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The Effect of Cave Entrances on the Distribution of Cave-Inhabiting Terrestrial Arthropods

by

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The entrance of a cave is generally regarded as having a number of effects on the environment and fauna of the cave. One of the prime effects is that the entrance is an input site of potential food materials (Barr, 1968; Barr and Kuehne, 1971: 49, 61; Poulson and White, 1969; Vandel, 1965: 328). The food input may be in the form of dead organic matter, such as leaves or wood passively falling or washing into the cave. The potential food may also actively enter the cave in the form of animals such as crickets and bats and result from their death, or from the deposition of their wastes.

Populations of cave-inhabiting arthropods are generally considered to be food-limited. If this is so, it would be expected that cave faunas, relying on food input from the external environment, would have a greater species diversity and larger population sizes in the parts of a cave with the greatest food availability. My own empirical field observations in temperate North American caves have convinced me that arthropod faunas are often most abundant a short distance inside the dark zone of a cave entrance. This phenomenon has also been noted in Europe by Deleurance-Glacon (1963: 162). Some further studies indirectly support these observations and expectations. Poulson and Culver (1969) found that terrestrial arthropod species diversity is higher in parts of the Mammoth Cave system of Kentucky where substrates have a higher organic content. Culver and Poulson (1970) investigated species diversity in a very small Kentucky cave and found it to be highest at the cave entrance, where cave and epigean faunas mixed. Such observations and results, however, are usually true only in the summertime. In the wintertime, the parts of any cave near the

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entrance experience coldness and dryness unfavorable to terrestrial cave arthropods (Barr, 1967).

In 1967 and 1968 I quantitatively investigated the effects of a cave entrance on the abundance of a population of scavenging troglobitic catopid *Ptomaphagus* beetles. The data gained, however, allow generalizations on the effects of an entrance on all the scavengers and some of the other members of a terrestrial arthropod cave community.

THE EXPERIMENTAL SITE

A simple way to test the summertime relationship of cave entrances to faunal abundance is to quantitatively sample the fauna at intervals from the entrance into the deep cave. Environmental variables other than distance from the entrance should be made minimal. The ideal cave should be long, relatively linear, without side passages and streams, and without varying substrate and moisture conditions. There should be only one entrance serving as a food input site. Under such conditions, it would be expected that the population densities should rise, and then fall at progressively deeper sampling stations.

Such an ideal experimental cave is almost non-existent. The best approximation that I could find in the over 300 caves that I have studied in northeastern Alabama and parts of adjacent states, was Crossings Cave, at Paint Rock, Jackson County, Alabama, at the edge of the cavernilerous Cumberland Plateau. The cave meets the above ideal requirements except for substrate variability, as is explained later.

The entrance is on a forested and gently sloping northfacing hillside, is roughly oval with a maximum height of 2 m and width of 1 m, and is at the lower end of a slight sink depression. It was formed by the collapse of a cave passage which maintains a general width of from 10 to 15 m throughout the length of the study area. The cave ceiling is flat and regular, and because of floor irregularities, is from 20 to 10 m above the floor in the center of the passage. No streams are present in the cave. The substrate in the first 20 m is loose soil which has washed into the cave from the entrance (figure 1). This soil contains visible organic detritus mostly in the form of leaves which have fallen in the entrance. Organic debris may, under very unusually wet conditions, be washed into the cave for up to 60 m. Otherwise, the floor throughout the study area is composed of moist rock, flowstone, or mineral soil. Conditions in 1967 were more moist than in 1968. Rimstone pools located from 20 to 40 m in the cave were full in 1967. They were empty in 1968, but the substrate here and elsewhere was still suitably moist. At distances over 200 m from the entrance, the substrate becomes drier, and is composed of fine silt and gravel.

