

NRPP ENTRANCE BIOMONITORING FINAL REPORT
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CONCLUSIONS, PERSPECTIVES, AND RECOMMENDATIONS

Multiple A Priori Hypotheses

As Poulson argued in 1995: "Inventory and monitoring that is conceptually and hypothetically-driven forces us to critically determine the relevant measures needed to develop and distinguish among alternative hypotheses. As we proceed in a scientific study, we attempt to falsify original and develop new hypotheses. In addition to solving management problems efficiently, this approach has the added bonus that natural differences among caves and anthropogenic impacts comprise natural and inadvertent experiments that give greater insights into processes and mechanisms. If we understand processes and mechanisms then we are in a better position to do effective proactive management and reactive mitigation." In addition we add that development of multiple hypotheses avoids the trap of a favorite hypothesis,

For our entrance biomonitoring grant, to again quote Poulson 1995, "The main management issue is whether cave gates or doors compromise [or help] cave resources by modification of microclimate, restriction of animal movement, or restriction of the inwash of organic matter. Clearly sizes of entrances, diameter of passage, volume of cave beyond the entrance area, and location of passages and other entrances above or below entrance elevation all influence the distance into the cave that microclimate will be influenced by outside weather (Tuttle and Stevenson 1975) and the kinds of organisms that are likely to use the entrance (Poulson 1992, Poulson et al. 1993)." With respect to the possible influence of retrofitting cave entrances, with the aim of further restricting air flow and thus eliminating any drying effects of cold winter air, we developed the following a priori hypotheses.

H1. Both cave fauna and cave formations can be protected without complete air-sealing. There are several rationales for this hypothesis. First, cave entrances accessible to humans open and close on all time scales but accessibility to small organisms lasts longer. For our study entrances the evidence is that the cave cricket guano in Frozen Niagara and Great Onyx (enlarged for human access about 50-80 years ago) is about equivalent in apparent extent and thickness to that around indisputably natural entrances (White and Little Beauty) and very much greater than around entrances that were blasted through >10m of solid rock 60-80 years ago (New Discovery and Carmichael). Second, with the entrances scheduled for retrofits, the drying effect on formations of cold winter air can be mitigated while still keeping micro entrances open to small organisms, especially those toward the ceiling which stay warm and wet even with cold and dry microclimates at the floor. This is one reason we recommended keeping natural micro openings and installing bypass tubes around door seals if there are no micro entrances.

H2. Different species will have different requirements at cave entrances. Not all entrances have all possible fauna. Some of this may be stochastic effects on colonization, as with orb spiders and salamanders. In addition cave salamanders require a wet area just inside the entrance, pack rats prefer a dry area near the entrance for their nests, and pipistrelle bats seem to roost only where is deep cave temperature and 100% humidity near the entrance. In addition, to support

the maximum diversity of species that live on feces of pack rats and cave crickets requires a substrate that is not too wet and not too dry (Poulson 1992). And different species may exit the cave to forage at night through different sizes and positions of openings. For these reasons we recommended different positions and sizes of bypass tubes around entrances to be air-locked. We recommended ceiling level openings for cave crickets and floor level openings for pack rats and salamanders.

H3. The cave cricket lives at least five years and will vary in how well it does among years and among cave entrances. We picked the cave cricket as our main species for monitoring because it has roosting aggregations at virtually all entrances. The evidence for long life of cave crickets comes from comparisons with camel crickets that are demonstrably annual. Unlike camel crickets, cave crickets do not have distinct size classes and molt 305 times less frequently (Poulson et al. unpublished data: 16 out of 2019 stygius = 0.79% and 7 out of 181,957 cave crickets = .00385%). The evidence for temporal variation comes from our previous study of cave cricket guano communities in two of our monitoring caves, Little Beauty and White (Poulson et al. 1995). These data strongly suggested that to us that diversity and abundance of cricket guano species is positively affected by wet, cool summers and negatively affected by drought. These are conditions that should positively and negatively affect cave cricket foraging outside at night. By extension any near entrance topography or forest maturity that ameliorates surface microclimate should have a positive effect on cave crickets and this effect will differ among entrances as will complex microtopography inside entrances. Complex ceiling microtopography just inside entrances provides a refuge from the cold, dry winter air at the floor and mid passage levels. In addition we knew that cave crickets reproduce away from entrance roosting sites and so roosting sites that are near reproductive sites should have better survival of young which do not feed as they travel to the roosting site. For these reasons we studied four entrances in addition to the five that were retrofitted and used each cave as its own control over a three year period. This allowed us to distinguish any changes due to retrofitting from those due to natural year to year variation in weather.

RATIONALE FOR MONITORING METHODS (See Monitoring Handbook for details of procedure)

Our census entrances were constrained by a number of factors. Our contract required us to census the five entrances that were to be retrofitted. In addition we picked Little Beauty and White Cave because they matched Frozen Niagara and Great Onyx in having vast deposits of cricket guano in areas of dense cave formations (and so had been accessible to cave crickets for at least hundreds of years), because we had data on entrance communities dating back to the 70s, and because they matched Great Onyx in having entrances in secondary forest without microclimatic protection from a large sinkhole. We picked Crystal because its entrance is in a large sinkhole with protected microclimate and this matched Violet City. And, we picked New Discovery because it has a blasted entrance of about the same 70 year age as Carmichael's blasted entrance and older than Austin's 40 year old blasted entrance. In addition New Discovery had a reproductive area close to the entrance and this matched Great Onyx.

