by sex for *C. stygius* and is the same for both sexes for cave crickets. This relationship has a high predictive value ( $R^2 = 0.902$ ) and allows us to measure the hind femur length and weight of a cricket, and by extrapolation determine its crop contents without having to sacrifice the cricket, using the equation:

$$\text{CEL W (mg)} = 2.698 \text{ HFL}^2 - 50.07 \text{ HFL} + 274.1 \quad (1)$$

In this study, wild-caught females started at 101% of their crop-empty live weight. These adult female *H. subterraneus* lost weight at a rate that would make them crop-empty in 11.5 days. Adult males lost weight at a slower rate, but they had consumed only 72% of their body weight, so these males should leave the cave to feed at least every 9.9 days. *H. subterraneus* exiting White Cave had nearly empty crops and 65.2% of exiting crickets were males (Studier et al., 1986). Helf (2003) reports that some crickets can consume in excess of 200% of their body weight in food in a single feeding. Most full wild-caught crickets had 110–130% of their crop-empty live weight (CELW) in their crops. Higher starting crop contents would extend these projections of time between feedings by up to 2–2.5 times which would be the maximum time they could stay in the cave before leaving to feed to avoid using up body energy reserves.

Adult *C. stygius* lost weight at two rates over the five days of the study, which we interpret as a rapid phase due to crop-emptying, followed by a slower rate of weight loss when fat reserves are being utilized (Studier et al., 1986). If they are to avoid using fat reserves, female camel crickets must forage at least every 3.0 days and males every 2.3 days. *C. stygius* are able to consume only 34% to 39% (males vs. females) of their body weight in food. Because camel crickets have very little flexibility in how often they

## RESPONSES TO TEMPERATURE AND RELATIVE HUMIDITY



**Figure 6.** Cross section of the cuticle of a) *H. subterraneus* and b) *C. stygius* taken at 400 $\times$ .

must feed to maintain their fat reserves, they must be able to leave the cave more frequently and endure a wider range of environmental conditions than cave crickets.

Cave crickets are also very sensitive to moisture loss by evaporation because their outer cuticle is thin compared to camel crickets (Fig. 6). The cuticle of *H. subterraneus* is approximately half as thick and appears to lack epicuticular wax compared to *C. stygius*. Yoder et al. (2002) reported that extractable cuticular lipids were significantly lower from *H. cumberlandicus* compared to *C. stygius*.

The metabolism of the three species of *Ceuthophilus* crickets from Carlsbad Cavern show the expected differences with degree of troglomorphy (Northup et al., 1993). Based on an in-cave weight loss study, calculated metabolic rates (cal h<sup>-1</sup>) were 1.04 for *C. carlsbadensis* and 0.52 for *C. longipes*. These metabolic rates are half those predicted for epigeic species of similar size. The long-term weight loss patterns are linear for all three species over the five days of the weight loss study. Foraging intervals are inferred for females and males, respectively, of 5.1 and 4.4 days for *C. carlsbadensis*, 4.6 and 5.7 days for *C. longipes*, and 5.0 and 4.2 days for *C. conicaudus*. Again, these wild-caught crickets had fed at some unknown earlier time, and the actual feeding intervals are certainly longer.

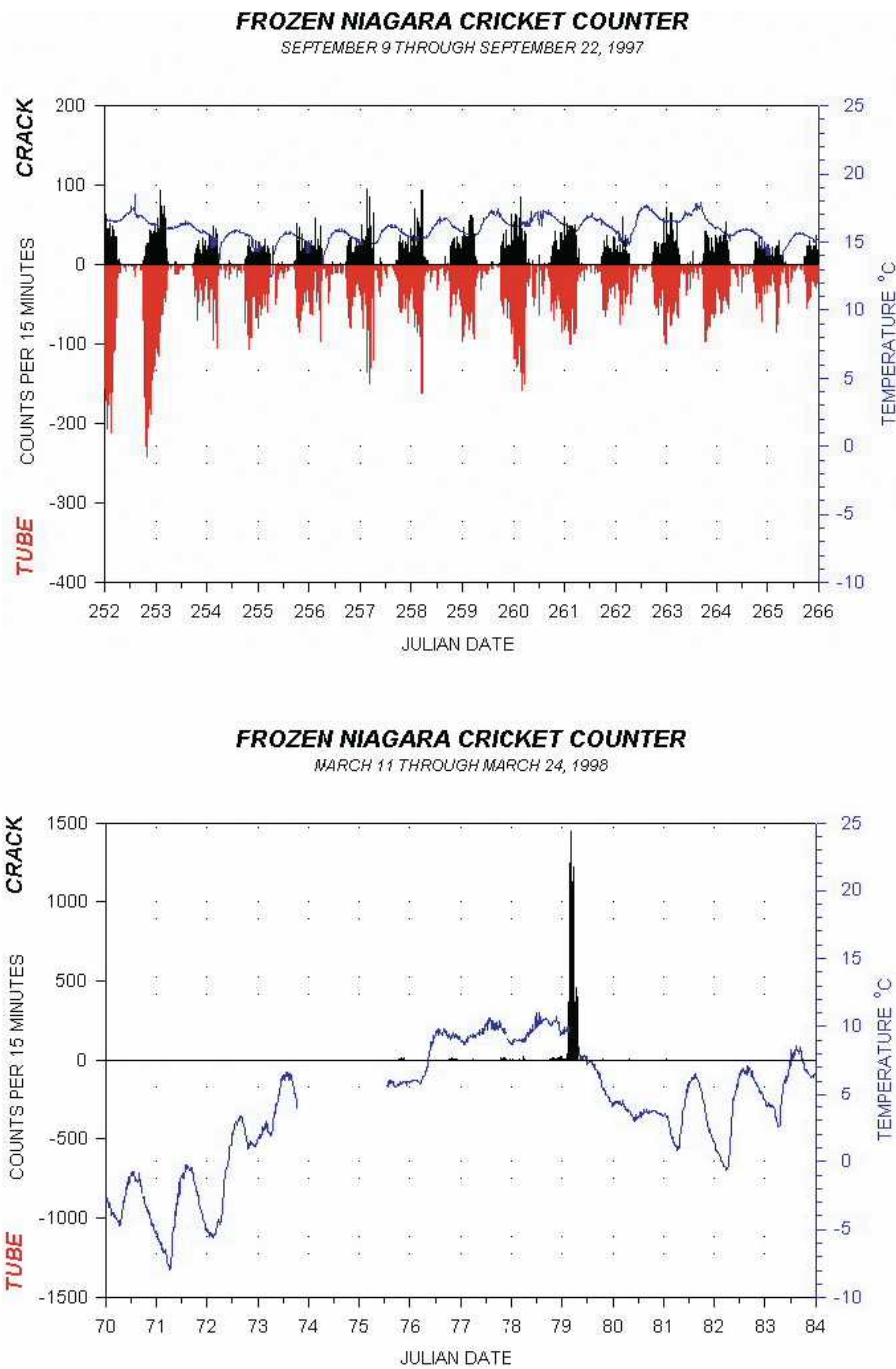
In central Kentucky, cave crickets must forage for food outside the cave, but foraging is very restricted by surface temperature and relative humidity (Leja and Poulson, 1990; Studier and Lavoie, 1990; Helf, 2003). Outside temperatures must be close to cave temperatures of 13°C (55°F) and relative humidity must be close to saturated. Tracings from an electric eye cricket counter are shown in Figure 7 for two times of the year at Mammoth Cave (Helf, 2003). In summer, a pattern of two peaks (exit and entry) is seen every night. In winter, crickets do not leave the cave when the temperature drops below about 5°C. Large numbers of crickets leave only on the warmest nights. Weather records for Mammoth Cave National Park indicate that on most nights throughout the year for at least a short time, surface conditions allow foraging. There are only a few weeks during the hottest months of summer and the depth of winter that are completely off-limits to foraging. Five degrees celsius was the lower temperature limit for surface foraging. At these low temperatures, *H. subterraneus* experience high evaporative water loss that may be made up by consumption of moister foods.

*H. subterraneus* rapidly lose water and die above even the mild temperature of 20°C (62°F). At 13°C, *H. subterraneus* lost water (0.35–0.53 mg% h<sup>-1</sup>) at a much higher rate than *C. stygius* (0.08 mg% h<sup>-1</sup>). At 23°C water loss was about 5 to 9 times higher for both species of crickets, but *H. subterraneus* (1.49–1.52 mg% h<sup>-1</sup>) again greatly exceed water loss for *C. stygius* (0.27 mg% h<sup>-1</sup>). In terms of Q10, a rough measure of the effect of temperature on physiology, the Q10 at 9.5°C–15°C was about 1.2, indicating no effect, temperatures from 15°C–20°C and 20°C–25°C were 2.5–3.0, which is a typical physiologic activity range. At 25°C–30°C, the Q10 was lethal.

