Section 6 (Texas Traditional) Report Review

Attachment to letter dated APR 2 2 2005

Project Title: Cave Crickets (*Ceuthophilus* sp.) in Central Texas; the Ecology of a Keystone Cave Invertebrate

Final or Interim Report? Final

Job #: **WER77** **Grant #:** E-7

Reviewer Station: Austin ESFO

Lead station was contacted and concurs with the following comments:
☐ Yes ☐ No ☒ Not applicable (reviewer is from lead station)

Interim Report (check one):

☐ is acceptable as is

☐ is acceptable as is, but comments below need to be addressed in the next report

☐ needs revision (see comments below)

Final Report (check one):

☐ is acceptable as is

☒ is acceptable, but needs minor revision (see comments below)

☐ needs major revision (see comments below)

Comments:

In previous reports under significant deviations, you stated that specimens of *C. secretus* were collected for a colleague for genetic relatedness research. Please identify the colleague conducting this research, explain how this project played a part in the genetics research, and provide the status.

Significant Deviations - under foraging behavior it states you deviated from proposed methods by not marking post forage crickets to determine their weight loss and thus how often they forage because "it was clear from the beginning of the study that *C. secretus* foraged every night." Please explain how you made this determination.

In Location, please correct the appendices numbers in the last sentence in this section to read as follows: "Only three of six study caves had maps of publishable quality (Appendices 2-4)," rather than Appendices 1-3.

In Methods, under Foraging Behavior, shouldn't fourth sentence in this section read as follows: "Thus, there were 3 bait patches at each distance for a total of 12 bait patches per cave entrance per evening," rather than "4 bait patches"?

In Methods, under Foraging Behavior, the 11th sentence in this section refers to Appendix 4. While there is an Appendix 4, it doesn't appear to be the one referred to and appears to be missing from the report. Also, add "that" after bait in the 12th sentence.

In Results and Discussion under Foraging Behavior p. 15, it states: "One might expect variation in the distribution of *S. invicta* mounds among cave entrances, and concomitant variation in the strength of their interactions, given that both taxa are opportunistic foragers, with *C. secretus*." Please change sentence to read as follows for clarity: "One might expect variation in the distribution of *S. invicta* mounds among cave entrances and concomitant variation in the strength of their interactions with *C. secretus*, given that both taxa are opportunistic foragers."

The caption for Figure 9 states *C. secretus* "food intake was significantly higher at caves with *S. invicta* mounds treated with hot water than untreated caves" although the text referring to Figure 9 in the body of the document states "*C. secretus* food intake at untreated caves was higher, in some cases significantly higher, than that at treated caves (Figure 9)." Please explain this contradiction. Also, please explain how you were able to determine the quantity of food eaten by *C. secretus* as opposed to that eaten by *S. invicta* at bait patches.

Please italicize *S. invicta* on p. 19 under Results and Discussion.

On p. 19 the sentence regarding Figure 12 states" Examining the data it is clear there is a different mechanism operating on *C. secretus* foraging behavior on 9/03 relative to 8/03 and 7/04 (Figure 12)." Should this sentence read as "7/04 relative to 8/03 and 9/03?"

Please provide black and white reproducible figures.

Poulson and Lavoie 2000, and Elzinga 2001, #441 are missing from literature cited.

FINAL REPORT

As Required by

THE ENDANGERED SPECIES PROGRAM

TEXAS

Grant No. E-7

Endangered and Threatened Species Conservation

State Project WER77: Cave Crickets (Ceutholphilus spp.) in Central Texas: the ecology of a keystone cave invertebrate

Prepared by: Kurt Lewis Helf

TEXAS PARKS & WILDLIFE

Robert Cook
Executive Director

Ron George
Program Director, Wildlife Science, Research & Diversity

Mike Berger
Division Director, Wildlife

16 February 2005

FINAL REPORT

STATE: Texas **GRANT NUMBER:** E-7

GRANT TITLE: Endangered and Threatened Species Conservation

REPORTING PERIOD: September 1, 2001 through August 31, 2004

PROJECT NUMBER: WER77

PROJECT TITLE: Cave Crickets (Ceutholphilus spp.) in Central Texas: the ecology of a keystone cave invertebrate

OBJECTIVE:

To investigate potential correlations among weather patterns and the population dynamics and foraging behavior of cave crickets (*Ceuthophilus* sp.) in caves of central Texas during 2001 – 2004 and formulate recommendations for management of cave crickets.

Approach Objectives:

1. Population Dynamics: Use ontogeny-based size classes (e.g., small juveniles = size class 1, juveniles = size class 2, etc.) developed during a three-year survey of cave crickets (*Hadenoecus subterraneus*) in Mammoth Cave National Park, to examine populations. At least two times each year I will collect data on entire cricket populations in each cave I examine. These data will permit me to determine population growth rates over the course of the study. Separating these data into ratios of adults to juveniles will enable me to determine if caves are sources or sinks (Helf et al. 1995). I will consult local experts in the Texas caving community (e.g., George Veni, Logan McNatt, etc.) for information on caves on private lands in central Texas. Written permission would be obtained from landowners if caves on private lands are censused. Thus, each year I will have at least two (i.e., one in winter one and one in summer) complete censuses of cave cricket populations in each cave I examine.

2. Foraging Behavior: Use techniques developed during a five-year study of cave cricket (*H. subterraneus*) foraging behavior in Mammoth Cave National Park. Using petri dishes filled with white albacore tuna, I will collect data on how much crickets eat per foraging bout and preferences among experimental versus natural foodstuffs. The tuna will be color-coded to distance from the cave entrance to determine how far crickets venture from the cave entrance. I will mark a subset of crickets in some populations and examine weight loss to determine how often crickets forage. All these data will be separated by sex and ontogeny. I will also

monitor climatic conditions during foraging bouts. These data will be collected at least three times per year (i.e., in spring, summer, and winter) and so I will have data on cave cricket foraging behavior each year of the study.

3. Consult experts (e.g., William Elliott, James Reddell, George Veni) for qualitative data on diversity of cave invertebrates at same eight caves where population and foraging data are collected.

4. Use a thermohygrometer to determine important data on abiotic factors pertinent to cricket surface and subsurface habitat (e.g., temperature and relative humidity). Long-term weather data, important for examining population trends and foraging behavior, will be obtained from meteorological records on U.S. Naval, NOAA, and National Weather Service websites. Using these data I will examine the effects of climatic factors on population data and foraging data. These tests will be performed at the end of the three-year study which will permit me to examine 'long-term' trends in cave cricket populations and foraging behavior.

5. Write Final Report on ecological conditions for cave crickets in central Texas. Recommendations for management of cave cricket populations will be an addendum to Final Report or separate report altogether.

Summary Of Progress:

See Attached

Significant Deviation(s).

Consult experts: No action was needed.

Genetic Analysis Among Caves: While this part of the project was not mentioned in the original proposal, I believe it directly addresses my original intent of the proposal. Specifically, examining genetic relatedness among local cave cricket populations in Government Canyon will reveal whether panmixis, or interbreeding among local cave cricket populations, occurs there or not. If populations are panmictic, then the source/sink population model may apply to Government Canyon cave crickets and caves with source populations export cave crickets to nearby sink caves. If cave cricket populations do not follow source/sink population dynamics, then each population may harbor its own unique genetic signature. Thus, each cave cricket population should be conserved accordingly.

Logistics: When I wrote the grant proposal I was near to finishing graduate school and so was looking toward further studies in cave invertebrate ecology as well as seeking employment. I did not suspect that I would receive funding for this grant and a job offer from Mammoth Cave National Park. While I gratefully accepted both my ability to travel to GCSNA as often as I wanted to carry out the proposed methodology, due to constraints imposed by my new job, was severely curtailed. My relative inability to travel became a chronic problem throughout the time span of the grant and permeated the entire study to varying degrees. I attempted to compensate by recruiting volunteers to help with the study from local caving grottoes but this met with very limited success (only one older couple helped out with preparing bait patches). Thus, I had to hire two technicians to perform a scaled down version of the original proposal. Under these constraints I elected to concentrate on the proposed methods I felt would be most successful, i.e., population dynamics and foraging behavior, rather than attempt to perform all proposed methods and very likely compromise all data collected. However, I am quite satisfied with the way the study turned out and I think I have some valuable insights to share in this report.

Location.

Initially, foraging data were recorded at eight caves in GCSNA (i.e., 10K Cave, Government Canyon Bat Cave, Goat Cave, Lithic Ridge Cave, Lost Pothole Cave, Purple Mushroom Cave, Sure Sink Cave, and Surprise Sink Cave). However, a paucity of volunteers and the remoteness of Lithic Ridge Cave and Purple Mushroom Cave forced me to eliminate these caves which leaves the remaining six study caves, i.e., 10K Cave, Government Canyon Bat Cave, Goat Cave, Lost Pothole Cave, Sure Sink Cave, and Surprise Sink Cave.

Cost: $ 56,876.50 (Total)
$ 42,657.39 (Federal)

Prepared by: Kurt Lewis Helf **Date:** February 16, 2005

Approved by: [signature] **Date:** February 25, 2005
Neil (Nick) E. Carter
Federal Aid Coordinator

Introduction

Cave cricket population dynamics and ecological interactions may be significant to resource managers throughout many National Parks and Natural Areas with cave and karst features. Two cave-dwelling cricket genera (i.e., *Ceuthophilus* spp. and *Hadenoecus* spp.) often inhabit caves throughout the southwestern and southeastern United States (Campbell 1976, Hubbell and Norton 1978, Northup et al. 1992, Mays 2002, Taylor et al. 2003). These genera are important to cave food webs because they are frequent in time and space, usually dense where they are found, and have a high impact per individual.

Ceuthophilus spp. and *Hadenoecus* spp.are typically the primary conduits for the input of allochthonous organic matter, i.e., eggs and feces, into the terrestrial habitats of caves they inhabit. This allochthonous organic matter supports subsurface communities that may include rare, sometimes endemic, obligate cave-dwelling invertebrates (Culver et al. 2000). For example, in southeastern Texas the endangered Tooth Cave ground beetle (*Rhadine persephone*) feeds largely on the eggs and nymphs of a cave cricket (*Ceuthophilus secretus*). In Mammoth Cave National Park, *Hadenoecus subterraneus* subsidizes three distinct subsurface communities with its eggs and feces (Poulson and Lavoie 2000). The effects of natural variation (e.g., drought), exotic species (e.g., Red Imported Fire Ants (*Solenopsis invicta*)) and management decisions on surface and subsurface habitat (e.g., altered cave entrance configuration) on cricket population structure and dynamics have the potential to affect the flow of allochthonous organic matter into caves (Poulson et al. 1995).