We had reasons for including and excluding particular species from our censuses, particularly related to ease of training personnel who will continue the monitoring after our grant expires. We included the cave cricket (Hadenoeus subterraneus) because it has a high importance value including high frequency of occurrence among entrances, dense roosting aggregations where it occurs, and very large size compared to other cave organisms. In addition it is easy to census because it roosts in the open and it is a surrogate for a number of species that depend on its feces. We did not regularly census the guano community because most species are tiny and cryptic and would be difficult to census reliably without compacting the guano. Poulson censused the three good guano communities (White, Little Beauty, and Frozen Niagara - Moonlight Dome) late May or early June to provide continuity with earlier studies and to

provide consistency in expertise needed to identify and census the many species. We did not search for the cave species that depend directly on sparse scattering of cave cricket feces (e.g. millipedes and bristletails and springtails) or predators that depend indirectly on the feces (e.g. cave spiders, daddy-long-legs, sand beetles and pseudoscorpions) because they are cryptic and/or sparse in the census areas. And we did not census the community that occurs in pack rat fecal latrines because reliable census is not possible without disturbing the latrines and we could not find the latrines for most of the pack rats. We did census the largest species that occur on the walls and ceiling along with the cave crickets and so could be censused with no extra effort and without disturbing the animals. These included the orb spider (Meta americana), the sacweb spider (Nesticus carteri), camel crickets (Ceuthophilus gracilipes and Ceuthophilus stygius), the heliomyzid flies (the "large" Amoebalaria defessa or A. sackeni and the "small" Heleomyza brachypterna or Aecotheca specus), the pipistrelle bat (Pipistrellus subflavus), and the cave salamander (Eurycea lucifugus).

We originally intended to do censuses for three years in mid December and early June of each year but subsequently decided that a year and a half of data taken every 2-3 months would be appropriate to capture some shorter term dynamics and get a more reliable census of adults and the smallest immatures. For example, we knew that the time of year of maximum cave cricket egg-laying varies from December to April in different years. Thus the timing of exodus of adults from entrance roosts to reproductive areas and the appearance of small immatures from reproductive area could also vary among years.

We censused four size classes of cave cricket. Hind femur lengths in mm for the size classes are "ones" 5-9, "twos" 10-14, "threes" 15-19, and "fours" = adults 20-24. These are the largest number of size classes that we could teach our assistants to reliably distinguish without touching the animals. Size distributions are an index of whether a population is growing, just sustaining itself, or declining. If $1s > 2s > 3s > 4s$ then a population is growing and is called a source because crickets may emigrate due to density dependent competition. But if $1s < 2s < 3s < 4s$ then a population is declining and is called a sink because it depends on immigration if it is not to go extinct.

We used 10m transects for censuses and continued into each cave until numbers of crickets in a transect was less than about five percent of the total number. Even in winter this meant that we usually had 8-16 transects (in Little Beauty 4 transects included the whole cave). A 10m transect length was short enough to pick up clear gradients from entrance inward and changes from summer to winter. Since cave passage sizes and shapes varied among caves, we also measured rough areas of the transects so we could express the data as relative densities.

We coordinated our studies with NPS studies of cave entrance microclimate. In addition to the microclimate "CAM" stations, where relative humidity and temperature were data-logged every 15 minutes, we recommended use of less precise "hobo" loggers that measured hourly temperature at 2-4 spots where we expected gradients to be steep. NPS-S&RM tried to place the CAM stations where we knew that crickets were dense and/or where there was a seasonal change because we wanted to be able to detect positive mitigation by the retrofitting of doors at entrances (the stations were 30-60m from the entrance). The main mitigation we hoped for was elimination of drying which is bad both for continued growth of cave formations with large sparkling crystal faces and is bad for survival of animals. Drying may not be measured using temperature and relative humidity because it is due to the interaction of absolute humidity and wind speed. There are no instruments made to measure evaporation so Poulson and Meiman designed a large scale evaporimeter. Using it we got an index of either evaporation or condensation per 100 square centimeters of cloth wick on a monthly basis by volumetrically measuring water in a reservoir.

ADAPTIVE MANAGEMENT

Without changing our basic transect census methodology we did consult with NPS Managers in order to streamline our methodology and improve their methodology of retrofitting different entrances. By and large our suggestions were followed. We submitted addendums to change our methods and argue for changes by NPS on 2/25/95 and on 2/29/96 (revision in response to S & RM queries on 4/17/96). On October 25, 1996 we provided a precis of retrofitting problems in Austin and Great Onyx and suggested mitigations. As of June 1999 these mitigations had not been done and the final data show that the lack of mitigation has had increasing deleterious effects, in the Great Onyx blockhouse and especially in Austin where we know of no other entrance closer than the Unknown Entrance.

Modifications of Our Procedures

Early on we decided to abandon the use of simulated cricket guano and rat fecal baits to assess the status of those two fecal community types. The time dynamics were too short, on the order of weeks, to allow adequate monitoring with the constraints of twice or thrice yearly trips to Kentucky. In addition the ground rat feces did not attract the same species as the cricket guano it was meant to simulate and in winter the cave crickets ate the rat fecal baits. Instead, once yearly, at the zenith of guano deposition in late May or early June, Poulson monitored the cave cricket guano communities in White and Little Beauty as a followup of the 1970-1991 data (Poulson et al. 1995) and in Moonlight Dome as a follow up of fragmentary data taken by Barr and Kuehne (1971).

Changes We Suggested for Retrofitting

We had reasonable success at getting NPS to modify retrofitting designs to make them more creature friendly. Lavoie tested pvc tubing and found that the minimum diameter and maximum length that all adult cave crickets would use to escape from a closed window screen container was 1.5 inches ID (Report to NPS 22 May 1995). In retrospect it is unfortunate that she did not try pipes longer than 12 inches because the Austin retrofit has a tube close to 36 inches long and is apparently not being used by cave crickets. And, it would have been better to place the cricket bypass tubes at the ceiling or along the walls, where crickets travel if they have a choice, instead of part way in between the door and the wall and ceiling. Except for Great Onyx and Austin, NPS followed our recommendations on size and on placement of larger pvc bypasses, around the human-sized air lock retrofits, at the floor for rats and salamanders. Part of the problem was getting effective communication between NPS managers and construction crews. To obtain a finer resolution of changes after retrofitting of all entrances was complete in July 1996, we censused every 2-3 months for a year and a half from July 1996 to December 1997. To check whether there was a progressive deterioration of animal populations at Austin and Great Onyx, we had John Fry, Rick Olson, and Virginia McDaniels do partial censuses on 15 June 1999.