Ectotherms such as invertebrates, fish, and reptiles, cannot metabolically regulate their body temperatures, so body temperature changes in response to changes in environmental temperature. The metabolic rate in these animals is expected to increase with increasing temperature. The absolute increase in metabolic rate is much greater in *H. subterraneus* than in *C. stygius* (Studier and Lavoie, 1990). The fact that *H. subterraneus* die very quickly and could not even be tested at temperatures exceeding 25°C indicates that they have much greater thermal sensitivity than *C. stygius*. These marked thermal sensitivities indicate adaptation to nearly constant ambient cave temperature and result in greatly increased metabolic demands at higher temperatures. As a result, we expect voluntary epigeic foraging at ambient temperatures much above cave conditions to be reduced.

Because *H. subterraneus* forages on the surface throughout the year, it is exposed to highly variable climatic conditions relative to those in the subsurface environment. Helf (2003) examined the impact of climatic conditions on *H. subterraneus* exit patterns in Mammoth





**Figure 7.** Counts of exiting crickets at Frozen Niagara Entrance, Mammoth Cave during optimal foraging temperatures in 1997 and suboptimal foraging temperatures in 1998. Solid Lines reflect crickets exiting through a crack 3 m above ground level. Dotted lines indicate temperature (Helf 2003).

Cave National Park. He analyzed data from 1996 to 1998 on surface temperature, precipitation, and *H. subterraneus* exit patterns using an electronic eye placed at a narrow crack just outside a cave entrance known to be heavily used by crickets. Overall, significantly greater numbers of cave crickets exited the cave nightly in summer (approximately  $460 \pm 50$ /night) versus winter (approximately  $190 \pm 25$ /night). In spring/summer, there was a significant positive

correlation between numbers of cave crickets exiting caves and rainfall. Cave cricket biology supports this conclusion in that evenings with significant rainfall would reduce their evaporative water loss and increase the volatility of odoriferous food patches, thus increasing cricket success in finding food.

Even more important is the effect of cold winters and summer droughts on cricket survival. From 1994–1997 we

censused *H. subterraneus* populations 2–6 times per year in nine cave entrances in Mammoth Cave National Park (Poulson et al., 1998). The overall numbers of size classes 1 (smallest), 2, 3 and 4 (large adults) generally increased in all caves over the four years with mean numbers per cave of 1,026, 1,998, 1,645, and 2,670. In the two caves with the largest populations there was a steady increase of 1,250, 2,180, 2,895, and 4,148 both for a weak source cave (Great Onyx) and 1,980, 2,133, 2,597, and 2,695 for a sink cave (White). The initial low numbers were probably the lingering effect of a severe late 1980s drought and severe early 1990s winters. From 1994 to 1997 the Taylor Drought Index generally decreased as did the number of long winter cold snaps that absolutely preclude foraging by crickets. We also know from indirect evidence of cricket guano communities that drought has had a negative effect on cricket populations in the interval from the early 1970s to late 1980s (Poulson et al., 1995). The presumed mechanism is that crickets preferred moist and/or rotting fruit, feces, micro-carrion, and mushrooms are largely unavailable during droughts. In this context it is not surprising that our best source caves have moist, protected, mature forests around their entrances.

The three closely related gryllid cricket *Caconemobius* species from Hawaii are an appropriate comparison among a cave-adapted species and its two closely related surface species. Ahearn and Howarth (1983) studied water balance physiology and metabolic rates of these species and, as expected, found that their ability to conserve water is strongly correlated with their environment. *C. sandwichensis*, the marine rock zone ancestor, is rarely, if ever, subjected to extremes in temperature or to relative humidity less than 98%. *C. fori*, the lava flow species, is exposed to extremes in temperature and relative humidity from daily cycles, and may also have to contend with geothermal heat. The cave species, *C. varius*, lives in a constant temperature environment and is extremely sensitive to relative humidity below saturation. After 12 hours in a dry environment near their normal ambient temperature (19 °C), the cave species lost significantly more water ( $14.7 \pm 0.7\%$  of body mass) than did either surface species, *C. fori* ( $8.8 \pm 0.7\%$ ) and *C. sandwichensis* ( $11.5 \pm 0.6\%$ ).

#### DIET AND DIGESTION

What do crickets eat in the wild is a simple question, yet is one of our enduring mysteries of cave cricket biology. They act as scavengers, eating whatever is smelly enough to get their attention and soft enough to chew. *H. subterraneus* have been observed eating mushrooms, dead insects, animal droppings, berries, and flowers. Taylor et al. (2005) observed one foraging *C. secretus* cave cricket with a live hemipteran in its mandibles. Crickets come readily to a wide range of baits, including rotten liver, limburger cheese, cat food, grape jelly, and peanut butter. Examination of gut contents shows mostly unidentifiable mush,

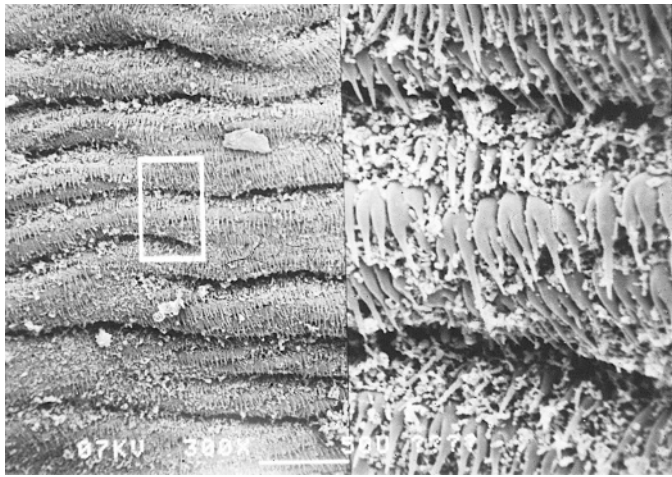
with an occasional recognizable insect part or piece of moss (Levy, 1976). Crickets seem to eat a much more varied diet in summer than in winter. They are also cannibalistic and will eat any cricket that is injured, but they will not eat the crop of the injured cricket. Crops may be a source of injury or death, and crickets may avoid eating them to prevent the cricket equivalent of food poisoning (Janzen 1977).

A study of caged *H. subterraneus* fed different types of foods one at a time (Lavoie et al., 1998, Helf 2003) shows that crickets do not eat partially decomposed leaf litter, moss, lichen, or live earthworms. Crickets gained 5–35% of their crop-empty live weight (CELW) on overripe fruit, deer fecal pellets, or fresh mushrooms. Crickets gained 70–120% of CELW from eating rotting mushrooms. Offering crickets artificial baits of cat food or wet cereal caused them to really tank-up, eating 100–250% of their CELW. We have done extensive searches for cricket foods in the wild, and we have a lot less success at it than the crickets do with their well-developed sense of smell. The natural crop contents are low in sodium relative to potassium, and low in total calories, which suggests that the crickets do not commonly find such high-quality foods as carrion or dead insects in the wild (Studier, 1996).

Organisms that consume plant detritus, decaying fruit, rotting wood, and herbivore dung ingest a variety of bacteria, protozoa and fungi along with their food (Martin and Kukor, 1986). If ingested microbes survive and proliferate in the digestive tract or excrete enzymes that remain active in the gut, then ingested microbes can augment or extend the digestive and metabolic capabilities of the organism that consumes and harbors them (Martin and Kukor, 1986, Kaufman and Klug, 1991). The crop of *H. subterraneus* is a very thin-walled structure that lies between the esophagus and hindgut (Fig. 8). These crickets frequently eat to the point of physical distortion by consuming very large amounts of food in a single foraging bout. The crop may act as a storage and fermentation chamber where an assemblage of microbes pre-digests the food. Some Orthopterans, including crickets, grasshoppers and cockroaches, depend on both resident and ingested microbes to aid in digestion, fermentation, and production of secondary metabolites, including potential toxins.

*H. subterraneus* may be partially restricted to a narrow temperature range to keep their crop microbes, including bacteria and yeast, under control. As reported by Studier and Lavoie (1990), cave crickets die in a few hours if held at temperatures above room temperature (23°C). Some of these crickets, as well as an occasional field-collected specimen, had crops visibly distended with gas, occasionally to the point of rupture. We think that crickets were killed by unregulated growth of crop microbes that produce excessive gaseous or toxic metabolites at elevated temperatures.

Most microbes isolated at 20°C from cave cricket crops or hindguts grew best above ambient cave temperatures of



**Figure 8.** *Hadenoecus* cave cricket crop walls have chitinous structures for grinding and mixing food, and large numbers of resident bacteria.

13.5°C with only one isolate showing optimum growth at cave ambient temperature (Phillpotts, 1989). The pattern of growth at different temperatures is largely due to the activity of enzymes at different temperatures. Enzyme activity generally increases up to the temperature optimum, and crop enzyme activity was optimum at 23°C. One limitation on cave cricket foraging is the need to slow down the metabolic activities of crop microbes that are largely responsible for food digestion. When cave crickets were fed diets rich in either carbohydrates or protein and compared to the natural diet, the activities of specific enzymes responded rapidly to the different diets, as would be expected if microbes were producing the digestive enzymes (White, 1989; Collier, unpublished data).