One crucial management question regarding cave crickets, particularly southwestern species, is how biotic and abiotic modifications to their foraging environment impact cricket populations and the communities they subsidize.,This is because anthropogenic and natural stressors can cause fluctuations in cricket populations over time and so initiate a trophic cascade throughout a cave's terrestrial food web. For example, variable climatic conditions over a thirty year period affected the favorability of surface foraging conditions for crickets and so caused fluctuations in the amount of cricket guano available to the guano community; fluctuations in these subsidies in turn affected guano community population dynamics (Poulson et al. 1995).

Resource managers at Natural Areas with cave and karst features and significant cave cricket populations may want to implement long-term protocols to monitor cricket populations. Long term monitoring of cricket population dynamics and ecological interactions will elucidate the effects of management actions on cave cricket populations and provide resource managers with an index of overall robustness of cave terrestrial invertebrate communities.

Significant Deviations

When I wrote the grant proposal I was near to finishing graduate school and so was looking toward further studies in cave invertebrate ecology as well as seeking employment. I did not suspect that I would receive funding for this grant and a job offer from Mammoth Cave National Park. While I gratefully accepted both my ability to travel to GCSNA as often as I wanted to carry out the proposed methodology, due to constraints imposed by my new job, was severely curtailed. My relative inability to travel became a chronic problem throughout the time span of the grant and permeated the entire study to varying degrees. I attempted to compensate by recruiting volunteers to help with the study from local caving grottoes but this met with very limited success (only one older couple helped out with preparing bait patches). Thus, I had to hire two technicians to perform a scaled down version of the original proposal. Under these constraints I elected to concentrate on the proposed methods I felt would be most successful, i.e., population dynamics and foraging behavior, rather than attempt to perform all proposed methods and very likely compromise all data collected. However, I am quite satisfied with the way the study turned out and I think I have some valuable insights to share in this report.

Population dynamics

The significant deviation that occurred in this portion of the proposal was that there was no time to perform censuses of cave cricket numbers at each study cave. However, this could be viewed as serendipitous as my opinion of the usefulness of this technique has changed considerably. During these times of increased budget constraints, a monitoring method developed for GCSNA must be cost effective and meet the needs of park management to be efficacious. However, censusing cricket populations is highly labor intensive in that it involves a total count of every visible cricket within tens of meters of cave passage. Thus, the time investment for GCSNA employees performing complete census of more than a few caves would be considerable. Further, if examinations of census data from Mammoth Cave National Park are any guide, the population data produced with this technique would be highly variable among years and minimum detectable changes in populations would be on the order of ≥30%. Because crickets are keystone species, minimum detectable changes in cricket populations useful to GCSNA management should be lower, on the order of ≤10%, so as to trigger studies to identify potential causes of the decline and to determine mitigation of the problem {Elzinga, 2001 #441}. Thus, this technique would most likely have been jettisoned in favor of a less time consuming more data rich technique. The recommendations I make, based on the sampling technique we used of necessity, will result in a more efficacious monitoring method than the total census method. Incorrect data collection by field technician during the mark/recapture procedure precluded the use of Lincoln-Petersen index to examine populations. In any case, numbers of recaptured of marked individuals were so low that the data would likely not have been useful.

Foraging Behavior

The only deviation from the methods proposed is that I did not mark post forage crickets in an effort to determine their weight loss and thus how often they forage. This technique was jettisoned because it was clear from the beginning of the study that *C. secretus* foraged every evening.

Hypogean Invertebrate Inventory

No invertebrate inventories were performed. Texas Speleological Survey mapping expeditions GCSNA had already generated a list of adequate collection/ observational data on invertebrate distribution among the six study caves (Miller et al. 2002); these are excerpted in Appendix 1.

Location

This study occurred in Bexar County, Texas at Government Canyon State Natural Area (GCSNA), 12861 Galm Road, San Antonio, TX 78254. Geologically, GCSNA is situated in the Austin Chalk and Edwards Limestone (Veni 198[illegible]). GCSNA management requested I not disclose exact locations of the six caves from which I collected data but their general locations are given in Figure 1. Only three of six study caves had maps of publishable quality (Appendices 1-3).

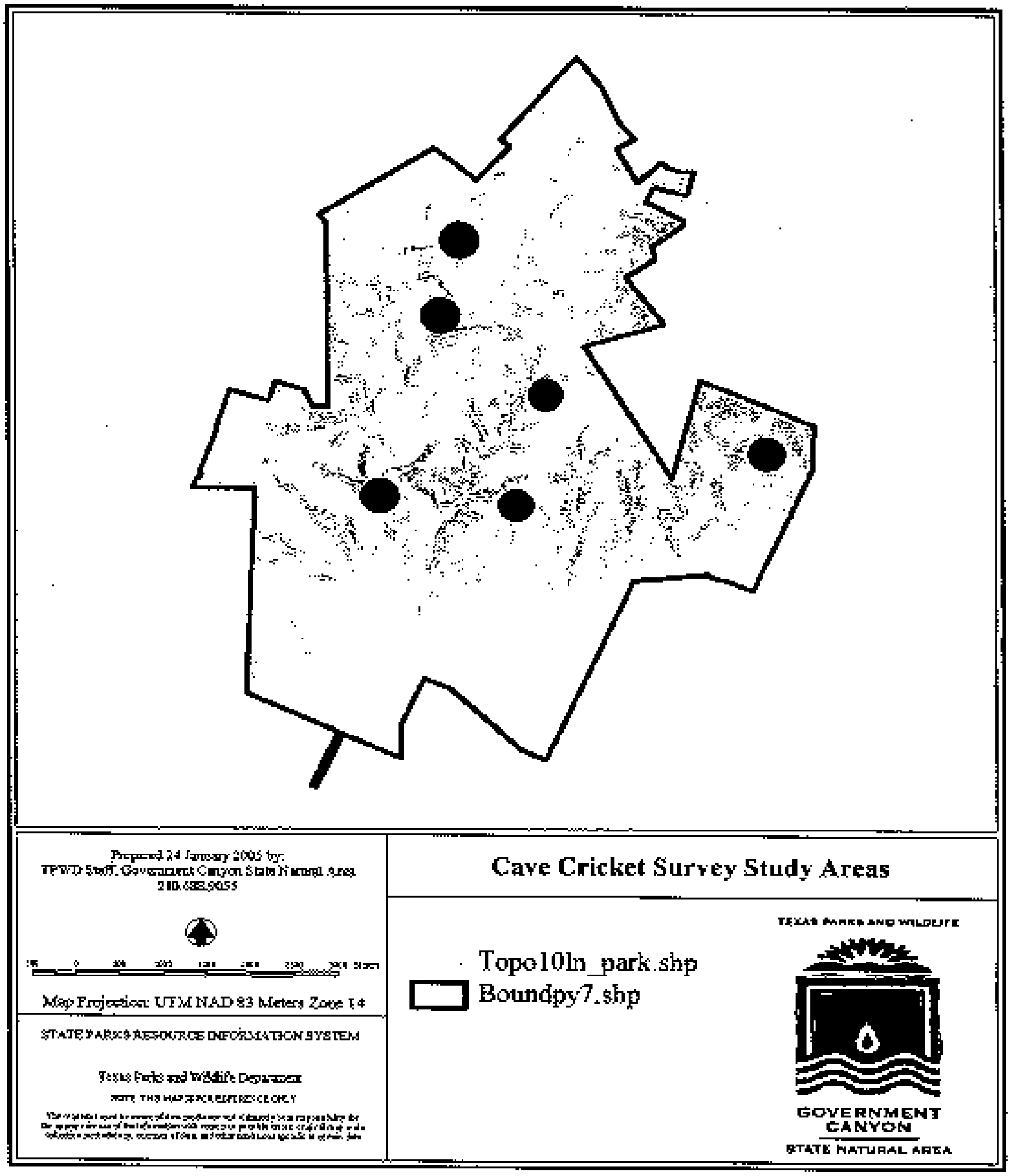

Figure 1. Topographical map of Government Canyon State Natural Area. Red dots indicate general location of six study caves. Locations are vague by GCSNA request.

Methods

1. *Population Dynamics*

In 2003, we investigated cave cricket (*Ceuthophilus secretus*) population dynamics using several methods. Throughout 2003 we collected crickets in groups of 200 at our six study caves (i.e., 10K, Surprise Sink, Sure Sink, Goat Cave, Lost Pothole Cave, and Government Canyon Bat Cave), recorded their sex and hind femur lengths, and released them at their respective cave entrances. In early 2003, we counted and collected all the crickets we could locate at Surprise Sink (1/11/03), 10K (1/17/03), Goat Cave (3/8/03) and Government Canyon Bat Cave (3/8/03); we subsequently marked the crickets using queen bee markers. We returned the following day and counted all the marked crickets we could find.

2. *Foraging Behavior*

We filled bait dishes (60x15mm petri dishes) with 30 g of pureed albacore tuna, determined on an electronic balance, prior to their placement around six cave entrances. Thirty minutes before we took our first readings, we placed bait dishes just outside cave entrances, at 5m, and at 10m distance away from cave entrances. At each of these distances we placed one bait patch at each cardinal direction, i.e., North, South, East, and West (Figure 2). Thus, there were 4 bait patches at each distance for

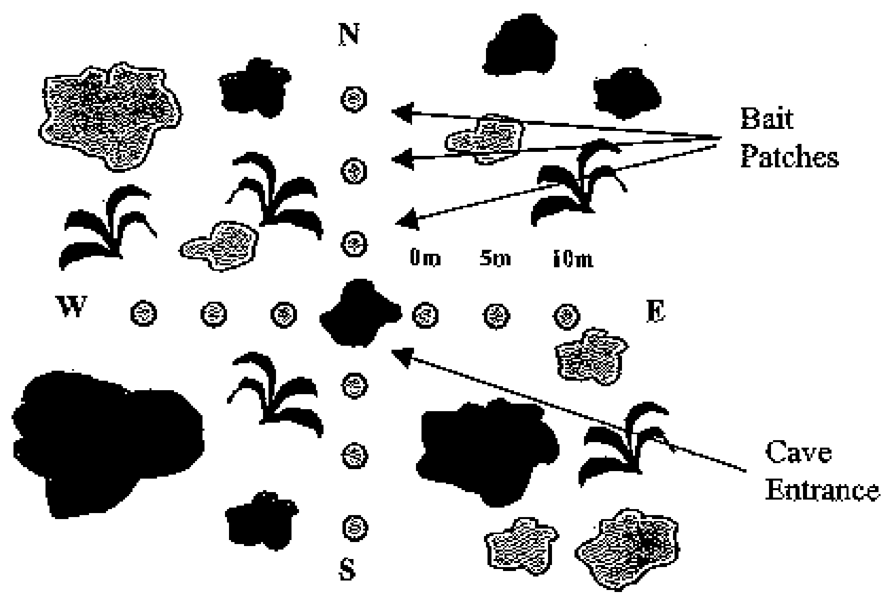

Figure 2. Diagram of bait patch arrangement we used to examine cave cricket foraging behavior.