As a result of the 1999 censuses we reiterate earlier suggestions. We suggest placement of 2 inch ID tubes at the ceiling by the inner Great Onyx door and floor level 4 inch ID tubes by both inner and outer doors if the weather strip sweeps on the doors are improved to make animal passage impossible. We would also like to see the former ceiling opening along the wall of the blockhouse opened up again though the presence of a mouse nest suggests that it may already be open. At Austin we suggest that the rock ramp at the inner edge of the large culvert pipe be made permanent using concrete and larger rocks. We also suggest releasing as many large cave crickets as possible from outside into the exit bypass tube so that they must move into the cave and perhaps leave a scent trail that will encourage other crickets to use the tube and conduit. Another possibility is to put a bait trail along the conduit and exit tube so the crickets will start to use it.

RESULTS AND CONCLUSIONS

This section is presented in three parts. First we analyze the overall effects of retrofitting compared to any trends among years in the control entrances. Second we consider trends among years that might be due to weather. And third we consider each species and how the natural experiments (control caves) and manipulative experiments (retrofitted caves) give us insights into each species requirements.

Effects of Retrofitting

Except for pipistrelle bats in several entrances, effects on salamanders at Great Onyx, and effects on many species in Austin, there have been no or minor unwanted consequences of entrance retrofitting. In fact numbers of cave crickets, camel crickets, heliomyzid flies, and orb spiders increased as much in manipulated as in control entrances, probably as direct and indirect results of shorter cold snaps in winter, possibly longer growing season, and possibly due to fewer dry periods in summer (see below).

Bats. Pipistrelles died in each entrance where they occurred before retrofitting. Apparently pipistrelles are creatures of habit and would not try to find the new exit routes when the traditional ones became blocked. Even though we rescued some seen flying around the entrance of Violet City, the events at Austin were clearest because it had the highest population of pipistrelles. In October of 1996 seven bats had died trying to get out around the door frame and we saw very few roosting in our census transects. When we censused the usual number in December of 1996 and February and May of 1997 we thought, erroneously, that new bats had learned to enter the cave via the bypass tube. In retrospect these were bats that had come from deeper in the cave and would not crawl through the bypass tube and we should have realized that there were problems when Poulson picked one off the ceiling and it did not arouse from torpor. In early June John Fry found 19 dead bats around the outer door frame. He rescued 30 more that were hanging in Pohl Avenue but only 2-3 were strong enough to arouse from torpor and fly away. As of June 15 1999 seven new pipistrelles have found the exit/entry bypass at Austin and recolonized or have arrived at that area from the Unknown Entrance much farther down Pohl Avenue. We suggest that these are young of the year males (only males use caves in summer) that never had a home cave before. Since pipistrelles live up to 20 years, it may be a while before their numbers build to pre retrofit levels.

Great Onyx Blockhouse. The retrofit of the blockhouse entrance of Great Onyx has compromised the cave salamanders and inhibited movement into the blockhouse from the cave by cave crickets. The salamanders can still move under the doors and before retrofit the summer filling of puddles by water entering under the front wall and door seemed to their liking. However now these puddles now dry out faster because there is much less cool, moist air exiting the cave in summer with the new inner door. This may explain why the numbers of cave salamanders seen in May and June has steadily declined since retrofit (F. Scott, pers. comm. 1995 - 1999, 63, 55, 25, 27, 7 in May but 38, 15, 20, 14, 0 in June when puddles from spring rains have dried). Cave crickets and camel crickets still use the blockhouse in summer but are apparently colonizing from outside and not using the narrow pvc tubes around the inner door. We infer this since the density of crickets drops dramatically from just outside to just inside the inner door. The problem may be that the bypass tubes in the door frame are slightly less than the minimum 1.5 inches ID that Lavoie found that adult cave crickets would move through when the only exit from a plastic screening bag was the pvc pipe. Another possibility is that the crickets do not readily use tubes at midwall elevations since they usually move along the ceiling when given a choice. Fortunately the blockhouse crickets are a small proportion of the censused population and nearby there is an alternative tiny entrance nearby (the so-called natural entrance) that is used by crickets and pack rats and perhaps the five pipistrelle bats seen on 15 June 1999. It may be that the old ceiling crack exit from the

blockhouse is open again since a mouse has a nest in the blockhouse and a large aggregation of camel crickets is on the ceiling in the area of the former exit crack. The blockhouse could become unuseable if the weather strip sweeps on the outer and inner door are made fully functional and our recommended exit tubes from the blockhouse are not installed.

Austin Entrance. The continued slow decline in numbers of cave crickets in Austin and the sudden decline in their numbers just inside the entrance just after retrofitting convinced us that the problem was that the bypass tube and entrance combination was not sufficiently creature friendly. There were problems of stabilizing the entrance which apparently required about a 10m long 1m ID culvert pipe with expanding foam around it to stabilize loose rock and a steel plate with a solid door tightly fitted to the outside rock face to provide an air seal. At the inside end the culvert terminates away from walls and about 40cm off the ground. There is about a 1m long 20cm ID plastic corrugated pipe bypass tube for animals that starts inside in the side of the culvert and ends off the ground in the steel plate outside. To make the slippery surface of the culvert more traversable by animals, NPS glued sand to roughen the inside floor of the culvert and plastered a tacky "goop" from the floor of the culvert to the bypass tube mouth. In October 1996 we removed most of the sand in the culvert because we thought that salamanders would not walk on the dry sand. We added mud and sand to mitigate the tackiness of the "goop" on the miniramp from the floor of the culvert to the bypass tube. We also cut off the projecting bypass tube exit outside so it was flush with the wall and constructed a rock and dirt ramp to the opening. And in December we built a rock and dirt ramp for crickets and salamanders from the inside lip of the culvert to the cave floor (this ramp needs to be permanent because it deteriorates which each passage of a surveying party). In October and December 1997 the number of cave crickets was at an all time low for that season, though salamander numbers were higher than in previous Decembers due possibly to the warmer and damper microclimate produced by the new door system. This, along with the high percentage of crickets with empty crops convinced us that the crickets were not exiting to forage and would gradually decline as fungal food on the old rotting timbers and opportunitites to eat dead crickets declined. Thus we were surprised when the overall numbers of cave crickets rebounded to pre retrofit levels in May of 1997, though not to all time highs as in other retrofitted entrances, and the numbers in the first two transects reached an all time high. However since that time the numbers have dropped to an all time low in June 1999. Here we consider multiple hypotheses to explain these results. Some of these are not mutually exclusive.