Whatever the reason or reasons for the extreme thermal sensitivity observed in *H. subterraneus*, even a modest increase in cave ambient conditions could have profound negative effects on cave crickets. Since caves maintain the average annual temperature of the area where they are located, global warming would result in increased cave temperatures. Even a modest increase of 2–6°C over the next 50 years (Schneider, 1989) would greatly increase metabolic demands and evaporative water loss, which would force more frequent foraging bouts and exposure to surface conditions and predators. These changes would probably result in extinction of cave crickets and the concomitant loss of the major source of fixed carbon energy inputs into caves in central Kentucky and many other areas around the world (Poulson, 1991).

#### FORAGING

Most cave crickets must leave the cave to forage for food. They have to consider many factors in deciding when to leave the cave. They will leave only when it is dark and conditions on the surface are close to cave conditions of 15

°C and 100% humidity, which are obviously influenced by season. How full the cricket is and its risk of being eaten are other factors they have to consider. Adult crickets have the advantage of having greater fat reserves than juveniles, so they can afford to wait longer for better foraging conditions than smaller crickets.

Campbell (1976) used a directional electric eye counter to show that decreasing light intensity was the trigger for *C. conicaudus* to emerge from Spider Cave. Total numbers emerging were influenced by temperature, relative humidity, and moonlight intensity. Numbers could change drastically in a short time. From July 3–4, 110 crickets emerged compared to July 7–8 when 1,195 crickets emerged. In lab studies, hungry crickets were more active. The highest emergence occurred on nights with low temperatures, high relative humidity, and low light intensity.

Levy (1976) observed that *H. subterraneus* use odor to differentiate among food choices. Small crickets are less fussy about what they eat than medium or large crickets. Small crickets fed on the first food item they encountered, compared to larger crickets with longer legs and antennae that can sense food from a greater distance away, and get to pick and choose among the different feeding opportunities. She described *H. subterraneus* as scavengers on stilts. Odor is highly correlated with caloric value; smelly foods tend to have more calories, but Levy could not determine whether crickets showed a real preference for higher calories or just smell.

DeLong (1989) did a deceptively simple caloric density preference study in the cave by offering *H. subterraneus* a buffet of three food choices. He used two extremes; pure peanut butter, which has a strong smell and is high in fat and calories (5.9 Kcal g<sup>-1</sup>), and pure corn starch, which has no odor and is a pure carbohydrate with much lower caloric value (4.1 Kcal g<sup>-1</sup>). A third bait choice was a 50:50 mixture that reduced available calories (down to 5.0 Kcal g<sup>-1</sup>), but kept the strong odor associated with peanut butter. The bait buffet was offered for one hour under separate live traps (a plastic ring capped with screening and propped up with a stick), traps were set by remotely yanking a string attached to the stick, and captured crickets were counted, sexed, and had their HFL measured (Table 1).

Consistent with Levy's scavenger on stilts model (Levy, 1976), non-sexable small crickets (HFL < 10 mm) were evenly distributed among the baits, while large adult (HFL > 20 mm) and medium (HFL 10–19 mm) crickets were preferentially found in the higher calorie baits. These size-related differences suggest that small crickets do not forage for the optimum caloric pay-off, but stop to feed at the first available foodstuff. These results also show that medium and large crickets do select for higher calorie foodstuffs based on odor, but are not able to select the highest calorie food. Data by gender for medium and large crickets show nearly equal numbers of males and females attracted to the 100% and 50% PB baits.



**Table 1.** *H. subterraneus* captured by size at three different energy level baits.

Bait	Large <sup>a</sup>	Medium <sup>b</sup>	Small <sup>c</sup>	Total
100% Peanut butter with 0% cornstarch	18	17	22	57
50:50 Peanut butter and cornstarch	13	22	23	58
0% Peanut butter with 100% cornstarch	2	1	22	25

HFL=Hind Femur Length (DeLong 1989).

<sup>a</sup> Large crickets = HFL>20 mm

<sup>b</sup> Medium crickets = HFL 10–19 mm

<sup>c</sup> Small crickets = HFL< 10 mm

Understanding the extent of the distance away from an entrance that cave crickets forage is an important consideration in cave management. If the crickets are the base of the food input into the cave, efforts have to be made to ensure that they have suitable habitat for foraging. Taylor et al. (2005) used UV bright paint to mark about 2000 *C. secretus* out of about 15,000 as they exited at night from Big Red Cave in Texas in late spring and summer 2003. The researchers used UV lights to locate marked crickets on the surface over a total of 17 sampling nights. The location of all 291 crickets on the surface (marked and unmarked) was recorded with GPS and a flag, and later measured and mapped. About half the crickets (51.1%) were located within 40 m of the entrance. Densities were uniform out to about 80 m, and some (8.1%) were located up to 105 m from the entrance, which is much greater than expected. On average, adults were found further from the entrance than sub-adults, and no male:female differences in distribution were noted. Crickets were typically found close to the ground, and almost evenly distributed in grasses, leaf litter, or herbaceous vegetation, although the authors noted that the vegetation type, such as cacti, may have influenced search efforts. In addition to managing suitable foraging environments around entrances, the authors noted the need to control fire ants in these areas.

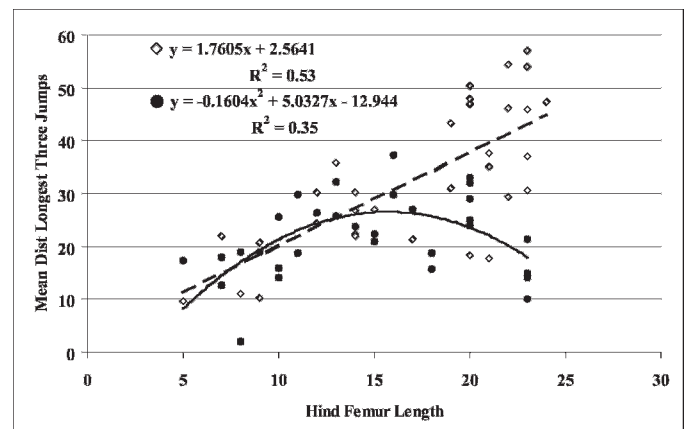
#### FORAGING AND PREDATION RISK

During a foraging bout on the surface, cave crickets likely use their prodigious jumping ability as their primary means of escape from predators. However, cave crickets' highly distensible crop enables them to increase their weight by more than >200% which could compromise their jumping ability and thus their means of escaping from predators. Helf (2003) showed that increasing crop fullness compromised large cave crickets' jumping ability (Fig. 9). Thus, cave cricket foraging decisions may be based on the tradeoff between food intake and biotic factors with the strongest impact (e.g., perceived predation risk or competition).

Helf (2003) hypothesized that the advantage a full crop conveys to an adult cricket would be outweighed by the negative effects it has on their jumping ability and predicted there would be a negative correlation between how much food large cave crickets eat at bait patches and