a total of 12 bait patches per cave entrance per evening. We performed these procedures at our six study caves from mid-late 2002 until mid 2004 (Table 1). We perched one extra bait patch atop a cardboard box to serve as a control patch to

Cave	10K	Goat Cave	Surprise Sink	Govt. Canyon Bat Cave	Lost Pothole	Sure Sink
Expt. Date	6/4/02	5/10/02	5/21/02	6/2/02	5/3/02	5/14/02
	6/18/02	5/31/02	6/14/02	8/30/02	5/31/02	6/4/02
	7/30/02	6/11/02	8/13/02	9/20/02	6/11/02	6/21/02
	8/17/02	9/6/02	8/30/02	**2/9/03**	7/26/02	7/19/02
	9/17/02	9/20/02	10/1/02	4/18/03	8/20/02	8/6/02
	1/17/03	3/7/03	3/14/03	**4/19/03**	9/24/02	9/13/02
	3/28/03	**5/24/03**	**3/15/03**	5/29/03	1/24/03	1/7/03
	5/3/03	5/31/03	5/15/03	**7/27/03**	**2/2/03**	3/21/03
	6/29/03	8/12/03	**5/24/03**	8/15/03	4/11/03	**4/12/03**
	7/19/03	**9/14/03**	8/13/03	9/28/03	**4/12/03**	**6/14/03**
	8/11/03	9/24/03	8/28/03	10/16/03	**5/14/03**	7/25/03
	8/21/03	10/20/03	10/9/03	11/19/03	7/31/03	8/16/03
	10/6/03	2/27/04	11/13/03	12/26/03	8/14/03	9/16/03
	12/4/03	5/21/04	12/11/03	1/21/04	**9/14/03**	**9/19/03**
	1/8/04	7/26/04	1/28/04	3/26/04	9/29/03	11/6/03
	3/5/04		3/19/04	5/25/04	10/23/03	12/22/03
	4/23/04		5/18/04		12/23/03	2/6/04
	7/18/04		7/13/04		2/20/04	4/9/04
			7/27/04		4/16/04	7/17/04
					7/21/04	8/10/04
					8/21/04	

Table 1. List of caves and the dates on which we set bait patches at GCSNA. Bold font indicates dates on which we collected cave crickets and measured their hind femur lengths.

determine weight loss from evaporation; the loss was negligible and, curiously, on some nights the dishes gained weight. In the interim between bait patch placement and our first reading, we searched for active fire ant (*Solenopsis invicta*) mounds within a 20 meter perimeter of each cave entrance. After counting active fire ant mounds we would sit quietly ca. 5m away from the cave entrance with our lights off so as not to disturb the foraging crickets. We took readings, which consisted of recording the numbers and sex of all crickets feeding at each bait patch, every 30 minutes for 2 hours. We counted the number of crickets from a distance so as not to disturb their feeding before approaching more closely to sex them. From spring through late summer, crickets were precluded from foraging at some 5m and 10m bait patches after the 2 hour period due to large numbers of *S. invicta* feeding at them (Figure 3 and Appendix 4). Thus, the petri dishes were collected after two hours and stored in a refrigerator until they could be reweighed to determine their post forage weight, that is, the amount of bait had been eaten over two hours. These data served as my dependent variable in statistical analyses. We tried to remove and/or prevent fire ants from precluding crickets' access to bait patches but these measures usually

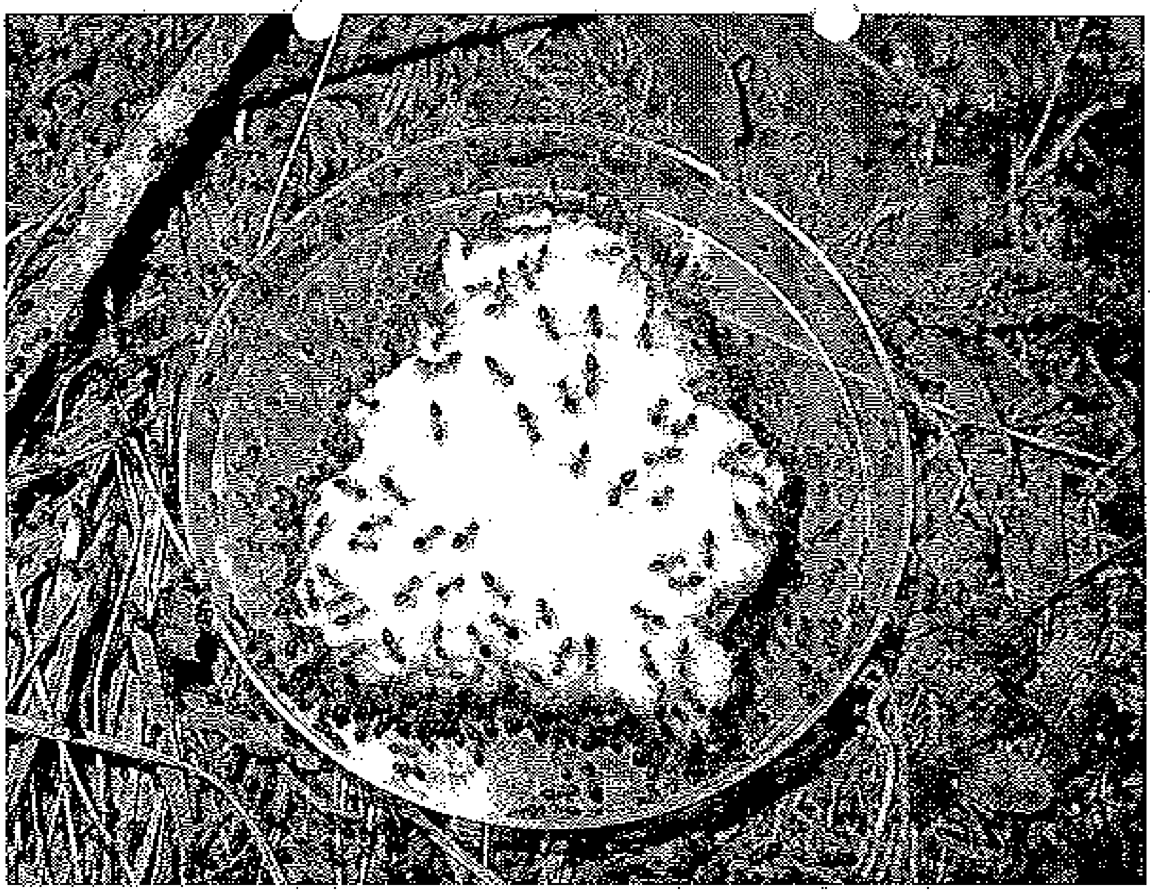

Figure 3. Fire ants (Solenopsis invicta) swarming a bait patch at Government Canyon Bat Cave. Note the lack of cave crickets (Ceuthophilus secretus) feeding at this patch.

failed. Between readings we recorded cricket feeding behavior at bait patches on Hi8 video tape using the infrared "night shot" setting on a Sony Handicam. We reviewed videotapes later and recorded the time crickets spent feeding at bait patches, their stage, and sex.

To examine the degree to which the independent variables explained the variation in my dependent variables I used the General Linear Model (GLM) in Systat 10.2 (Wilkinson and Coward 2002). I used GLM rather than ANOVA because the data I gathered on each stage in crickets' foraging behavior involved one dependent variable (e.g., mean patch weight) and both continuous (e.g., temperature) and categorical (e.g., year) data for my independent variables. Further, I did not want to be constrained by having to test interactions among all independent variables as required by ANOVA in Systat 10.2 (Wilkinson and Coward 2002). In my analyses years, seasons, and patch distance were represented by dummy variables (e.g., 1=just outside, 2=5m, and 3=10m). The dummy variable 'seasons' represented data from twelve months of the year pooled into three numerical categories, i.e., 1=winter=January-March; 2=spring/summer=April-August; and 3=fall=September-December. Dummy variables were assigned nonrandomly, in linear order, to represent years, seasons, and patch distance because these variables can be measured linearly. I also assigned numerical dummy variables to the six study caves but I chose these randomly, by repeated die casts, because I could think of no logical way to order them. To increase the normality of dependent variables, bait patch weights were log transformed and numbers of fire ants were square root transformed prior to analysis (Sokal and Rohlf 1981). Timed feeding bouts at bait patches, determined from video tapes, were also transformed for analysis using an angular conversion (Zar 1999). Climatic data on rainfall and temperature from 2001-2004 were obtained from the National Oceanic and Atmospheric Administration's website http://www.srh.noaa.gov/ewx/html/cli/sat/sclidata.htm. Planned post hoc comparisons among means were made with the Tukey test for unequal sample sizes (Zar 1999).

Results and Discussion

I. Population Dynamics

The hind femur length data we collected throughout 2003 among all six study caves suggests some populations could be net exporters of individuals to other caves. Indeed, the wide range of hind femur lengths at Goat and Lost Pothole indicates adult crickets are present and possibly still laying eggs. Clearly, these caves contain overlapping generations rather than single cohorts; this may be more widespread among the study cave due to field observations of overlapping generations at other caves (Figure 13).