H1. The cave crickets are in fact using the bypass tube: We were misled by thinking that the retrofit arrangement was not at all creature friendly. The retrofit was completed in early July and cricket numbers were way down in late July but the next July also showed a decline in numbers at the entrance from a high peak in May to July. Thus the crickets were exiting via the bypass tube and we missed it by not being there at night and because crickets could not roost on the slippery ceiling of the culvert tube. It is possible that they are coming from other caves by above ground travel because at White, which is surrounded by high quality mesic forest, seven 4s and one 3 were trapped, along with 59 camel crickets, far from the cave entrance while hundreds are trapped using the same baits within 40 m of the entrance when they forage outside at night. The critical experiment to differentiate overground dispersal at Austin from the second hypothesis will be to use colored bait outside and see if crickets inside have colored crops. If they are using the tube then the continued slow decline in numbers must have another explanation.

H2. The crickets are not using the bypass tube: they are either using another nearby entrance or represent crickets that have come underground from a more suitable distant habitat. This would explain why they are never full but neither scenario explains why they would aggregate where they cannot or will not exit the cave.

That a few cave crickets are coming from deeper in the cave is consistent with observations of marking adults in other caves where there is rapid loss of marked adults (4s) but no obvious change in population density of adults in the marking area. In most caves regular exchange with a deep cave population could explain the rapid dropoff of marked adults but not in White Cave which has no underground connections to the Mammoth Cave system. The inescapable conclusion is that marked adults are more vulnerable to predation since, if they were only spooked to move into crannies then we would expect them to reappear after a few days. In addition there could be many more unmarked crickets in inaccessible crannies than we believed could exist and it is those individuals that are replacing the lost marked animals.

In Austin the rarity of full crickets, and even of intermediate fullness, may be explained if they eat much smaller amounts inside the cave than they always do if they can forage outside. They could be subsisting on carcasses of other crickets that slowly die and on bits of fungi and bacteria that still exist on the old rotting timbers. Or they are starving and moving back into the cave in an attempt to find another entrance.

We have not done the baiting experiments to falsify H1 but our data post retrofit are all consistent with H2. Extrapolating the May 1997 data to lower June numbers using May, June, and July numbers from other years, we see that cave cricket numbers have progressively declined from 1790 ('95) to 1617 ('96) and then precipitously after retrofitting to 977 ('97) and continuing down to 310 ('99). At the same time other entrance populations have slightly or greatly increased. Furthermore the visual fullness data suggest that the crickets were not exiting after retrofitting. Before retrofit the percents were 33-51% empty, 25-30% intermediate, and 24-30% full. On 22 July 1996 (two weeks after completion of retrofit) the percents were 71% empty, 21% intermediate, and 8% full and one week later they were 89% empty, 8% intermediate, and 3% full. This means that the crickets were probably not exiting and were surviving on what little fungus remained on the rotting timbers, on cave crickets that die, and on feces of cave salamanders that eat starving cave crickets. Thus the cave salamander population, that is at the same May and June numbers of 17-30 as in previous years, will eventually die out as the cave cricket population drops to near zero in a year or two. The small crickets are probably better at subsisting on bits of salamander feces and cricket feces while the larger crickets probably get most of the dead crickets. This could explain why there has not been a differential loss of one or another size class.

Improved microclimate due to retrofits? The microclimate possibly improved inside all retrofitted entrances but the improvements were subtle since we could detect effects on organisms or cave formations only in Great Onyx and Frozen Niagara. We can only compare the effects of retrofitting at each entrance separately since the CAM and HOBO stations were not at the same distances from the entrance and elevations between floor and ceiling. In addition each entrance is likely to have its own microclimatic dynamics.

In Violet City and Carmichael the CAM and evaporimeter data showed that there was never much of a problem with cold, dry winter air and so the tighter door only decreased winter temperatures and temperature fluctuation a little. In Violet City the near entrance area is quite wet and the passage quickly opens into a huge room. In addition the adjoining cave passages are huge and much lower than the entrance but there was never the severe wind and cold seen at the Historic entrance. The CAM station was at 15m inside and winter relative humidities remained high and temperatures dropped no lower than 9 Centigrade even during cold snaps before retrofitting. In the case of Carmichael the original door was reasonably tight and so there were never obvious windy and dry winter conditions despite the fact that the blasted entrance is long, narrow, and steeply descending. The CAM station was in a breakdown at the bottom of the stairs, about 55m from the entrance, and the only change after retrofitting was a great dampening of the low amplitude daily fluctuations in temperature in spring and fall when outside and inside temperatures were similar.

In Great Onyx the CAM station was at about 21m from the blockhouse entrance and influenced both by the blockhouse entrance and the other entrance 37m away. There was no discernible change in the CAM station microclimate and the HOBO network showed that there was still a strong temperature gradient from the unmodified entrance inward. There continued to be an increase of humidity, with no change in temperature, within a day of rain at the CAM station, especially in winter. However use of a temperature - humidity probe showed that the blockhouse is now warmer and drier in summer. The reason is that the inner door effectively stops outward flow of cool, moist air in summer. With summer rains, water still accumulates on the blockhouse floor but it now dries out faster. This may be why the salamander population in the blockhouse is down and the numbers are up slightly in the unmodified entrance area. Food supply for the salamanders is not lower since the cave cricket numbers for the blockhouse show no discernible trend from pre to post retrofit. An alternative hypothesis is that the old exit crack at the top of the blockhouse was filled and the salamanders are not as effective at catching crickets as they exit under the door along a wider area than in the former ceiling crack.