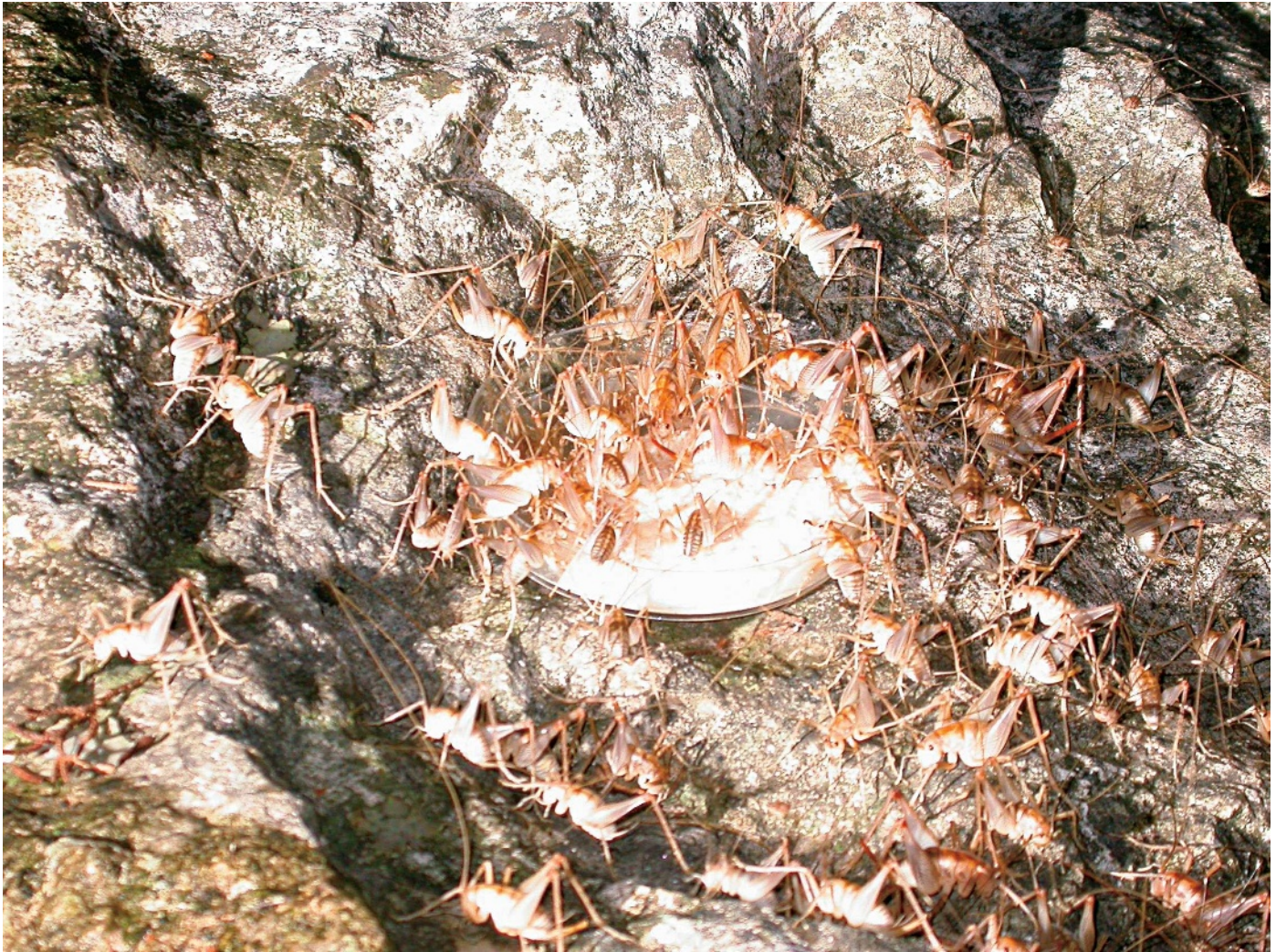
its distance from a cave entrance. Helf (2003) used color-coded bait patches placed at different distances from cave entrances to examine what effect *H. subterraneus* perceived risk of being eaten has on their foraging behavior. The data from these experiments, numbers, sizes, and fullness of crickets that fed at the bait patches on a given night, were obtained by censusing and weighing colored crickets in the cave the day following a foraging bout. There was no significant difference in food intake among bait patch distances. The data suggest that cricket foraging behavior was not affected by predation risk. Average food intake at all patch distances (ca. 100% of body weight) were well below cricket crop capacity of  $\geq 200\%$ .

Helf (2005) found aggregative responses to food patches in *Ceuthophilus secretus*, a widespread species in central Texas, can also lead to intense intraspecific competition (Fig. 10). Helf (2005) used bait patches centered on cave entrances at the four cardinal directions set just outside cave entrances, at 5 m, and at 10 m away to examine the foraging behavior of *C. secretus* at six caves in Government Canyon State Natural Area (GCSNA) in San Antonio, Texas. During summer and fall months the amount of food consumed by *C. secretus* declined significantly as a function of patch distance from cave entrances. Videotaped foraging bouts showed fierce intraspecific competition among *C. secretus* at bait patches. There was a significant positive



**Figure 9.** Effect of crop fullness on jumping ability of various sizes of *Hadenoeus* cave crickets. Error bars are  $\pm 1$  standard deviation (Helf 2003).





**Figure 10. Intense intraspecific competition among *Ceuthophilus secretus* at bait patches.**

correlation between their time spent feeding in bait patches and patch distance.

Red Imported Fire Ants (*Solenopsis invicta*) were usually found in large numbers at food patches, but 2003, a drought year, saw the largest numbers of *S. invicta* using the bait patches. Similarly, *C. secretus* food intake at bait patches was highest during 2003. GCSNA staff treated *S. invicta* mounds at half the study caves with boiling water that effectively reduces their number. Surprisingly, *C. secretus* consumed significantly less food from bait patches at treated caves relative to untreated caves. These data suggest that at caves with reduced *S. invicta* numbers, *C. secretus* was released from interspecific competition and so was able to exploit all available bait patches. At untreated caves, *C. secretus* increased food intake was likely due to their avoidance of distant bait patches being used by great numbers of *S. invicta*. Overall there were fewer available bait patches being exploited by many crickets. On one occasion there was a significant negative correlation

between *C. secretus* time spent feeding in bait patches and patch distance (Helf, 2005).

A study of numbers of three species of *Ceuthophilus* in three central Texas caves was made by Elliott and Sprouse from 1993 to 1999 (Elliott, 1994). Lakeline Cave was heavily impacted by construction of a mall, which left an undisturbed area around the cave entrance of only 0.9 ha (2.3 ac) in comparison to two other caves in large undisturbed areas. Cave cricket numbers in Lakeline Cave showed a steady decline with time while populations in the other two caves remained stable. These crickets generally forage 50–60 m from a cave entrance, showing the need for a larger undisturbed area around the entrance.

#### MOVEMENT AND ELONGATED APPENDAGES

Elongated appendages and gracile appearance are widely regarded as troglomorphic characteristics of cave animals. Elongated appendages, particularly antennae,



**Table 2. Averages of ranges [in brackets] of hind femur length (HFL), crop-empty live weight (CELW), and attenuation index (CELW/HFL<sup>3</sup>) for cricket species, both Rhaphidophoridae and Gryllidae.**

Species	Cave status	Number Location	CELW, mg (S.E.)	HFL,mm (S.E.)	Attenuation Index CELW/HFL <sup>3</sup>
<b>Rhaphidophoridae</b>					
<i>Hadenoeus subterraneus</i>	TP	425 KY	[11.3–556.8]	[7–25]	0.0334 [0.0296–0.0380]
<i>Ceuthophilus longipes</i>	TP	21 NM	120.2 (0.1)	12.6 (0.1)	0.0602
<i>Ceuthophilus stygius</i>	EP/TX	247 KY	[108.5–1338]	[10–25]	0.0996 [0.0508–0.1214]
<i>Ceuthophilus conicaudus</i>	EP/TX	20 NM	166 (9.3)	10.2 (0.2)	0.1546
<i>Ceuthophilus carlsbadensis</i>	EP/TX	29 NM	283.6 (0.1)	11.5 (0.1)	0.1879
<b>Gryllidae</b>					
<i>Caconemobius varius</i>	TB	19 HI	34.0 (2.4)	6.1 (0.1)	0.1474
<i>Caconemobius fori</i>	EP/TX	19 HI	59.4 (0.1)	7.2 (0.2)	0.1571
<i>Caconemobius sandwichensis</i>	EP	14 HI	80.9 (4.0)	7.4 (0.2)	0.1998
<i>Gryllus pennsylvanicus</i>	EP	20 MI	291.7 (0.1)	10.1 (0.1)	0.2831
<i>Acheta domestica</i>	EP	20 ???	142.2 (4.0)	7.4 (0.2)	0.3543

Values in parentheses are standard errors. Crickets are ranked specifically by attenuation index and in decreasing order by status of cave adaptation where TB=troglobite, TP=troglophile, TX=trogloxene, and EP=epigean. (Studier *et al.*, 2002).

could increase sensory perception, while elongated legs may be an adaptation for walking on irregular surfaces in total darkness (i.e., in a three-dimensional dark maze where stepping across gaps may be safer than jumping or walking around). Elongated appendages also could be an adaptation for metabolic economy; with longer legs, the animal could move farther with each step. Continuing Levy's (1976) scavenger on stilts concept, long legs and antennae allow crickets to reach above surface boundary layers to detect food or mates better. Vandel (1965) generalizes very broadly that cavernicolous crickets show extreme appendage elongation, even within a group that tends to have long appendages.

Studier *et al.* (2002) did a study of leg attenuation in a range of cave and surface crickets. When possible, they measured a range of sizes of individuals of each species and found that a relationship exists between body mass and a linear measurement of hind femur length. In both *H. subterraneus* and *C. stygius*, the relationships differ between sexes, with adult females routinely being heavier than adult males of similar HFL. With *H. subterraneus*, the relationships also differ by season. Individuals of similar HFL are lightest in the spring and heaviest in the fall. We have a limited amount of information from other species, but adults of the three *Ceuthophilus* species from Carlsbad and the three *Caconemobius* species from Hawaii generally fit the proposed model. An attenuation index of the ratio of crop empty live weight to hind femur length, cubed (CELW/HFL<sup>3</sup>) inversely ranks the studied cricket species to their level of adaptation to a cavernicolous existence, and is proposed as a potentially useful non-lethal quantitative indicator of the extent of cave adaptation in crickets (Table 2).

Jumping behavior in *H. subterraneus* was studied by Sevick (unpublished data). He used a photographic system

with a strobe light to evaluate the cricket jumping response to a threat. The pictures reveal something quite unexpected; the crickets somersault during their escape jump. He thought that the somersault allows the cricket to make contact with the underside of a ledge or the ceiling of the cave, which are safer places to avoid predators than just landing on the floor several centimeters away from where it started.