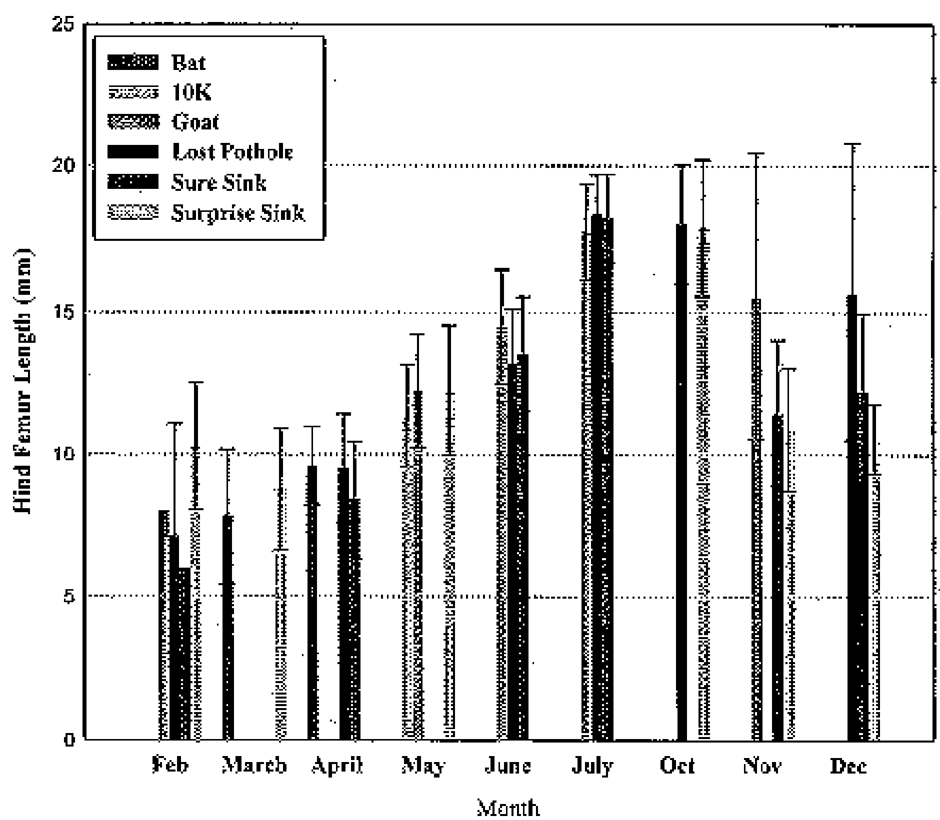

Figure 4. Varation in hind femur length by month among four caves in 2003. Note the wide range in hind femur lengths at Goat and Lost Pothole Caves in November and December.Error Bars are ±1 StDev.

I analyzed interactions among several biotic and abiotic factors that, given my research experience with southeastern cave crickets (*Hadenoecus subterraneus*), I hypothesized should strongly affect southwestern cave cricket (*Ceuthophilus secretus*) foraging behavior on the surface. However, I also attempted to incorporate the hypothesized interactions between *C. secretus* and *S. invicta* (Elliott 1993, 2000, Taylor et al. 2003) in my analyses. The factors I analyzed explained a large amount of variation in cricket food intake for all three years of the study (R^2=.66, N=1013). A significant interaction between patch distance and season ($F_{4, 992}$ = 10.65, P<.0001) reveals one problem with using bait patches: most crickets will use the closest bait patches and skew the results (Figure 5). However, these results are quite revealing ecologically in that during the winter season there was no difference in food intake among bait patches. This strongly suggests some of the early instar nymphs feeding at bait patches in winter missed the bait patches just outside the cave entrance; a likely explanation is their search acumen is poor relative to late instar and adult crickets. An alternative, not necessarily mutually exclusive, explanation is that low winter temperatures reduced the volatility of the odor producing compounds in the bait patches and so they were harder for nymphs to detect (O'Neill et al. 1994). Another alternative is that nymphs have seasonal food preferences and so largely avoided my bait patches (Cokendolpher et al. 2001). It is also interesting to note the very low temperatures (3.89 °C) at which *C. secretus* forages in winter; particularly because low temperatures can increase cave crickets' evaporative water loss and

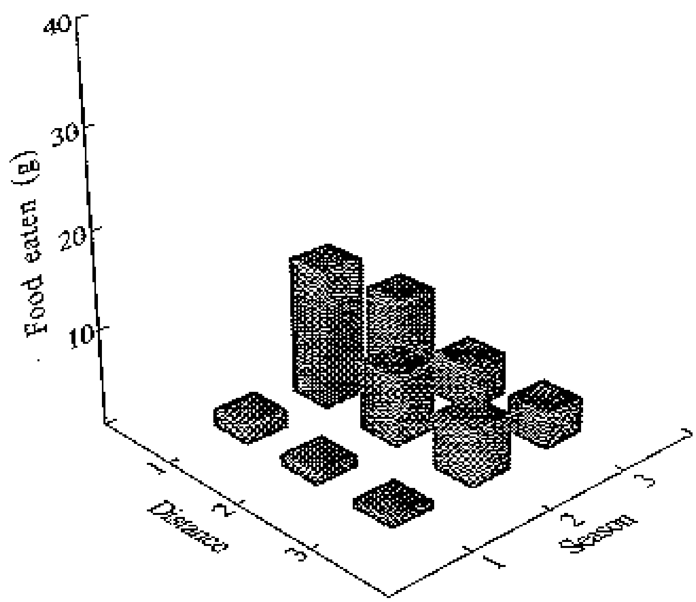

Figure 5. The overall amount of bait consumed at bait patches as a function of season (1=Jan-April, 2=May-August, 3=September-December) and bait patch distance (1=just outside cave entrance, 2=5m, and 3= 10m). Note significant increases in food consumption among all bait patches only occur in seasons 2 and 3 when large late instar and adult crickets are abundant; this suggests intraspecific competition at my relatively rich bait patches.

decrease their jumping ability and so preclude foraging bouts at very low temperatures. However, these data strongly suggest that *C. secretus* can function at low temperatures unlike *H. subterraneus* and *H. cumberlandicus* in the southeast, which are precluded from foraging at these temperatures due to reduced jumping ability and increased evaporative water loss (O'Neill et al. 1994, Yoder et al. 2002, Helf 2003). Indeed, *C. secretus* exhibits a shiny exoskeleton that indicates a thick waxy epicuticle which aids in retarding evaporative water loss (Gullan and Cranston 1994). Foraging opportunistically throughout the winter also enables nymphs to continue their growth cycle uninterrupted by hibernation, unlike their southeastern congeners (e.g., *C. latens* which hibernates in caves in great numbers during winter), and provides a temporal refuge during foraging bouts from competitive interactions with *S. invicta* which are less likely to forage at low temperatures (Porter and Tschinkel 1987).

The significance of the temperature term on food intake at bait patches ($F_{1, 992} = 86.81$, $P<.0001$) strongly supports these inferences since the lowest food intake at bait patches is associated with the lowest winter temperatures (Figure 6) when foraging crickets are almost exclusively early instar nymphs. The significant

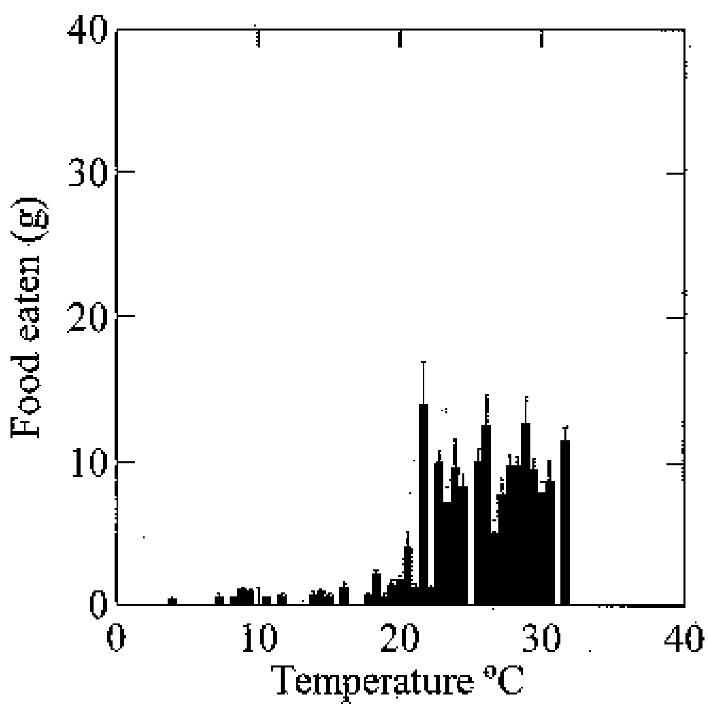

Figure 6. Food eaten at bait patches as a function of temperature. Lowest temperatures are during winter when foraging crickets are almost all early instar nymphs. Significant increases in food intake at higher temperatures are during summer and fall when many late stage instars and adults forage and support inferred increased intraspecific competition. Error bars are ±1 SE.

overall increase in food intake at bait patches, highest during summer, and fall (Figure 5) when late stage instars and adults are found in the greatest numbers (Hubbell 1936), suggests increased intraspecific competition among *C. secretus* feeding at my relatively rich bait patches. Indeed, the increased food intake among all bait patches during summer and fall suggests increased competition (Figure 5).

While there are drawbacks in using bait patches to examine foraging behavior in cave-dwelling orthoptera, I found one of the apparent advantages is the insight I gained as to the effect of primary productivity, as predicted by rainfall, on *H. subterraneus* foraging behavior (Helf 2003). The availability of crickets' natural food patches is directly related to primary productivity. Indeed, several studies indicate a large portion of above-ground net primary productivity (ANPP) in temperate forests enters detritus-based food webs and that ANPP, as predicted by rainfall, is highly seasonal and greatly reduced during cold months (Edwards et al. 1970, Crossley 1977, Webb et al. 1983, González-Hernández et al. 1998, Chen and Wise 1999, Knapp and Smith 2001). Thus, I hypothesized that *C. secretus*, more properly classified as an opportunistic scavenger like *H. subterraneus* as there is no direct evidence that either is predaceous, use of my bait patches would be inversely correlated with primary productivity as predicted by rainfall. I found the interaction of year with average monthly precipitation was highly significant ($F_{2, 992} = 80.50$, $P<.0001$) and indeed the data show that 2003, the year with

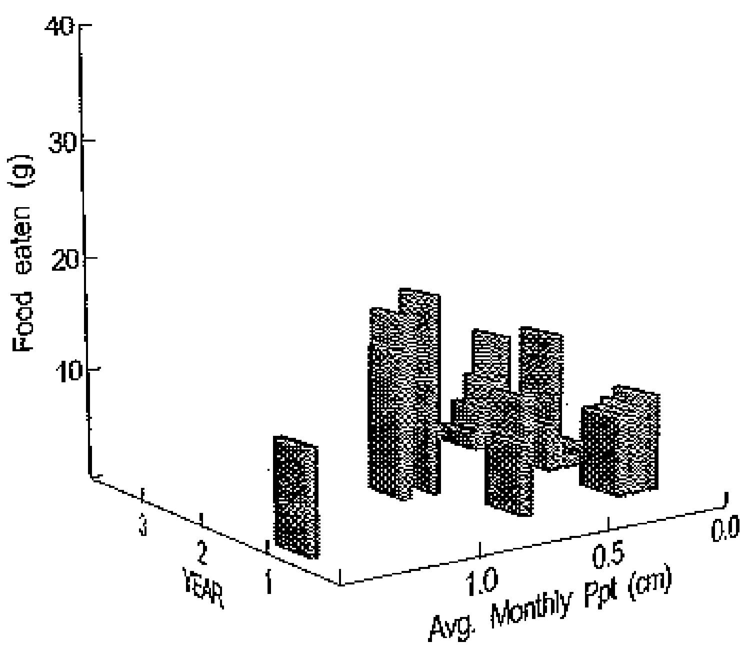

Figure 7. Food eaten at bait patches as a function of year (1=2002, 2=2003, 3=2004) and average monthly precipitation. Note highest food intake in year 2 and similar high food intake between years 1 and 3, all during summer and fall. Year 2 had the lowest precipitation levels during the growing season whereas years 2 and 3 had similar precipitation levels. Low food intake was during winter months, when food intake was generally low.