In Frozen Niagara after retrofit there was virtually a complete cessation of inward winter air flow as detected by the CAM station but only a slight change in the temperature gradient as detected by the HOBO network. The effects of increased moisture and/or decreased air flow were most obvious in the Onyx Colonnade which had previously been dry and devoid of life due to a slight heating and drying by the lights and/or cold, dry winter airflow. Now both cave crickets and spiders occur and the formations appear wet with algae beginning to grow.

Population Trends of Censused Animals from 1995 to 1997 Analyzed Cave by Cave

Interactions of weather, retrofitting, and species longevity. Population responses to the short-term changes in weather are expected to be seen only in short-lived species. Thus camel crickets live only ≥ 1 year and their numbers in winter, when many move from outside to caves to hibernate, reflect the weather during their growing season from April through October. We predict a similar situation for heliomyzid flies based on a guess of short life span and their need to feed outside caves. For cave crickets we should only expect to see changes in population size and proportions of small to large individuals. This is because they forage all year long when temperatures are above 10 C at night and they roost in caves where they are protected from the most severe cold of winter and drought of summer. In addition they need only feed every 10 - 12 days to maintain their weight. The orb spiders are only in caves and can live a long time without food so their reproductive success only indirectly reflect the outside weather via their cave cricket prey. The cave salamanders may mainly eat cave crickets but also eat a large variety of other invertebrates and may forage outside near the entrance. They live many years, perhaps 10 - 20, and so will only be affected by weather if it dries out the cave entrances where they live. Bats are known to live 15 - 20 years and the pipistrelles that we census use the caves to roost in summer and hibernate in winter. They do not reproduce in caves and can feed on the adults of aquatic insects during droughts and so we should expect changes in their numbers only if we interrupt their movements to and from the cave or disturb them during hibernation.

Effects of prolonged cold in winter and drought in summer. Weather, both in winter and summer, explains much more of the temporal change in invertebrate populations within most entrances than differences among caves due either to retrofitting or entrance configurations. For all invertebrate species there was an overall trend of increasing populations from 1995 to 1997. Except for Little Beauty and Austin, when compared at the same times of year, most of the other study caves showed either a trend of increased populations of all invertebrate species censused

and/or all time peaks in May of 1997. We infer that the growing season weather had independent effects on camel crickets and heliomyzid flies, neither of which depend on cave crickets, but that orb spider populations increased along with their cave cricket prey which in turn are affected by weather all year long since they do not hibernate.

Cave cricket population size. As detailed in the 1997 Science Conference Proceedings (Poulson, Lavoie, and Helf and Poulson and Helf) for cave crickets, over the three years there was less fluctuation in numbers of 1s and 2s with most of the spring increases due to higher and higher numbers of 3s and 4s. During the three years, growing seasons were never warmer than average and were all wetter than average. Winter average temperatures and temperature extremes did not show a trend of decreasing rigor but there was a 1994-95 to 1996-97 decrease in frequency and duration of periods that remained below 0 Centigrade and an increase in frequency of "respites" where night time temperatures remained above 10 Centigrade and when there was rain associated with the short warm spells. We infer that this allowed the 3s and 4s to forage more frequently and this increased their survivorship. In addition it meant that adults (4s) and subadults (3s) did not have to metabolize their fat supplies or maturing gonads to survive and that this translated to higher fecundity and recruitment of 1s. Those 1s and 2s in entrance roosts, with their lower reproductive values and less fat and no possibility of resorbing gonads as hedges against starvation, probably foraged under suboptimal conditions in all years so were less favored overall by the three year decrease in frequency and duration of winter cold snaps.

Heliomyzid flies. There was no pattern of change in populations of either small or large heliomyzid flies from 1995 to 1997.

Orb spiders (Meta). Orb spiders mainly eat cave crickets and so it is not surprising that their overall numbers from 1995 to 1997 increased in parallel to those for cave crickets and that numbers of adults did not change seasonally. In White Cave, where over 50% of the total occurred, the summer season numbers (when most of the population was adults) were 28 in '95 < 63 in '96 < 96 in '97.

Camel crickets (Ceuthophilus). For camel crickets both species occurred in all study caves and there was a huge difference between species in seasonal occurrence and trends over time. For gracilipes during the hibernation season (the only time we can census them because they are essentially absent from caves during the growing season) their numbers were remarkably stable from 94 to 97 varying from a low of 1995 to a high of 2214. Thus the differences in duration of the growing season did not affect their numbers over time. This is surprising because the numbers of stygius did increase over the three years and, since they also hibernate in caves, this could only have been because of less droughty summers and increased duration of the growing season. Their December numbers for the four years were 720, 1291, 1929, and 1592 and their May numbers, that reflect the previous growing season, were 264 < 598 << 2251!

Sink Caves and Source Caves for Cave Crickets

Recall that source caves are those where populations are growing if there is no emigration and sink caves are those where persistence depends on immigration because otherwise populations are declining.

Sink caves. There are definite sink caves for cave crickets. Little Beauty, White, and Austin are sinks for cave crickets because $4s \gg 3s > 2s = 1s$. In Austin there is a lot of substrate for egg-laying but it is of marginal quality because of layering of mud and sand and the spring peaks for 4s suggests that they are returning from a reproductive area farther back in the cave or that

crickets are immigrating by below-ground routes. But in Little Beauty and White there is very little even marginal substrate for egg-laying and no current connection to the Mammoth Cave System. There is a little local reproduction because we regularly census a few new hatched "whiteys" and there is no winter decline in fours because there is no place for them to go to reproduce. Thus cave crickets must be maintained largely by above-ground immigration of 4s and a few 3s. There is little fluctuation in numbers of 1s and 2s and yearly peaks of 4s tend to be in the December. In Little Beauty there was no trend for increase in total numbers or for any size class from 1994 through 1997. We could argue that this is as expected for a sink cave but White had a steady increase in total numbers with some of this due to 3s but mostly due to increase in 4s. A possible explanation is that the forest outside White is more mesic and there are several other small caves that could be refuges for cave crickets moving overland.