The evasive behavior of *H. subterraneus* has also been studied. Individual cave crickets were captured and tested in the cave by forcing them to hop to exhaustion (Fig. 11), defined as being unresponsive to touch (Mason, 1989). Crickets with longer hind femurs hopped greater distances both per hop and cumulatively, while the amount of food in the crop reduced the hop length, but not the total distance hopped. In winter 1988, 32 adult crickets with HFL ≥ 20 mm, hopped an average of 11.5 ± 0.6 times (range 7–20 hops). The average hop length was 36.7 ± 1.2 cm (range 23.8–46.9 cm) for a total average distance hopped of 419 ± 1.2 cm (range 212–898 cm). Time to exhaustion was 15.3 ± 0.2 seconds (range 8–24 seconds). The compass direction of the initial and subsequent hops were random. Comparing winter to summer, crickets showed an increased ability to hop for a longer time and total distance, although the average hop length remained the same.

Helf (2003) measured the impact of surface temperature on large *H. subterraneus* locomotory ability by measuring the distance they walked and jumped over sixty seconds at a temperature conducive to foraging (9°C) and a temperature that precluded foraging (3°C). There was a significant decrease in the distance walked by large crickets from 9°C to 3°C. No statistical comparison was even possible for jumping ability between 9°C and 3°C because crickets could not jump during the 3°C trials. As an ectotherm, *H.*





**Figure 11. Exhausted *Hadenoeus* cave cricket does not respond to touch and is unable to use its hind legs for jumping (muscles are in tetany).**

*subterraneus* cannot respond to the negative effect of low surface temperatures, so it waits inside the cave for better conditions.

In the Mammoth Cave entrance biomonitoring study, Poulson, Helf and Lavoie expressed concern about plans to develop gates for some entrances to the Mammoth Cave system. The use of airlock doors would eliminate the evening movement of *H. subterraneus* out of the cave to forage and their morning return to roosts in the caves. We wanted to know what size openings would need to be left around gates to permit free movement of cave crickets. Four large adult crickets were placed in a fiberglass window screen bag attached to PVC tubing of different lengths and shapes. The bags were placed horizontally on the ground and the number of crickets remaining after one hour and 12 hours was noted. A diameter of 1¼ in was the minimum that allowed for free movement of adult crickets. The shape of the tubing had no appreciable effect on cricket movement, so baffling the tubes should be possible to reduce air flow without a negative effect on crickets. We recommended that several openings be included in the design of airlock gates, with a single 3–4 in opening low down for movement of cave rats (*Neotoma* spp.) and multiple openings of 1½ in closer to the ceiling for crickets. Salamanders could make use of any of these openings. The Park Service agreed. Caves with gated bat entrances would already allow free movement of crickets and rats, and were not part of these recommended modifications.

#### CRICKETS AS PREY

If you have ever watched a nature show, you have probably noticed that many things like to eat crickets and grasshoppers. Cave crickets are no exception. Inside the cave, they are preyed upon by spiders and salamanders. In

some caves, specialized beetles prey on cricket eggs and injured young crickets. Outside the cave, crickets are eaten by many animals, in particular, mice. In Texas caves *Ceuthophilus* are eaten by many species including a scorpion and a spider. In addition dead crickets are scavenged by a rove beetle, a harvestman, and springtails, if other crickets do not find them first.

A cave sand beetle, *Neaphaenops tellkampfi*, is a specialized predator on cricket eggs in Kentucky. Some aspects of the relationship between crickets and beetles have been well studied (Poulson, 1975; Norton et al., 1975; Kane and Poulson, 1976; Griffith, 1991). Beetles dig in areas of sandy soil that have been disturbed by oviposition. It has been suggested that female crickets from caves with populations of beetles have co-evolved to have longer ovipositors than females from un-predated populations (Hubbell and Norton 1978). The difference is only one millimeter, but inserting eggs that much deeper decreases the risk of the egg being found by a sand beetle. In laboratory studies, Griffith (1991) carefully measured the depth of buried cricket eggs and the depth of holes dug by beetles. The overlap of graphs showed that beetles are likely to find only 25% of eggs laid. A reduced harvest rate due to lower, seasonal cricket egg availability was shown by Griffith and Poulson (1993) to decrease beetle fecundity. Cave cricket eggs that escape predation hatch into nymphs that move to the ceiling where they are less vulnerable to predators (Norton et al., 1975). A similar situation of coevolution or parallel evolution between predator and prey is seen in the Cumberland Plateau area, involving *H. cumberlandicus* and a different species of cave beetle, *Darlingtonia kentuckensis* (Hubbell and Norton, 1978; Marsh, 1969), *Ceuthophilus* in Texas by *Rhadine subterranea* (Mitchell, 1968).

*Ceuthophilus maculatus*, a cave cricket, may be an intermediate host for an intestinal parasite of mice. Fish (1974) studied the food of two species of meadow mice (*Microtus* sp.), and determined that the mice would eat these crickets when they encountered them in a confined space. The mice discarded the hard parts of the crickets, eating only internal organs. The lack of identifiable cricket parts in the stomachs of the mice may have led researchers to underestimate the use of insects in the diet.

The use of cave entrances by mice (*Peromyscus leucopus*) as a reliable source of food in the form of cave crickets was studied by Viele and Studier (1990). At some entrances, numbers of exiting crickets can be in the hundreds or even thousands per night. Viele and Studier set up a grid of traps around the entrance to a small, biologically rich cave in Mammoth Cave National Park called White Cave. Sherman live traps were set at 10 m intervals and baited with peanut butter. Traps were set at night and checked in the morning for several days. Trapped mice were marked to identify specific individuals and then released. The data were plotted to determine the home range of each trapped mouse. Only four white-footed deer

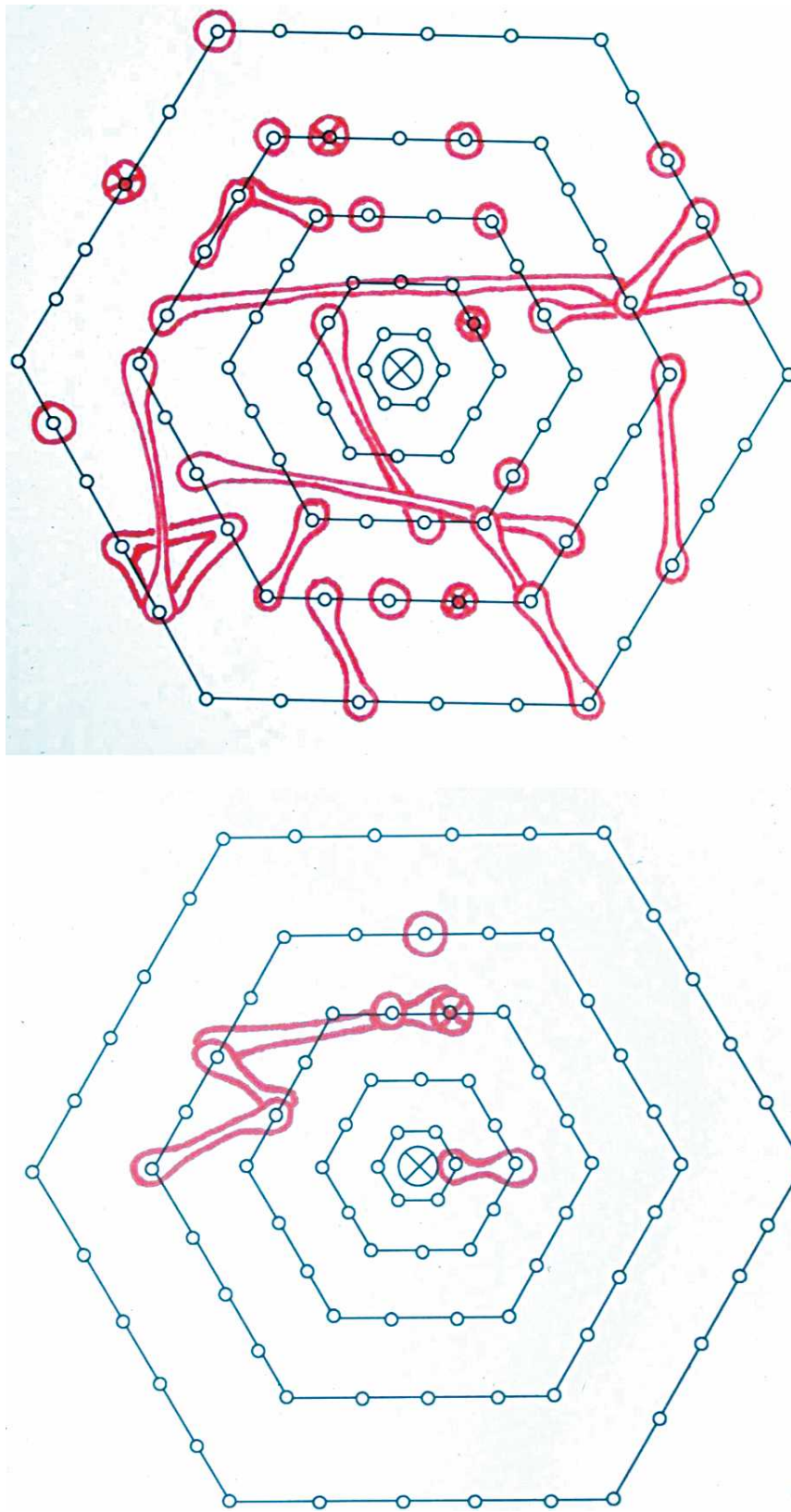
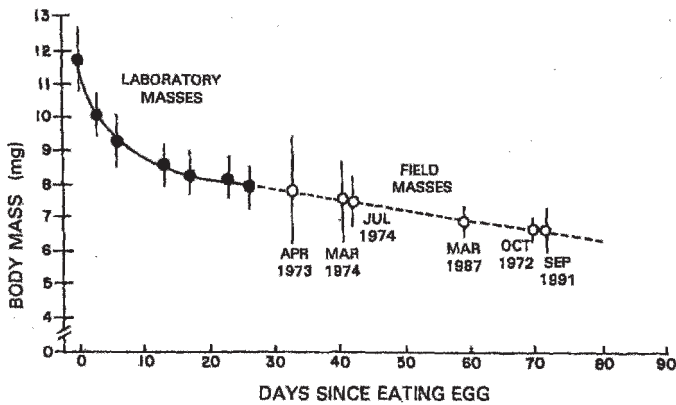