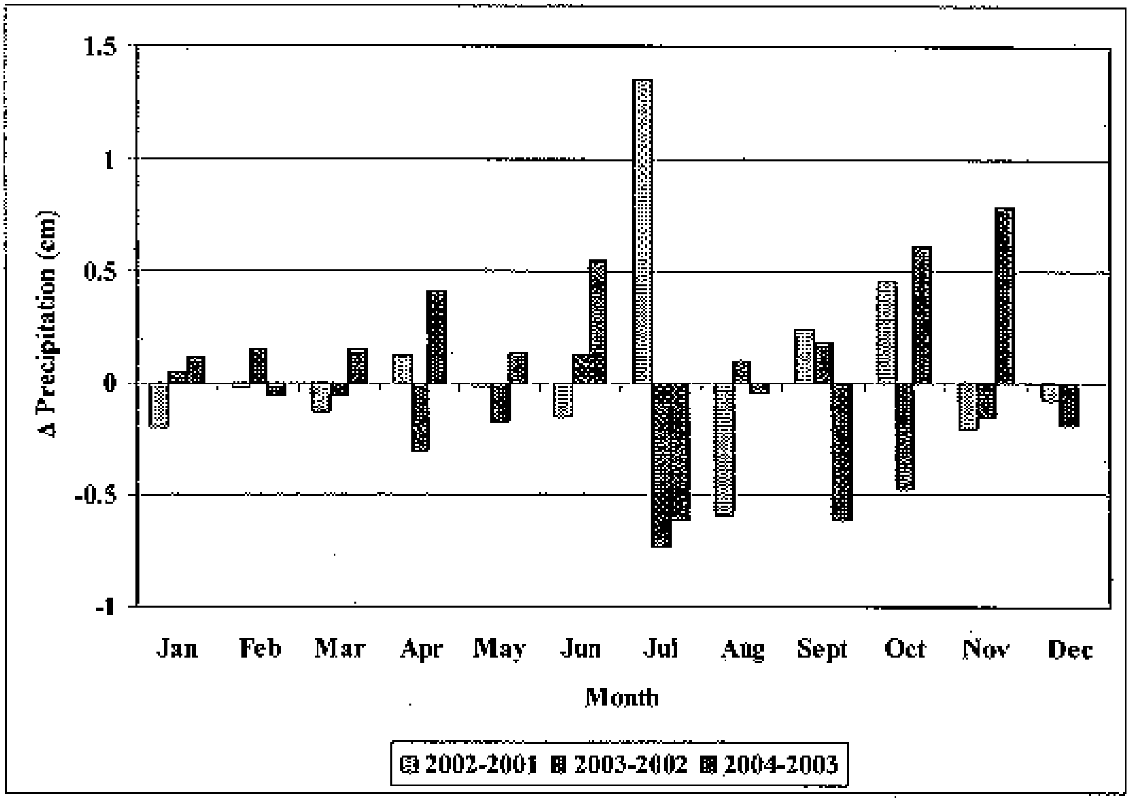

Figure 8. Monthly differences in the cumulative precipitation among years (Δ=current year-previous year). Total precipitation in 2002 and 2004 was higher than in 2003. Total monthly differences in precipitation were significantly higher in 2004 than that in 2003 (Wilcoxon signed test, $Z=1.61$, $P=.05$); note among-year differences in precipitation in the early growing season.

the highest food intake (Figure 7), had the lowest annual rainfall and the lowest proportion of rainfall from April-October during the study, when most of the biomass contributing to ANPP is generated (Webb et al. 1983, González-Hernández et al. 1998, Knapp and Smith 2001). Further, only 2004 showed consistent increases in precipitation during the early growing season from the previous year (Figure 7). Thus, *C. secretus* foraged more heavily at my bait patches during years when ANPP was relatively low (i.e., 2002 and 2003) and relied on preferred, natural foods when ANPP was relatively high (i.e., 2004). Indeed, food intake during 2002 suggests I observed "the ghost of ANPP past" in that differences in monthly precipitation, particularly during the early growing season, was reduced from 2001 to 2002 (Figure 7 and 8).

One might expect variation in the distribution of *S. invicta* mounds among cave entrances, and concomitant variation in the strength of their interactions, given that both taxa are opportunistic foragers, with *C. secretus*. This was particularly true throughout this study because three cave entrances (i.e., Government Canyon Bat Cave, Lost Pothole, and Surprise Sink) had all visible mounds within at least 20m dug up and

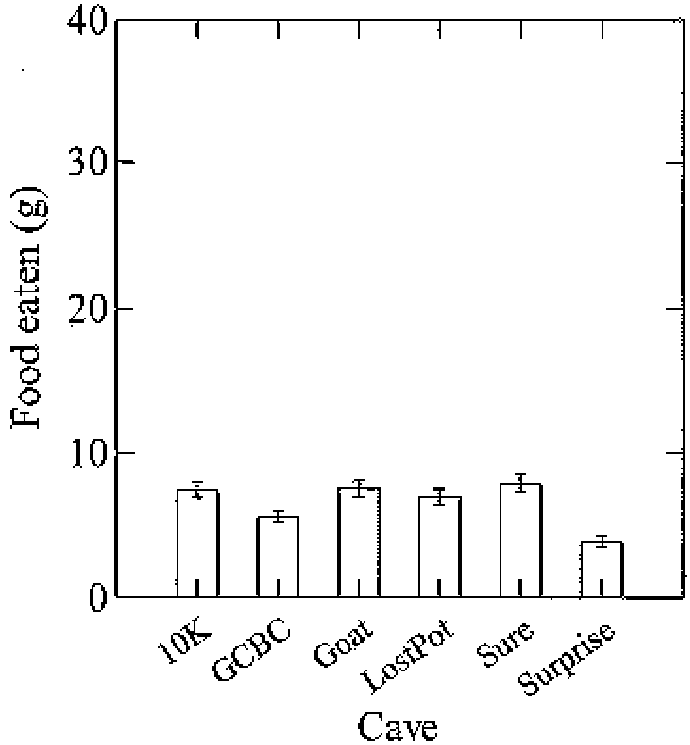

Figure 9. Effects of cave entrance on *C. secretus* food intake at bait patches (GCBC=Government Canyon Bat Cave and LostPot=Lost Pothole). Note food intake is significantly higher at caves with *S. invicta* mounds treated with hot water than untreated caves (10K > Surprise Sink; Goat > GCBC, Lost Pothole, and Surprise Sink; Sure Sink > Surprise, Tukey Test $p<.0001$). Error bars are ±1 SE.

"treated" with boiling water and three study cave entrances were left untreated (i.e., 10K, Sure Sink, and Goat Cave). While cave entrance had a significant effect on *C. secretus* food intake ($F_{5, 987} = 23.19$, $P<.0001$) surprisingly it was the opposite of what I hypothesized in that *C. secretus* food intake at untreated caves was higher, in some cases significantly higher, than that at treated caves (Figure 9).

Much has been written in the scientific literature regarding the potential long-term negative effects of non-native *S. invicta* on native taxa (but see (Morrison 2002): competitive replacement of native ant species, depredation of native arthropods, and altered foraging behavior are just a few examples (Porter and Tschinkel 1987, Porter and Savignano 1990, Jenkins and Matthews 2003, Orrock and Danielson 2004). Indeed, scientific studies of Texas cave invertebrate communities typically mention the potential negative effects of *S. invicta* as a predator or a competitor relative to *C. secretus* (Elliott 1993, 2000, Taylor et al. 2003). Thus, I hypothesized *C. secretus* food intake at the treated caves would be significantly greater due to their release from competition with or perceived predation risk from *S. invicta*. But my results do not necessarily reject the hypothesis that *S invicta* competes with *C. secretus* and in fact may support it. Indeed, one possible explanation for these results is that at untreated caves *S invicta* may have precluded *C. secretus* from some bait patches, leaving them with fewer patches, increased intraspecific exploitative competition among bait patches and so increased bait removed from patches collectively. Finally, the effect of the average number of *S invicta* at bait patches on *C. secretus* food intake ($F_{1, 992} = 26.64$, $P<.0001$), while significant, examination of the data yields another unexpected result: many instances where there were low average numbers of *S invicta* yet *C. secretus* food intake was low (Figure 10). These data points are likely winter data, when food intake is low (Figure 5), but generally these data support a negative interaction between *S invicta* and *C. secretus* but whether their relationship is competitive or predator-prey is still in question. How *S invicta* affects the amount of time *C. secretus* spent in bait patches, if at all, may provide an answer.