Great Onyx and Frozen Niagara. These two caves appear to be sinks for cave crickets based on the ratios of $4s \geq 3s > 2s \geq 1s$ but these ratios are not as weighted against small size classes as in the clear sink caves of Austin, Little Beauty, and White. In addition, absolute abundance of smaller sizes is higher and this indicates better recruitment. Indeed Frozen Niagara and, especially, Great Onyx have some small areas with substrate suitable for egg-laying near the entrance roost areas. In Great Onyx there was a clear and steady increase in numbers from 1994 through 1997 both with respect to spring maxima and winter minima. Almost all of this increase was due to 3s and 4s and so the likely explanation is immigration, either above- or below-ground, and higher survival of large immigrants with better winter weather for foraging. In Frozen Niagara there was only a slight increase in winter minima but, as in Great Onyx, the all time spring peak occurred in May 1997.

Clear source caves for cave crickets. On the basis of size ratios, averaging $4s \geq 3s > 2s \geq 1s$, four caves are sources (New Discovery > Crystal > Carmichael = Violet City). These sources are also characterized by a seasonal shift from $1s > 2s = 3s > 4s$ in winter to $4s \geq 3s \geq 2s = 1s$ in spring and early summer. This shift is due to movement of adults (4s) out of roosting areas in winter and back from reproductive areas in spring; with a lag of a month or two 1s also move from reproductive areas to entrance roosting areas. The rapidity of these shifts is greatest in New Discovery where the beginning of the reproductive area is contiguous with the roosting area. In Crystal and Carmichael we have seen some small areas with substrate suitable for egg-laying within 500m of the end of the roosting area but we have been able to find no suitable reproductive areas within 1000m or more of the Violet City entrance roost.

Even though all four source entrances had all time peak numbers in May 1997, the 1995 to 1997 increase in winter minima (1.3 - 2.1 times) and spring maximas (1.4 - 2.4 times) overlap the increases for one of our sink entrances, White, and one of our intermediate entrances, Great Onyx. Why? We offer four hypotheses, each of leads to the prediction that there should be increased survivorship, especially for 1s and 2s.

H1. All four sources and two other caves have outside conditions which should ameliorate microclimatic rigor and favor the kinds of foods crickets prefer by being in sinkholes (Violet City > Crystal > Carmichael), adjacent to a deep valley (New Discovery), and/or in mesic forests (Violet City > New Discovery > Carmichael $\geq$ White).

H2. A reproductive area with good substrate for egg-laying near entrance roosting areas is especially helpful in increasing survivorship of 1s (New Discovery $\gg$ Great Onyx).

H3. Cool, moist air flowing out of entrances in summer allows prolonged foraging at night in hot weather, especially for 1s and 2s (Carmichael > Crystal).

H4. Complex ceiling and wall microtopography just inside an entrance keeps a warm and damp microclimate refuge in winter and so allows 1s and 2s to roost nearer the entrance and respond

more quickly to thaws (Great Onyx > Violet City). [In White there is no winter influx of cold, dry air so small crickets do not need complex microtopography to stay near the entrance.]

Other Species Patterns Analyzed by Cave

Other species patterns of distribution and abundance bore no obvious relation to whether the cave was a sink or source cave for cave crickets.

Definite sink caves for cave crickets. For White, there were virtually no heliomyzid flies of either species, gracilipes camel crickets declined from 446 in 1December 95 to 238 in December 97, and stygius camel crickets remained the same in December (118 in 95 and 120 in 97) but increased dramatically in May (7 in 95 and 296 in 97). As with their cave cricket prey, orb spiders increased from 95 to 97 both in December (58 to 78) and in May (28 to 60).

For Austin, there has been a slow decline in all sizes of cave crickets, both in winter and spring, from 1994 through 1997 but the heliomyzid flies remained the same or increased. Austin is the best of all caves for heliomyzid flies and numbers of both species increased from 1995 to 1997. Small heliomyzids increased in December from 15 to 28 and in May from 27 to 187 while large heliomyzids decreased in December from 67 to 26 but increased in May from 496 to 1045. The numbers of camel crickets did not show a clear pattern of change from 1995 to 1997. C. gracilipes declined in December from 65 to 45 and increased in May from 8 to 21 while C. stygius increased slightly in December from 68 to 78 and increased dramatically in May from 6 to 65.

Possible sink caves for cave crickets. In parallel to the slight increase in number of cave cricket prey, the number of orb spiders in Frozen Niagara in December increased slightly from 1995 to 1997 (27 to 27 in December and 23 to 34 in May). There are no orb spiders in Great Onyx.

Frozen Niagara is apparently not a good cave for heliomyzid flies with only small numbers of both species. There were no small heliomyzids in December and in May their number decreased from 47 in 95 to 13 in 97. The number of large heliomyzids in December increased from 2 to 4 and in May their number decreased from 8 to 6.

Compared to Frozen Niagara, Great Onyx is a somewhat better cave for heliomyzid flies, probably because a number of our transects are away from wet formation areas avoided by the flies. For small heliomyzids December numbers increased from 17 in '95 to 41 in '97 but May numbers only increased from 40 in '95 to 46 in '97. For large heliomyzids the increases were greater. In December there were 43 in '95 and 72 in '97 and in May there were 228 in '95 and 314 in '97.

Great Onyx is also a better cave for camel crickets (Ceuthophilus) than Frozen Niagara, especially for winter hibernation. In Great Onyx gracilipes numbers in December increased from 243 in 95 to 896 in '96 and then declined to 347 in 97. There were no gracilipes in May of any year while for stygius numbers in May increased dramatically from 5 in '95 to 155 in '96 to 254 in '97. Numbers in December increased from 113 in '95 to 196 in '96 to 371 in '97 and in Frozen Niagara stygius numbers in May also increased dramatically from 1 in '95 to 283 in '96 to 430 in '97 but in December numbers increased only from 18 in '95 to 41 in '97. For gracilipes in Frozen Niagara there were none in May and only a few in December (19 in '95, 10 in '96, and 13 in '97). The tiny cracks and ceiling pockets preferred by gracilipes for hibernation are much less common in Frozen Niagara than in Great Onyx.