Figure 12. Sherman live trap grid of 90 live traps at Great Onyx cave 6–8 June, 1996. The upper grid was centered on the cave entrance used by crickets and the lower grid was set in similar terrain without a cave entrance several hundred meters away from the cave grid. All traps in the grid were 10m from the next nearest trap. Marks indicate captures of white-footed mice (*Peromyscus leucopus*). Connected points and circles with an 'X' indicate multiple captures of one individual (Helf 2003).



**Figure 13.** Mass loss in *Neaphaenops* sand beetles (mean  $\pm$  SD). Solid circles represent mass loss in the laboratory after consuming a single cricket egg (distended). Open circles are field masses, placed on an extended line (—) at a slope of 0.031 mg/d that equals the average rate of mass loss of non-distended beetles (Griffith and Poulson 1993).

mice were captured, but the home ranges of three of the mice were not randomly or evenly distributed. Three of the mice had home ranges that overlapped at the cave entrance, indicating the importance of the cave entrance to the mice.

Helf (2003) examined the effect of a cave entrance actively used by foraging *H. subterraneus* on the density of *P. leucopus* at Great Onyx Cave in Mammoth Cave National Park. Helf set a 90-trap grid centered on the cave entrance with another 90-trap grid set several hundred meters away in similar terrain without a cave entrance. Helf (2003) found 26 *P. leucopus* individuals within 50 m of the cave entrance whereas only six *P. leucopus* individuals were found in the control area (Fig. 12). Helf concluded that such high *P. leucopus* densities, since they are insectivorous, could affect the local community around cave entrances.

Studier (1996) measured the size, mass, nitrogen and mineral concentrations of crop-free carcasses of *H. subterraneus*, their eggs, and the egg predator sand beetle, *Neaphaenops tellkampfi*. Body magnesium, iron, and nitrogen concentrations decrease with size in the cave crickets, and accumulation of these minerals occurs very slowly in hatchling cave crickets. Nutrients needed for egg growth greatly exceed needs of the cricket for growth. Compared to cricket eggs, the beetles contain similar concentrations of iron and calcium, lower concentrations of magnesium and potassium, and higher concentrations of nitrogen and sodium. Growth rates of body mass in crickets is about one-tenth the growth expected for epigeal insects, so nitrogen and mineral accumulations are likewise expected to be very slow.

A single cricket egg represents about 75% of the mass of a *N. tellkampfi*, making it a huge meal. Based on a weight-

loss study in the laboratory (Griffith and Poulson, 1993), a single cricket egg will sustain a beetle for 2–3 weeks before it has to begin using body fat reserves (Fig. 13). As an example of you are what you eat, the nitrogen and mineral composition of the *N. tellkampfi* carcass is quite different from levels found in other beetles, and much more similar to that of cave cricket eggs (Studier, 1996).

Female *H. subterraneus* exhibit two strategies to avoid egg predation. One strategy is predator satiation, in which timing of egg production results in an overabundance of eggs for a short duration. Predators become satiated during this short period, and the surviving young quickly grow beyond a size easily handled by the predator (Smith, 1986). One cricket egg completely satiates a sand beetle for approximately a week or two (Norton et al., 1975; Griffith and Poulson, 1993). A reduction in predation rates is associated at the population level with high egg densities (Kane and Poulson, 1976). The second predator avoidance strategy involves making large numbers of ovipositor holes to increase search time for *Neaphaenops* beetles, which preferentially dig in areas of disturbed substrate. Caged crickets consistently made more ovipositor holes than eggs laid. Both of these strategies may increase egg survival rate. Oviposited eggs have a minimal hatching success rate of 82.6%, with an approximate time to hatching of 12 weeks, which agrees with estimates by Hubbell and Norton (1978). Females may also be testing the soil for suitable conditions of egg development. None of these explanations is mutually exclusive.

Ten-meter transects (32.8 ft transects) of nine entrances in Mammoth Cave National Park were censused regularly from 1995–1997 by the authors. All entrances had *Nesticus* spiders or a similar-sized spider, while only five had populations of the large orb-weaver *Meta americana* (Fig. 14). At the five entrances with *Meta*, there was a positive correlation between spider number and reproduction, and cave cricket abundance both in transects in a cave and between caves. This finding suggests that cricket prey numbers have a strong influence on success of the spider predator.

Fungi may have the potential to reduce cave cricket populations. In a study of the internal and external species of fungi associated with a troglonecric cave cricket, *Hadenoeus cumberlandicus*, Benoit et al. (2004) isolated a range of soil saprophytes that you would expect to find in a cave. Two internal isolates were species of plant pathogenic fungi, which they attributed to feeding. One external isolate was a genus of fungus that is an insect pathogen. Presence alone does not indicate activity, but we occasionally observe dead crickets covered in a white mycelium of *Isaria densa* (Cali, 1897). We refer to them as cricket marshmallows, for obvious reasons (Fig. 15). We are not sure if the fungus kills the cricket or grows on it after the cricket dies, but it is certainly present at the time of death. The fungus is in a race with crickets and other scavengers for the carcass.





**Figure 14.** *Meta americana* spider with web. These large spiders are able to catch and consume adult cave crickets.

#### CAVE CRICKETS AS KEYSTONE SPECIES

The cave cricket is often considered a dominant species in cave ecosystems because of the large numbers of individuals and their contribution to the food base in many caves. Cave crickets enhance biodiversity in food-limited caves by a combination of their feces, eggs, and dead bodies. This might have been predicted just by their high importance value as by far the largest, the most numerous, and the highest metabolic rate species in caves where they occur. Their actual contribution to biodiversity has only been well studied in Texas caves by Mitchell (Mohr and Poulson, 1966) and in Kentucky (Poulson, 1992).

In the Mammoth Cave area their guano under entrance roosts only occasionally has the right moisture to support a very diverse community, but their scattered feces away from entrances support a community that includes some of the most troglomorphic springtails, beetles, millipedes, and spiders. In addition, their eggs are eaten by a carabid beetle,

*Neaphaenops tellkampfi*, which occurs in high densities where crickets lay most of their eggs in sandy or silty substrates away from entrances. The beetle's feces in turn support a moderately diverse community that includes springtails, mites, a pseudoscorpion, a dipluran, and a spider.

In Texas caves *Ceuthophilus* guano can also be an important community food base, supporting populations of troglobites and troglophiles (S. Taylor, personal communication). And, though not studied, the feces of a carabid beetle (*Rhadine*) that eats cricket eggs are certainly the basis of another community.