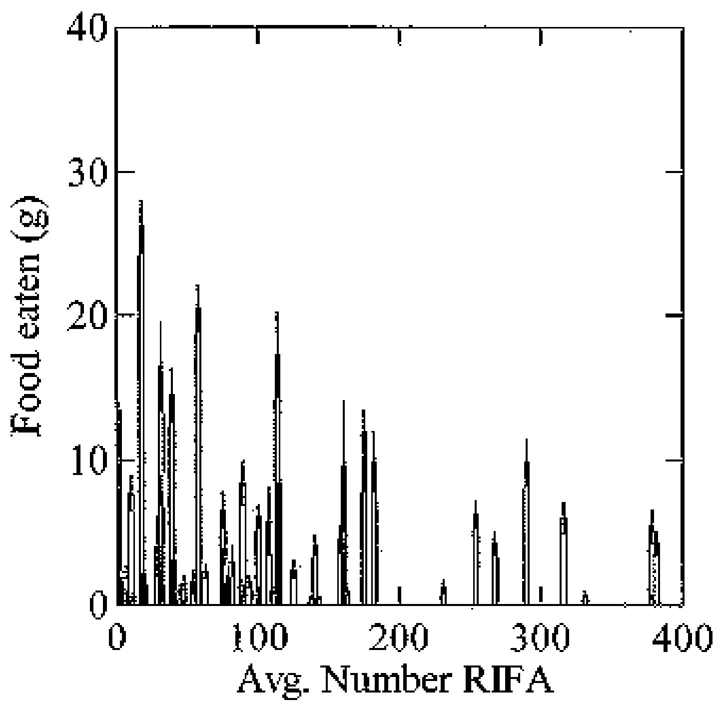

Figure 10. Effects of average number of *S. invicta* at bait patches on *C. secretus* food intake at bait patches. While this term was significant, the data appear equivocal. Error bars are ±1 SE.

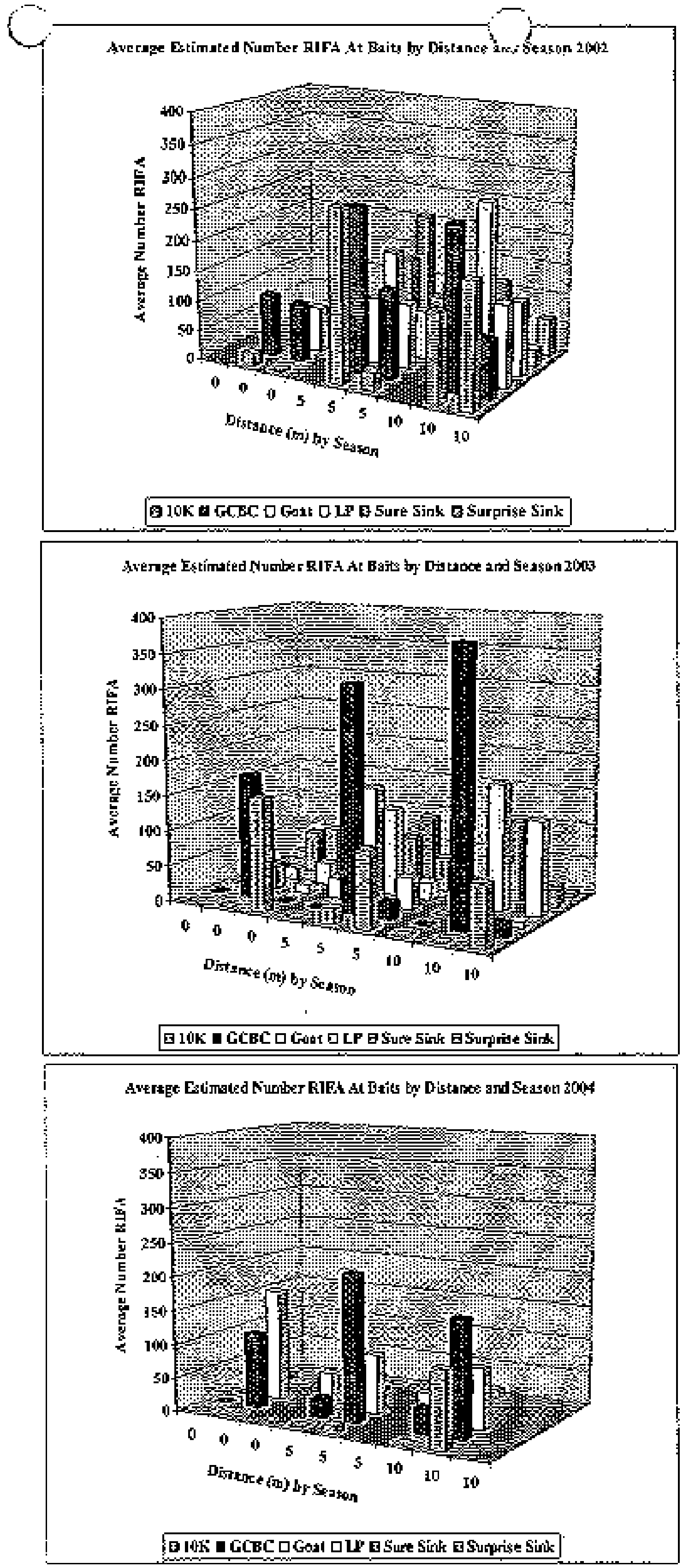

Figure 11. Average number of *S. invicta* at bait patches as a function of patch distance and season among all three years of the study (LP=Lost Pothole, GCBC=Government Canyon Bat Cave). Seasons are in order with patch distance, e.g., 1st zero=winter, 2nd zero=spring/summer, and 3rd zero=fall.

Clearly, on a gross time scale *S. invicta* is found at our bait patches in large numbers from spring through fall (Figure 11) but of interest is how the presence of S. invicta at bait patches affects *C. secretus* feeding behavior on a smaller time scale, e.g., one or several evenings, if at all and by what mechanism? I analyzed data from three dates, i.e., 8/03, 9/03, and 7/04, and though there was a significant interaction between cave and patch distance on 8/03 and 9/03 (two-way ANOVA, $F_{4, 132} = 5.95$, $P<.0001$; $F_{6, 232} = 3.73$, $P<.005$, respectively) on 7/04 only patch distance had a significant effect on the time *C. secretus* spent in bait patches (two-way ANOVA, $F_{2, 58} = 1.75$, $P<.0001$). Examining the data it is clear there is a different mechanism operating on *C. secretus* foraging behavior on 9/03 relative to 8/03 and 7/04 (Figure 12). In general, the time *C. secretus* spent in bait patches on 9/03 decreased as a function of patch distance from cave entrances and was negatively correlated with *S. invicta* numbers, which suggests perceived predation risk or interference competition due to *S. invicta*. However, the time *C. secretus* spent in bait patches on 8/03 and 7/04 increased as a function of patch distance from cave entrances, which suggests perceived predation risk due to *S. invicta*

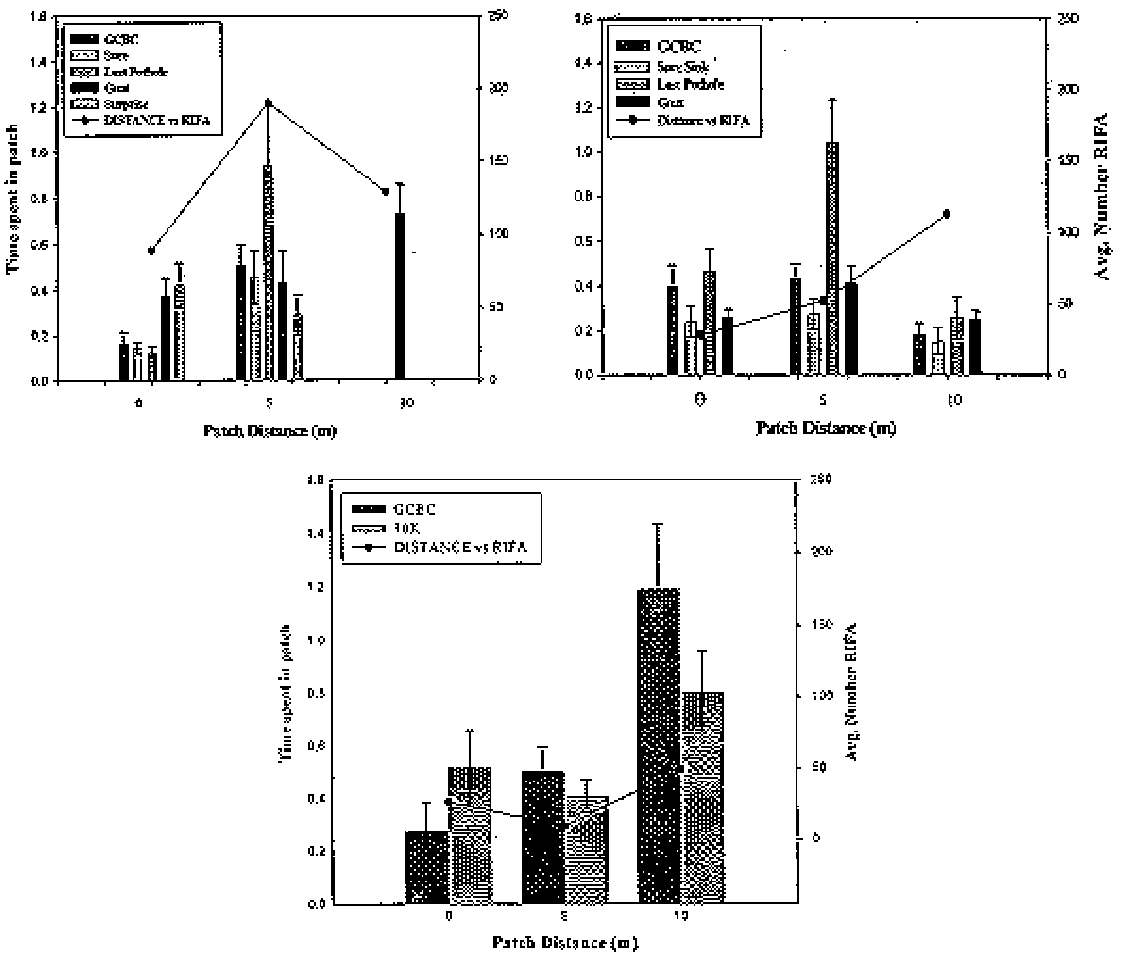

Figure 12. Mean time spent in patch by distance relative to *S. invicta* numbers on (clockwise, from left) 8/03, 9/03, and 7/04. Note the dissimilarity in the data on 9/03 relative to 8/03 and 7/04. Error bars are ±1 SE.

or interference competition due to conspecifics or *S. invicta*. Increased perceived predation risk from *S. invicta* appears unlikely because the time *C. secretus* spent at bait patches on 8/03 was positively correlated with numbers of *S. invicta* and the opposite would be true if this were the case. While it is plausible that *S. invicta* preys on juvenile *C. secretus*, it is unlikely that healthy adults, with their prodigious jumping ability, could be captured. Indeed, anecdotal observations (Appendix 5) indicate adult *C. secretus* often jumped in and out of bait patches that were swarming with fire ants. Some researchers have shown abundance of ground cricket increased significantly after an *S. invicta* invasion (Porter and Savignano 1990). More likely, *C. secretus* and *S. invicta* are competitors on some level. Indeed, I have strongly supported one criterion for interference competition in that *S. invicta* clearly diminish foraging effectiveness in *C. secretus* by reducing the time it spends in bait patches and therefore its food intake (Griffith and Poulson 1993).