Definite source caves for cave crickets. Orb spiders did not occur in New Discovery but the cave is suitable for spiders because there were quite a few medium sized linyphiid? spiders in

the blockhouse in summer. In the other caves normalized numbers for 10 censuses were 210 in Crystal, 149 in Violet City, and 65 in Carmichael. The differences seem to relate to the quality of web sites and clearly not to abundance of cave crickets.

Heliomyzids were common in New Discovery but nowhere near as abundant as in Austin which is a definite sink cave for cave crickets. There were always about three times as many large as small species and they were rare in December. Total large / small individuals were as follows: 682 / 354 New Discovery, 698 / 194 Crystal, 371 / 273 Carmichael, and 10 / 8 Violet City. All of these caves have areas with stable microclimates on flat ceilings, as with Austin which has by far the most heliomyzids, so we do not know why the numbers in these cave cricket source caves vary so dramatically.

Camel crickets ranged from abundant abundant in New Discovery, to moderately abundant in Crystal, to uncommon in Carmichael, to virtually absent in Violet City. This was true for both species except that, as usual, gracilipes was absent during the growing season. The summed summer counts for stygius ranged from 1439 to 174 and its counts for winter ranged from 2459 to 48.

Species Accounts

Population Structure of Cave Crickets. Data gathered over three years has allowed us to differentiate among three hypotheses for the overall population structure of cave crickets among cave entrances. The general biology of cave crickets has been covered in a number of publications (see Literature Cited and Annotated Bibliography in our original research proposal).

H1. Metapopulation model. According to this model, populations of a species are on "islands" in an "uninhabitable sea" and populations go extinct periodically and then are recolonized after a time. Area of habitat in which a population occurs, and the edge effect due to perimeter to area ratio, also have a large effect on chances of local extinction. This hypothesis was attractive to biologists because low gene flow would allow adaptation to local environments and there would still be spreading of the risk of extinction among populations. It also seemed consistent with the island biogeographic theory and the observation that large areas have more species. However a metapopulation structure turns out to be rare for terrestrial species and cave crickets are no exception. Around Mammoth Cave National Park, virtually every cave entrance without strong winter drying has cave crickets and there is no evidence that they go extinct periodically. This is probably because there is frequent movement by large crickets below-ground in the 500 km long Mammoth Cave System and regular movement above ground at least in areas with mesic forests with rockcrops and small caves.

H2. Source-sink model. According to this model, some populations are self-sustaining (sources) while many rely on immigration because there is not sufficient reproduction (sinks). In contrast to the metapopulation model, movement among populations is frequent enough that low population size does not much increase the chance of local extinction. In fact, as in our Mammoth Cave Region study caves, neither population size nor population density is well correlated with degree of approach to source population structure with $1s \geq 2s \geq 3s \geq 4s$. Some source populations have fewer cave crickets than some sinks and one sink (White) has the highest population density of all. And, as we just reviewed in the previous section on population trends, the relative suitability of the areas near the entrance for reproduction and foraging seem to be the main predictors of where a population lies on a source to sink continuum.

H3. Landscape ecology model. According to this model, the likelihood of dispersal and of local population extinction depends on the relative habitability of the landscape between local populations. This is incompatible with a metapopulation model but not incompatible with a source-sink model. It is more realistic than a strict source-sink model because there is likely to be a continuum of habitat suitability for a species that greatly affects the frequency and number of dispersing individuals. In the context of cave crickets, entrance populations that are separated by successional mature forests on north facing slopes forest are more likely to exchange dispersing individuals than ones separated by successional immature forest on south facing slopes. And, entrance populations interconnected by damp habitats and other entrance populations in the 500km Mammoth Cave System are more likely to exchange individuals dispersing below ground than those isolated from the large cave system (Little Beauty > White > Great Onyx).

Orb spiders (Meta). The rank order for abundance by cave of orb spiders normalized to 10 census dates was White 650 >> Frozen Niagara 207 = Crystal 210 > Violet City 149 > Carmichael 65; there were no orb spiders in Austin, Great Onyx, Little Beauty, or New Discovery. Spider rank order of abundance is poorly correlated with that for cave cricket abundance even though orb spiders diet is overwhelmingly cave crickets, especially for biomass. We suggest that the absence of orb spiders in caves with many cave crickets is a matter of chance and past history. For example they occur in the New Entrance, a blasted entrance, and in Cathedral Cave, a small Green River bluff cave, in addition to our censused caves which include both natural and blasted entrances. And one adult appeared in a cave cricket reproductive area at the back of Edwards Avenue in Great Onyx in the late '70s and remained in the same ceiling pocket for at least five years before a male chanced to arrive; a population explosion of spiders ensued that took about five years to return to a stable low number of mainly adult spiders.

Where orb spiders do occur their numbers match those for their primary cave cricket prey only if there are suitable web sites. These are spots where wall and ceiling meet at an acute angle, or among cave formations, or in mini depressions in the floor or in mini ceiling domes; thus flat ceilings or walls are not good sites. In White Cave the orb spider numbers match those for crickets well along the eight 10m transects. But in Crystal the near entrance transects do not have good web sites and the numbers of spiders in the last transects, with an especially high number of small spiders, is higher than for crickets. Among web sites that are suitable for building webs, spiders move to different sites to find ones where they can catch a cave cricket.

The numbers of large adult orb spiders does not fluctuate seasonally but there is a general increase in numbers of small and medium sized spiders in the fall and winter months. This coincides with appearance of egg cases that are pinkish yellow, slightly smaller than a gold ball, and hang from the ceiling. In the about ten cases when we have been in the cave at and soon after hatching, it appears that the 30 - 50 spiderlings disperse quickly. The rarity of small or medium small spiders in subsequent months suggest high mortality, unlike the adults which can live for at least five years. Unlike the adults, there is a rarity of prey small enough for the smallest spiders and we hypothesize that those that survive 'practice' density dependent cannibalism.