Long-term studies of cave cricket guano communities in two small caves in Mammoth Cave National Park show large fluctuations in the numbers of animals censused over 24 years between 1971 and 1994 (Fig. 16). Poulson et al. (1995) pose four hypotheses to explain the observed variation. The first hypothesis is that anthropogenic disturbances by cave tours cause the crickets to move their roosts to other areas, thus preventing renewal of the guano. After considering the frequency, group size, and path



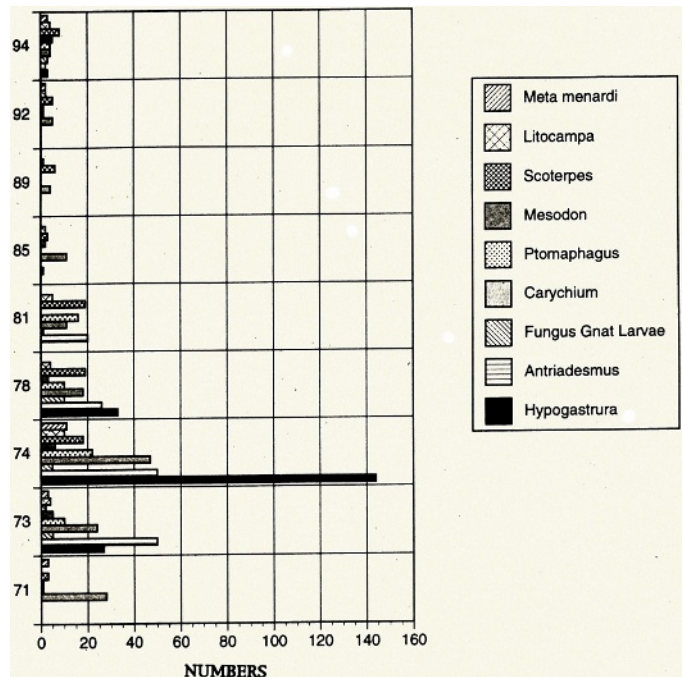
**Figure 15. Cricket marshmallow:** A dead *H. subterraneus* cricket surrounded by a dense white fungal mycelium.

followed by four groups, we rejected this hypothesis. A second hypothesis is that weather directly affects the guano, making it too dry or too moist to support the guano community. This hypothesis is rejected because the data are not consistent with the model. The third hypothesis is that weather changed the cave microclimate, causing the crickets to roost elsewhere, which reduces guano input to the community. However, we have observed that crickets do keep the same roosts for long periods of time, and new guano communities are not established elsewhere.

The final hypothesis, and the one supported by observations, is that weather effects are indirectly seen on the guano communities because weather forces change in cricket foraging, guano deposition, and cricket survival. Data comparing species diversity and abundance of the guano community with an increase in cricket numbers coincided with a period of favorable weather. Poor surface weather conditions negatively affect cricket foraging and the trophic cascade based on guano resupply.

#### PERSPECTIVES

Cave crickets are often important keystone species that support cave ecosystems by production of eggs, carcasses, and guano that serve as the food base in many caves. Tom Poulson is fond of using the phrase, *Mysteries of the Cave*, when discussing something we just don't understand about caves and cave life. The challenge of field research is to find answers to these mysteries (Poulson, 1996). Any research project in the field can be a humbling experience. You review what you know, develop alternate hypotheses to test, think, plan, and plan again, get your materials together, build devices, travel to the field site, and then nothing works as you planned. Generally, most experiments require two or more modifications, and plenty of



**Figure 16. Changes in abundance of cave cricket guano community organisms in White Cave over 24 years from 1971–1994 (Poulson *et al.*, 1995).**

duct tape, before they work. Cave cricket research is no exception. Although we know a lot about a few species, there are still tremendous opportunities for further study of cave crickets in order to solve more mysteries of the cave.

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#### REFERENCES

- Ahearn, G.A., and Howarth, F.G., 1982, Physiology of cave arthropods in Hawaii: *Journal of Experimental Zoology*, v. 222, p. 227–238.  
 Altman, P.L., and Dittmer, D.S., 1972, *Biology data book*, 2nd ed.: Bethesda, MD, Federation of American Societies for Experimental Biology, p. 156–157.



- Barr, Jr., T.C., 1967, Ecological studies in the Mammoth Cave system of Kentucky I, The biota: *International Journal of Speleology*, v. 3, p. 147–207.
- Barr, Jr., T.C., and Kuehne, R.A., 1971, Ecological studies in the Mammoth Cave system of Kentucky II, The ecosystem: *Annales de Speleologie*, v. 26, p. 47–96.
- Benoit, J.B., Yoder, J.A., Zettler, L.W., and Hobbs, III, H.H., 2004, Mycoflora of a troglonecric cave cricket, *Hadenoeus cumberlandicus* (Orthoptera Rhabdophoridae), from two small caves in northeastern Kentucky: *Annals of the Entomological Society of America*, v. 67, no. 5, p. 989–993.
- Caccone, A., and Powell, J.R., 1987, Molecular evolutionary divergence among North American cave crickets II, DNA-DNA hybridization: *Evolution*, v. 41, p. 1215–1238.
- Caccone, A., and Sbordoni, V., 1987, Molecular evolutionary divergence among North American cave crickets I, Allozyme variation: *Evolution*, v. 41, p. 1198–1214.
- Cali, R.E., 1897, Some notes on the flora and fauna of Mammoth Cave, Ky.: *The American Naturalist*, v. 31, no. 365, p. 377–392.
- Campbell, G.D., 1976, Activity rhythms in the cave cricket, *Ceuthophilus conicaudus* (Hubbell): *The American Midland Naturalist*, v. 96, p. 350–366.
- Cockley, D.E., Gooch, J.L., and Weston, D.L., 1977, Genetic diversity in cave-dwelling crickets (*Ceuthophilus gracilipes*): *Evolution*, v. 31, p. 313–318.
- Culver, D.C., 1982, *Cave life: Evolution and ecology*: Cambridge, Mass, Harvard University Press.
- Cyr, M.M., Studier, E.H., Lavoie, K.H., and McMillan, K.L., 1991, Annual cycle of gonad maturation, characteristics of copulating pairs and egg-laying rates in cavernicolous crickets, particularly *Hadenoeus subterraneus* (Insecta: Orthoptera): *American Midland Naturalist*, v. 125, p. 231–239.
- DeLong, M.J., 1989, Caloric density preference of cave crickets, *Hadenoeus subterraneus*: 1988 Cave Research Foundation Annual Report, p. 48–49.
- Downing, R.D., and Hellman, K., 1989, Long term intracave movements of the cave cricket, *Hadenoeus subterraneus*: 1988 Cave Research Foundation Annual Report, p. 51–52.
- Downing, R.W., 1989, Cave entry and exit patterns of the cave cricket, *Hadenoeus subterraneus*: 1988 Cave Research Foundation Annual Report, p. 50.
- Elliott, W.R., 1994, Conservation of Texas caves and karst, in *The caves and karst of Texas*, 1994 NSS Convention guidebook, Elliott, W.R., and Veni, G., eds., National Speleological Society, Huntsville, Texas, p. 85–98.
- Fish, P.G., 1974, Notes on the feeding habits of *Microtus ochrogaster* and *M. pennsylvanicus*: *American Midland Naturalist*, v. 92, no. 2, p. 460–461.
- Gregory, T.R., 2001, Animal Genome Size Database: <http://www.genomesize.com/> [accessed May 27, 2006].
- Griffith, D.M., 1991, The effects of substrate moisture on survival of cave beetles (*Neaphaenops tellkampfi*) and cave cricket eggs (*Hadenoeus subterraneus*) in a sandy deep cave site: *Bulletin of the National Speleological Society*, v. 53, no. 2, p. 98–103.
- Griffith, D.M., and Poulson, T.L., 1993, Mechanisms and consequences of intraspecific competition in a carabid cave beetle: *Ecology*, v. 74, p. 1373–1383.
- Harris, J.A., 1973, Structure and dynamics of a cave population of the guano mite, *Urobovella coprophila* (Womersley): *Australian Journal of Zoology*, v. 21, p. 239–275.
- Helf, K.L., 2003, Foraging Ecology of the Cave Cricket *Hadenoeus subterraneus*: Effects of Climate, Ontogeny, and Predation [Ph.D. dissertation]: Chicago, University of Illinois at Chicago, 170 p.
- Helf, K.L., 2005, Cave crickets (*Ceuthophilus* spp.) in central Texas: The ecology of a keystone cave invertebrate, Austin, Texas, Texas Parks and Wildlife Department, 40 p.
- Hellman, K., 1989, A preliminary study of apparent changes in the population density of the cave cricket (*Hadenoeus subterraneus*) at Frozen Niagara Entrance, Mammoth Cave National Park, Kentucky: 1988 Cave Research Foundation Annual Report, p. 52–54.
- Hobbs, III., H.H., and Lawyer, R., 2002, A preliminary population study of the cave cricket, *Hadenoeus cumberlandicus* Hubbell and Norton, from a cave in Carter County, Kentucky [abs.]: *Journal of Cave and Karst Studies*, v. 65, p. 174.
- Howarth, F.G., 1983, Ecology of cave arthropods: *Annual Review of Entomology*, v. 28, p. 365–389.
- Howarth, F.G., 1987, The evolution of non-relictual tropical troglolites: *International Journal of Speleology*, v. 16, no. 1–2, p. 1–16.
- Hubbell, T.H., 1936, A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacridae, Rhabdophorinae), v. 2, University of Florida Publications in Biology, Gainesville, Florida, 551 p.
- Hubbell, T.H., and Norton, R.M., 1978, The Systematics and Biology of the Cave-Crickets of the North American Tribe Hadenocini (Orthoptera Saltatoria: Ensifera: Rhabdophoridae: Dolichopodinae): *Miscellaneous Publication of the Museum of Zoology, University of Michigan*, No. 156.
- Janzen, D.H., 1977, Why fruits rot, seeds mold, and meat spoils: *American Midland Naturalist*, v. 111, no. 980, p. 691–713.
- Kane, T.C., and Poulson, T.L., 1976, Foraging by cave beetles: spatial and temporal heterogeneity of prey: *Ecology*, v. 57, p. 793–800.
- Kastberger, G., 1984, Gating of locomotor activity in the cave-cricket, *Troglophilus cavicola*: *Physiological Entomology*, v. 9, p. 297–314.
- Kaufman, M.G., and Klug, M.J., 1991, The contribution of hindgut bacteria to dietary carbohydrate utilization by crickets (Orthoptera: Gryllidae): *Comparative Biochemistry and Physiology*, v. 98A, p. 117–124.
- Lavoie, K.H., Poulson, T.L., and Helf, K.L., 1998, Cave crickets at Mammoth Cave National Park: You are what you eat [abs.]: *Journal of Cave and Karst Studies*, v. 60, no. 3, p. 180.
- Leja, W., and Poulson, T.L., 1984, Nocturnal cave exodus and return: cave vs. camel crickets: *Cave Research Foundation Annual Report*.
- Levy, E.S., 1976, Aspects of the biology of *Hadenoeus subterraneus* with special reference to foraging behavior [M.S. thesis]: Chicago, University of Illinois-Chicago Circle.
- Marsh, T.G., 1969, Ecological and behavioral studies of the cave beetle *Darlingtonia kentuckensis* [Ph.D. dissertation]: Lexington, Ky., University of Kentucky.
- Martin, M.M., and Kukor, J.J., 1986, Role of mycophagy and bacteriophagy in invertebrate nutrition, in *Gastrointestinal ecology*, University of Michigan Press, Ann Arbor.
- Mason, E.J., 1989, Preliminary quantification of several parameters of evasive behavior in the cave cricket, *Hadenoeus subterraneus*: 1988 Cave Research Foundation Annual Report, p. 54–55.
- Mitchell, R.W., 1968, Food and feeding habits of the troglolitic carabid beetle *Rhadine subterranea*: *International Journal of Speleology*, v. 3, p. 249–270.
- Mohr, C.E., and Poulson, T.L., 1966, *The life of the cave*, McGraw-Hill, New York, 232 p.
- Neilson, S.J., 1989, Short-term intracave distributional patterns for a cave cricket (*Hadenoeus subterraneus*) population: 1988 Cave Research Foundation Annual Report, p. 56–58.
- Nicholas, G., 1962, Nocturnal migration of *Hadenoeus subterraneus*: *NSS News*, v. 20, p. 102.
- Northup, D.E., and Crawford, C.S., 1992, Rhabdophorid “camel crickets” (*Ceuthophilus longipes* and *C. carlsbadensis*) from Carlsbad Cavern: *The American Midland Naturalist*, v. 127, p. 183–189.
- Northup, D.E., Lavoie, K.H., and Studier, E.H., 1993, Bioenergetics of camel crickets (*Ceuthophilus carlsbadensis*, *C. longipes* and *C. conicaudus*) from Carlsbad Caverns National Park, New Mexico: *Comparative Biochemistry and Physiology A, Comparative Physiology*, v. 106, no. 3, p. 525–529.
- Norton, R.M., Kane, T.C., and Poulson, T.L., 1975, The ecology of a predaceous troglolitic beetle, *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae) II. Adult seasonality, feeding, and recruitment: *International Journal of Speleology*, v. 7, p. 55–64.
- Otte, D., 1994, *The Crickets of Hawaii: Origin, Systematics and Evolution*: Philadelphia, The Orthopterists Society, 396 p.
- Phillipotts, S.G., 1989, Thermal sensitivity of microbes from the digestive tract of adult cave crickets, *Hadenoeus subterraneus*: 1988 Cave Research Foundation Annual Report, p. 60–61.
- Poulson, T.L., 1975, Symposium on life histories of cave beetles: an introduction: *International Journal of Speleology*, v. 7, p. 1–5.
- Poulson, T.L., 1991, Effects of recent and future climate change on terrestrial cave communities at Mammoth Cave: 1991 Cave Research Foundation Annual Report, p. 47–48.
- Poulson, T.L., 1992, The Mammoth Cave Ecosystem, in Camacho, A., ed., *The Natural history of biospeleology*: Madrid, Spain, Madrid Museo Nacional de Ciencias Naturales.