These data and my field observations indicate weak competitive interactions between *C. secretus* and *S. invicta*. *C. secretus* nymphs may possess similar or only slightly superior search acumen in finding natural food patches or items. However, my data clearly show early instar nymphs forage during the winter and so possess a temporal advantage over *S. invicta*. Further, adult *C. secretus*, with their long legs and antennae (scavenger on stilts), are likely superior to *S. invicta* in locating food patches or items and exploiting them before *S. invicta* arrives. Finally, *C. secretus* also utilizes diet refugia when it found my bait patches were being exploited by *S. invicta* (Figure 13). At Government Canyon Bat Cave I observed many crickets feeding on rotting Persimmon (*Diospyros* texana) fruit and *S. invicta* ostensibly did not utilize these food patches even though its diet can include fruit. There is a possibility that persimmon fruit contain some secondary compound unpalatable to *S. invicta*.

Figure 13. *C. secretus* feeding on ripe persimmon fruit at Government Canyon Bat Cave. Note size distribution of feeding crickets. Note also no *S. invicta* are present.

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I would like to acknowledge the United States Fish and Wildlife Service and the Texas Parks and Wildlife Department for funding and administering this study. I am grateful to Joel Brown, Alex Alonzo, and Thomas Lagen of the University of Illinois at Chicago. I would also like to thank my field assistants: Erik Holmback, Kyle McDaniel and Gail Denkhaus for all their hard work. In addition, I owe much gratitude to the staff of Government Canyon State Natural Area, particularly Deirdre Hisler, Erik Holmback, and Bruce Wilson. I am also indebted to George Veni, James Reddell, Marvin Miller, Rick Olson, and Bob Woodman. Last but not least I would like to thank my wonderful family, Carol, Brannon, and Hannah for their understanding and forebearance. Any omissions in these acknowledgements were unintentional.

Management Recommendations

Cave cricket population dynamics:
As I stated in the significant changes section, my thinking on this type of procedure has been radically altered. I suggest a test of a photomonitoring method similar to the one we are developing at Mammoth Cave National Park. This photomonitoring method requires only a digital camera and the software to examine the pictures. Several pictures, between 4 and 8, are taken from the same point, or landmark, at some interval during the year. We have typically used two landmarks per cave: one distal to the entrance and one proximal to the entrance. The pictures are examined back at the office and the animals counted and sexed and once the baseline data are established some descriptive statistics can be used to examine cricket population structure and dynamics. The data are archivable for later examination and easily stored on compact discs. This is an extremely low impact way to examine cave cricket population structure and dynamics.

Cave cricket foraging behavior
More study is required to elucidate some of the preliminary findings I made during this study. I have just scratched the surface with the data I gathered in this study.

One bit of basic cave ecology that is assumed, probably correctly, is the relationship between *C. secretus* and cave dwelling invertebrates. I am unaware of any studies that strongly support these relationships. This is a key piece of information that must be elucidated.

One thing I was particularly concerned with was the possibility of trees being cleared around caves with bat populations, ostensibly to facilitate their exiting caves. My concern is with Persimmon trees that provide *C. secretus* with a food source apparently free of competition with *S. invicta*. If trees must be cut from around cave entrances I suggest selective cutting that spares Persimmon trees.

A study could be commissioned examining the potential effects of persimmon trees and/or primary productivity on cave cricket populations and their dependent invertebrate communities.

Cave invertebrate populations
A comprehensive study should be made of the cave invertebrate communities at GCSNA; particularly the six caves I investigated in this study. A number of methods are available to do this; the methods I cited in the introduction are particularly good.

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Appendix 1

Excerpts from "Summary of biological collections and observations from caves at Government Canyon State Natural Area"

Goat Cave (19-9)

James Reddell and Marcelino Reyes collected in the cave on 24 May 1998. A sample of leaf litter and a bird nest was returned to the laboratory for Berlese funnel separation. The following is a fauna list:

Snails: Gastropoda undetermined
Terrestrial isopods: *Porcellio* sp. (?trogloxene)
Spiders: *Cicurina* sp. (troglophile)
Cicurina (*Cicurusta*) *varians* (troglophile)
Neoleptoneta sp.
Linyphiidae genus and species
Achaearanea porteri (troglophile)
Mites: Acarina undetermined
Harvestmen: *Leiobunum townsendii* (trogloxene)
Centipedes: Gosibiidae genus and species
Geophilomorpha undetermined
Millipedes: *Eurymerodesmus melacis* (accidental)
Springtails: Collembola undetermined
Insects: Insecta larvae undetermined
Cave crickets: *Ceuthophilus* (*Ceuthophilus*) *secretus* (trogloxene)
Ceuthophilus (*Geotettix*) *cunicularis* (troglophile)
Barklice: Psocoptera undetermined
Ground beetles: Carabidae genus and species
Rove beetles: Staphylinidae genus and species
Darkling beetles: *Embaphion muricatum* (trogloxene)
Fire ants: *Solenopsis* (*Solenopsis*) *invicta* (trogloxene)
Flies: Diptera undetermined
Mosquitoes: Culicidae genus and species
Cliff chirping frogs: *Syrrhophus marnocki* (trogloxene) (SIGHT)
Short-lined skink: *Eumeces tetragrammus* (trogloxene) (SIGHT)
Black vultures: *Coragyps atratus* (trogloxene) (SIGHT)
Bats: Chiroptera undetermined (trogloxene) (SIGHT)
Raccoons: *Procyon lotor* (trogloxene) (SIGHT)

Government Canyon Bat Cave

Collections were made in the cave on 11 August 1965 by John Fish and James Reddell; 24 May 1993 and on 24 May 1998 by James Reddell and Marcelino Reyes. The following is a fauna list:

Snails: Gastropoda undetermined
Terrestrial isopods: *Brackenridgia* sp. (troglobite)
Scorpions: *Pseudouroctonus reddelli* (troglophile)
Spiders: *Cicurina* (*Cicurella*) *vespera* (troglobite)
Cicurina (*Cicurusta*) *varians* (troglophile)
Neoleptoneta microps (troglobite)
Agyneta llanoensis (troglophile)
Eidmannella pallica (troglophile)
Eidmannella rostrata (troglobite)
Achaearanea porteri (troglophile)
Mites: Trombidiidae genus and species
Soft ticks: Argasidae genus and species (parasite)
Millipedes: *Cambala speobia* (troglobite)
Speodesmus sp. (troglobite)
Springtails: *Pseudosinella violenta* (troglophile)
Insects: Insecta larvae undetermined
Subterranean silverfish: Probably *Texoreddellia texensis* (troglobite)
Cave crickets: *Ceuthophilus* (*Ceuthophilus*) *secretus* (trogloxene)
Ceuthophilus (*Geotettix*) *cunicularis* (troglophile)
Ceuthophilus sp. B (trogloxene) (SIGHT)
Ground beetles: *Rhadine exilis* (troglobite)
Rhadine howdeni (troglophile)
Rhadine infernalis infernalis (troglobite)
Comb-clawed bark beetles: Alleculidae genus and species (troglophile)
Rove beetles: Rove beetles: *Belonuchus* sp. (troglophile)
Flies: Diptera undetermined
Mosquitoes: Culicidae genus and species (trogloxene)
Fleas: Siphonaptera undetermined (parasite)
Cliff chirping frog: *Syrrhophus marnocki* (trogloxene) (SIGHT)
Snakes: *Elaphe obsoleta lindheimeri* (accidental) (SIGHT)
Western diamondback rattlesnake: *Crotalus atrox* (SIGHT)
Blacktail rattlesnake: *Crotalus molossus* (trogloxene) (SIGHT)
Mexican brown bat: *Myotis velifer incautus* (trogloxene) (SIGHT)
Eastern pipistrelles: *Pipistrellus subflavus* (SIGHT)
Porcupines: *Erethizon dorsatum* (SIGHT)
Raccoon: *Procyon lotor* (trogloxene) (SIGHT)

Lost Pothole

Andy G. Grubbs, Geoff Hoese, and Chris Vreeland collected in the cave on 4 February 1995. The following is a fauna list:

Snails: Gastropoda undetermined
Terrestrial isopods: *Brackenridgia* sp. (troglobite)
Scorpions: *Pseudouroctonus reddelli* (troglophile) (SIGHT)
Spiders: *Cicurina* (*Cicurella*) sp. (troglobite)
Gaucelmus augustinus (troglophile)
Harvestmen: *Hoplobunus* sp. (troglobite)
Texella sp. (troglobite)
Leiobunum townsendii (trogloxene)
Millipedes: *Speodesmus* sp. (troglobite)
Springtails: *Pseudosinella violenta* (troglophile)
Subterranean silverfish: Probably *Texoreddellia texensis* (troglobite)
Ground beetles: *Rhadine* sp. (SIGHT)
Cliff chirping frog: *Syrrhophus marnocki* (trogloxene) (SIGHT)
Western diamondback rattlesnake: *Crotalus atrox* (trogloxene) (SIGHT)

Sure Sink

Spiders: Araneae undetermined (SIGHT)
Mites: Acarina undetermined (SIGHT)
Millipedes: Possibly *Speodesmus* sp. (SIGHT)
Cave crickets: *Ceuthophilus* sp. (SIGHT)
Earwigs: Dermaptera undetermined (SIGHT)
Ground beetles: ?*Rhadine* sp. (SIGHT)
Rio Grande leopard frog: *Rana berlandieri* (SIGHT)
Blacktail rattlesnake: *Crotalus molossus* (trogloxene) (SIGHT)

10K Cave

Snails: Gastropoda undetermined (SIGHT)
Earthworms: Haplotaxida undetermined (SIGHT)
Scorpions: Probably *Pseudouroctonus reddelli* (SIGHT)
Spiders: Araneae undetermined (SIGHT)
Cicurina sp. (SIGHT)
Harvestmen: *Leiobunum townsendii* (SIGHT)
Millipedes: Probably *Speodesmus* sp. (SIGHT)
Springtails: Collembola undetermined (SIGHT)
Subterranean silverfish: Probably *Texoreddellia texensis* (SIGHT)
Cave crickets: *Ceuthophilus* sp. (SIGHT)
Ground beetles: *Rhadine* possibly *howdeni* (SIGHT)
Rhadine infernalis (SIGHT)
Cliff chirping frog: *Syrrhophus marnocki* (SIGHT)
Gulf Coast toad: *Bufo valliceps* (SIGHT)