Heliomyzid flies. These flies are an enigma on several counts. They occur in the cave mainly in summer but do not occur in the near entrance transects and do not move toward the entrance at night as do the cave crickets which will exit to forage. They rarely move in the light or even if lightly touched. They do not come to various organic baits and we have never seen larvae in the several rat latrines in our study caves. Their numbers decline to near zero in December in some caves but in other caves 30 - 100 remain.

Heliomyzid relative abundance among caves gives us no clue about their biology or microhabitat needs for roosting. Nor do they have a pattern of doing well where other species are abundant such as camel or cave crickets. If they were foraging outside, like the cave and camel crickets, we might expect their numbers to have increased from 1995 to 1997 as growing season duration increased and wet summers continued. Instead their numbers are approximately stable in May and June with 1351 in '95, 1287 in '96, and 2200 in '97.

For both species of heliomyzid flies only a small number of the total (539 = 22% for small species and 810 = 11% for large species) were found in the non growing season (D, J, F, M) with 87% of the total (1897 = 78% for small species and 6516 = 89% for large species) in the growing season (M, J, J, O). Three caves (Austin >>> Great Onyx >> Frozen Niagara = New Discovery) had 92% of the large species and 74% of the small species. Both large and small heliomyzids had similar distributions by transect with no relation to density of cave crickets (in fact their numbers increased greatly in Austin while cave cricket numbers declined after retrofit) or to camel crickets. Neither the small nor large species had their highest numbers in near entrance transects so it seems unlikely that they go out at night to forage. They scarcely ever fly from their ceiling roosting spot unless touched and are never in even loose aggregations. What they do is a mystery. Why did Austin have ~ 50% of all individuals censused and why were there virtually none in White or Violet City? We do not even have hypotheses to offer as to what they do and what controls their numbers.

Camel crickets (Ceuthophilus). Compared to cave crickets, camel crickets are less adapted to finding scarce food, using a 'scavenger on stilts' mode of foraging (Levy 1976), but are better able to tolerate the rigors of warm and dry temperatures outside caves (Studier and Lavoie). Camel cricket's body build is more robust with shorter legs, antennae, and labial palps. They have a thicker exoskeleton and shiny epicuticular waxes.

Based on size distributions and frequency of molting camel crickets live only a year or two, in contrast to the 5 - 10 years for cave crickets. One can follow a cohort of camel crickets (C. stygius) from initial very small individuals and huge surviving adults in fall, to medium small hibernating individuals in winter, to increasing sizes during the growing season. There is never any obvious cohort of cave crickets within or among years. In addition 1 - 3 percent of camel crickets are molting or have recently molted in summer whereas less than .001 percent of cave crickets have molted recently across all caves, seasons, and years.

We do not know much about C. gracilipes because it does not occur in caves in summer. Only 0.67% of the total 11658 C. gracilipes occurred in the caves in growing season (M, J, J, O) even though they are regularly attracted to baits outside in summer and just as often as for C. stygius. Since gracilipes only hibernates in caves, it is not surprising that its numbers are not well correlated with those for stygius which both hibernates and roosts in caves in summer (growing season totals for stygius were 5612 with 8124 in the non growing season of D, J, F, M).

In addition both species use different microsites for hibernation, though both avoid the coldest areas near entrances. C. gracilipes wedges itself tightly into tiny ceiling pockets or cracks whereas stygius tends to occur in loose aggregations on the open ceiling or in bedding plane openings partly because overwintering individuals are larger than those of gracilipes. In summer stygius virtually all occur right inside the entrance in dense aggregations. There may be some advantage to roosting in caves in summer because the numbers of stygius increased with more favorable weather whereas those of gracilipes did not.

RECOMMENDATIONS

We start with some general recommendations that should apply to all contract work. First we suggest that there should be more flexibility in the early stages. Any proposal should have a priori protocols but observant scientists will always find ways to improve methodology with the first detailed field work. Examples in our study were modifications in the size classes of cave crickets censused, the elimination of the fecal bait stations, a more detailed focus on the biology of the cave cricket, and addition of a new study cave (New Discovery) that gave us a greatly broadened perspective. Our second suggestion is that chance for modification of management and mitigation details should be built into contracts at regular intervals. In our case this would have given even better communication among the scientists, resource managers, and the maintenance crews doing the construction. We certainly had some successes with informal communication. Successes included addition of tube bypasses for biota instead of having complete airlocks and determining what sizes and lengths of tubes cave crickets would use before they were installed. More regular communication might have avoided the problems that now require further. And seminars by the scientists with the construction crews might have made them more sensitive to the reasons for installing bypass tubes of different sizes and locations for different organisms. In these contexts we suggest the following mitigations to the retrofitted entrances.

1. Austin. Roughen the insides of the slippery culvert and build permanent ramps from cave floor to the lip of the culvert and from the exit of the bypass tube to the ground outside.
2. Great Onyx. Enlarge the current tubes around the inner door, or add new ones of larger size at the ceiling level, and add a salamander size exit in the ceiling area of the blockhouse, where crickets will certainly also use it, or at floor level by the outer door. This should be done before the weather strip skirts on the doors are made completely functional.
3. Frozen Niagara. Require tour guides to leave the inner door closed while tours are inside and suggest that they have people enter and exit in small groups so that the inner door adds effectiveness to the air lock, which otherwise pumps air in and out. Have more regular algal removal now that the Onyx Colonnade is damp and may have renewed active speleothem growth.

As with monitoring, management should be hypothetically and conceptually driven. To do this most effectively requires the interpretations of the data by an expert. In our case we continued to falsify some and modify others of our multiple hypotheses. This was critical in our ability to separate effects due to natural variation, over time and among caves, from anthropogenic impacts related to entrance retrofitting. It was also important to have the point resource manager on the project help us in the field regularly to hear our continued discussions about how the data related to the mitigation project.

And finally, take advantage of science and management in the interpretive tours. To do this we suggest regular seminars for the guides to give them information about the dialogue between scientists and resource managers. And we suggest leaving the evaporimeter and a mock CAM station in Frozen Niagara so it can be used by interpreters to reinforce the protection message.

LITERATURE CITED

(see also the annotated bibliography in the original grant proposal)

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