- Poulson, T.L., 1996, Research aimed at management problems should be hypothesis-driven: Case studies in the Mammoth Cave region, *in* Rea, G.T., ed., Proceedings of the 1995 National Cave Management Symposium, Spring Mill State Park, Mitchell, Indiana, Indianapolis, Indiana Karst Conservancy, p. 267–273.
- Poulson, T.L., Helf, K., and Lavoie, K.H., 1998, Distribution and abundance of cave crickets at Mammoth Cave National Park due to weather from 1995 to 1997 and entrance retrofitting in 1996 [abs.]: *Journal of Cave and Karst Studies*, v. 60, no. 3, p. 181.
- Poulson, T.L., Lavoie, K.H., and Helf, K., 1998, Cave crickets at Mammoth Cave National Park: Source and sink population dynamics [abs.]: *Journal of Cave and Karst Studies*, v. 60, no. 3, p. 181.
- Poulson, T.L., Lavoie, K.H., and Helf, K., 1995, Long-term effects of weather on the cricket guano community in Mammoth Cave National Park: *American Midland Naturalist*, v. 134, p. 226–236.
- Richards, A.M., 1971, An ecological study of the cavernicolous fauna of the Nullarbor Plain, southern Australia: *Journal of Zoology*, v. 164, p. 1–60.
- Schneider, S.H., 1989, The Greenhouse Effect: Science and Policy: *Science*, v. 243, p. 771–781.
- Smith, R.L., 1986, Elements of ecology, 2nd ed., p. 328–333: New York, Harper and Row Publishers.
- Studier, E.H., 1996, Composition of bodies of cave crickets (*Hadenoeus subterraneus*), their eggs, and their egg predator, *Neaphaenops tellkampfi*: *The American Midland Naturalist*, v. 136, p. 101–109.
- Studier, E.H., and Lavoie, K.H., 1990, Biology of cave crickets, *Hadenoeus subterraneus*, and camel crickets, *Ceuthophilus stygius* (Insecta: Orthoptera): Metabolism and water economies related to size and temperature: *Comparative Biochemistry and Physiology*, v. 95A, p. 157–161.
- Studier, E.H., Lavoie, K.H., and Chandler, C.M., 1991, Biology of cave crickets, *Hadenoeus subterraneus*, and camel crickets, *Ceuthophilus stygius* (Insecta: Orthoptera): Parasitism by hairworms: Proceedings of the Helminthological Society of Washington, v. 58, no. 2, p. 244–246.
- Studier, E.H., Lavoie, K.H., and Howarth, F.G., 2002, Leg attenuation and seasonal femur length: mass relationships in cavernicolous crickets (Orthoptera: Gryllidae and Rhaphidophoridae): *Journal of Cave and Karst Studies*, v. 64, no. 2, p. 126–131.
- Studier, E.H., Lavoie, K.H., Nevin, D.R., and McMillin, K.L., 1988, Seasonal individual size distributions and mortality of populations of cave crickets, *Hadenoeus subterraneus*: Cave Research Foundation Annual Report, p. 42–44.
- Studier, E.H., Lavoie, K.H., Wares, II., W.D., and Linn, J.A.-M., 1986, Bioenergetics of the cave cricket, *Hadenoeus subterraneus*: *Comparative Biochemistry and Physiology*, v. 83A, p. 431–436.
- Studier, E.H., Lavoie, K.H., Wares, II., W.D., and Linn, J.A.-M., 1987a, Bioenergetics of the camel cricket, *Ceuthophilus stygius*: *Comparative Biochemistry and Physiology*, v. 86A, p. 289–293.
- Studier, E.H., Wares, II., W.D., Lavoie, K.H., and Linn, J.A.-M., 1987b, Water budgets of cave crickets, *Hadenoeus subterraneus* and camel crickets, *Ceuthophilus stygius*: *Comparative Biochemistry and Physiology*, v. 86A, p. 295–300.
- Taylor, S.J., Krejca, J., and Denight, M.L., 2005, Foraging and range habitat use of *Ceuthophilus secretus* (Orthoptera: Rhaphidophoridae), a key troglone in Central Texas cave communities: *American Midland Naturalist*, v. 154, p. 97–114.
- Vandel, A., 1965, Biospeleology: The biology of cavernicolous animals (Translated from the 1964 French edition by Freeman, B.E.): Oxford, Pergamon Press, 524 p.
- Viele, D.P., and Studier, E.H., 1990, Use of a localized food source by *Peromyscus leucopus*, determined with an hexagonal grid: *Bulletin of the National Speleological Society*, v. 52, no. 1, p. 52–53.
- White, C.R., 1989, Digestive enzymes of the cave cricket, *Hadenoeus subterraneus*: 1988 Cave Research Foundation Ann. Report, p. 61–63.
- Yoder, J.A., Hobbs, III, H.H., and Hazelton, M.C., 2002, Aggregate protection against dehydration in adult females of the cave cricket, *Hadenoeus cumberlandicus*: *Journal of Cave and Karst Studies*, v. 64, no. 2, p. 140–144.