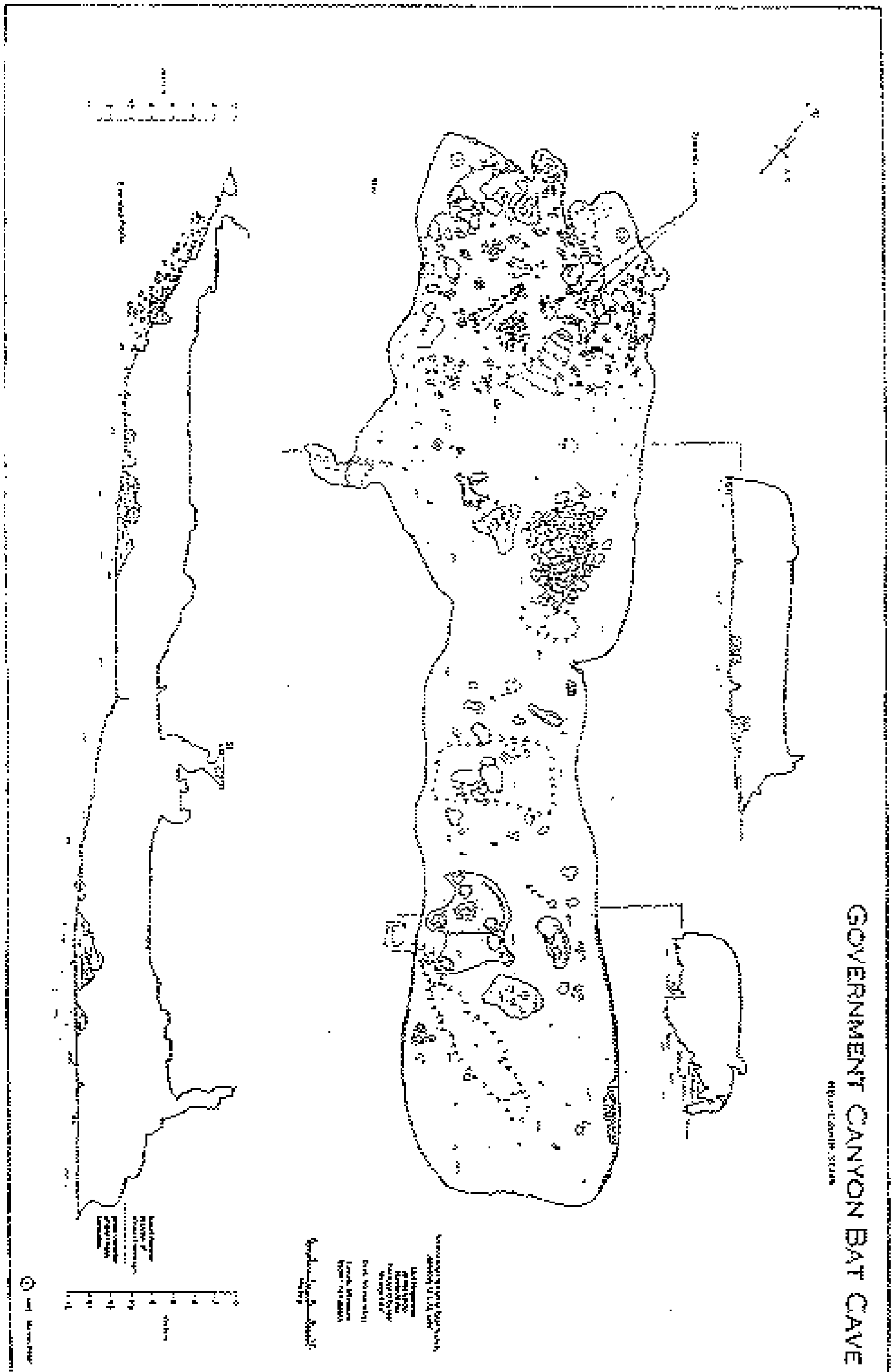
Surprise Sink

Collections were made in the cave on 5 February 1995 by Andy G. Grubbs; on 7 October 1995 by Alvis Hill and George Veni; on 21 April 1996 by George Veni, Karen Veni, and Jim Kennedy; 24 May 1998 by James Reddell and Marcelino Reyes; and on 29 May 2002 by Jean Krejca, Tannika Engelhard, and M. Holmback. The following is a fauna list:

Snails: Gastropoda undetermined
Terrestrial isopods: *Brackenridgia* sp, (troglobite)
Scorpions: *Pseudouroctonus reddelli* (troglophile)
Spiders: *Trachelas volutus* (accidental)
Cicurina (*Cicurella*) sp, (troglobite)
Cicurina (*Cicurusta*) ?*varians* (troglophile)
Neoleptoneta sp,
Linyphiidae genus and species
Eidmannella rostrata (troglophile)
Achaearanea sp, probably *porteri* (troglophile)
Pseudoscorpions: Pseudoscorpionida undetermined
Mites: Acarina undetermined
Trombidiidae genus and species (parasite of *Ceuthophilus cunicularis*)
Harvestmen: *Leiobunum townsendii* (trogloxene)
Hoplobunus sp. (troglobite)
Texella new species (troglobite)
Millipedes: *Cambala speobia* (troglobite)
Speodesmus sp, (troglobite)
Eurymerodesmus melacis (accidental)
Symphylans: Symphyla undetermined
Springtails: *Pseudosinella violenta* (troglophile)
Slender entotrophs: Campdeidae genus and species
Insects: Insecta larvae undetermined
Subterranean silverfish: Probably *Texoreddellia texensis* (troglobite
Cave crickets: *Ceuthophilus* (*Ceuthophilus*) new species B (trogloxene)
Ceuthophilus (*Geotettix*) *cunicularis* (troglophile)
Beetles: Coleoptera undetermined
Ground beetles: *Rhadine infernalis infernalis* (troglobite)
Comb-clawed beetles: Alleculidae genus and species (troglophile)
Rove beetles: *Belonuchus* sp. (troglophile)
Orus (*Leucorus*) *rubens* (troglophile)
Moths: Lepidoptera undetermined
Wasps: Hymenoptera undetermined
Fire ants: *Solenopsis* (*Solenopsis*) *invicta* (trogloxene)
White-throated slimy salamander: *Plethodon albagula* (trogloxene) (SIGHT)
Cliff chirping frog: *Syrrhophus marnocki* (trogloxene) (SIGHT)
Rio Grande leopard frog: *Rana berlandieri* (SIGHT)

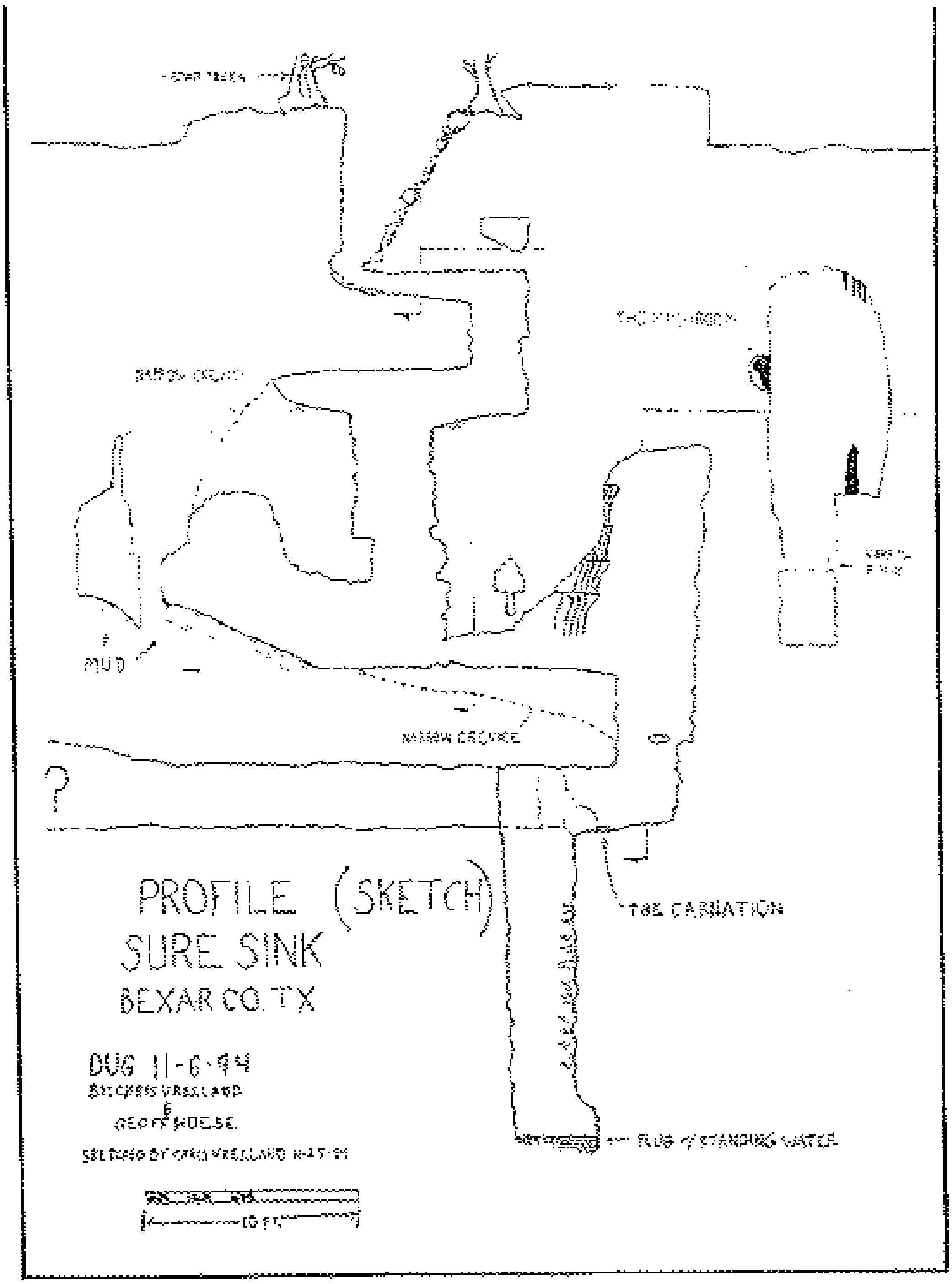
Appendix 2

Map of Government Canyon Bat Cave



Appendix 3

Map of Sure Sink



Appendix 4

Map of Surprise Sink Cave