The rocks and flowstone surfaces in the first 40 m are lightly stained by *Hadenoecus* cricket guano. The intensity of the black stain of cricket guano increases from 40 to 60 m inside the cave and is most intense from 60 to 100 m

Figure 1. Talus slope and soil floor just inside the entrance of Crossings Cave. The entrance itself is the two light spots above, behind, and to the right of the people. The trap at 3 m was set in the twilight zone in the talus below the entrance proper. The trap at 10 m was set in the cave dark zone in the flat soil floor at the base of the talus.

with deposits of up to 5 mm in thickness. The intensity of guano cover declines from 100 m onwards. At 130 m, the cover is thin and spotty, and little or no guano discoloration of the substrate is visible from 160 m onward into the cave. The heavy guano accumulation on the floor from 60 to 100 m shows that here, on the ceiling above, is the region of greatest adult cricket abundance. There are no apparent differences in the cave ceiling in this region to suggest reasons why the crickets prefer to roost in this section of the cave, other than that it is seemingly an appropriate distance from the cave entrance.

The cave is inhabited (personal data and manuscript on Alabama cave faunas) by a large suite of troglobites (obligate cave-inhabitants) including two species of beetles, three species of millipeds, two species of Collembola, a spider, and a dipluran. A large troglophilic fauna (facultative cave-inhabitants) is also present, including several species of beetles and spiders, and many species of flies. Two species of trogloxenic crickets complete the summary of the fauna. I have seen neither bats nor bat guano in the cave, so bat guano cannot be important as a food input in Crossing Cave. As noted above, an appropriate sampling technique could simultaneously determine the effects of the entrance on the abundances of many of these arthropod species.

METHODS

Baited pitfall traps were used as a sampling technique, as described by Poulson and Culver (1969), Peck (1973), Peck (1975), and Newton and Peck (1975). Thirty ml gobbets of slightly rotted pork liver were used as baits; Galt's solution was used as a preservative in the traps. Ten traps were placed at roughly 20 m intervals from the entrance up to a distance of 186 m from the entrance. The location of the traps was selected so that substrate variability was reduced as much as possible. The experiment was first performed in August, 1967, and was repeated in August, 1968, at the same trap sites. In both cases, the traps remained in the cave for exactly one week.

A visual census was made for one minute for any active fauna in an area of a one meter radius around each undisturbed trap site before placing the trap. Rocks or soil were not turned over or raked to detect any fauna which was hiding or inactive. No fauna was seen in the censuses, and this gave a strong impression of a fauna depauperate in both numbers of species and individuals. Although the cave has a fairly uniform and flat ceiling, irregularities in the floor did not allow an equal census of the ceiling for crickets at each trap site. Where the ceiling was close enough to be examined, at stations 5 to 8 and 10, no crickets were seen.

When the traps were picked up, another visual census was made of the area around the trap. No fauna was seen that was not in the trap or on the bait, except in 1968 when two *Ptomaphagus* were near trap 9 and one each was at traps 5 and 7. These were added to the totals for those traps.

RESULTS

The traps attracted and captured a total of 25 species of invertebrates. The most significant species in terms of numbers of individuals were three troglobites; the catopid beetle *Ptomaphagus loedingi longicornis* Jeannel, the lysiopetalid milliped *Tetracion jonesi* Hoffman (figure 2), and the entomobryid collembolan *Pseudosinella hirsuta* (Delouttevile): three troglophiles; the common phorid fly *Megaselia cavernicola* (Brues), the less common sphaerocerid fly *Leptocera* sp., and the less common sciarid fly *Sciara* sp.: and one trogloxene; the gryllacridid cave cricket *Hadenoecus* sp., of which all captured individuals were small nymphs. All these species are scavengers or mycetophages (*Sciara*) as adults and/or immatures, except for *Hadenoecus* sp. which has unknown nymphal feeding habits. The numbers of captured individuals of these species, which are judged to be the most important scavengers (or omnivores) of the Crossing Cave community, are presented by graphs for the stations progressively deeper in the cave in figure 3.

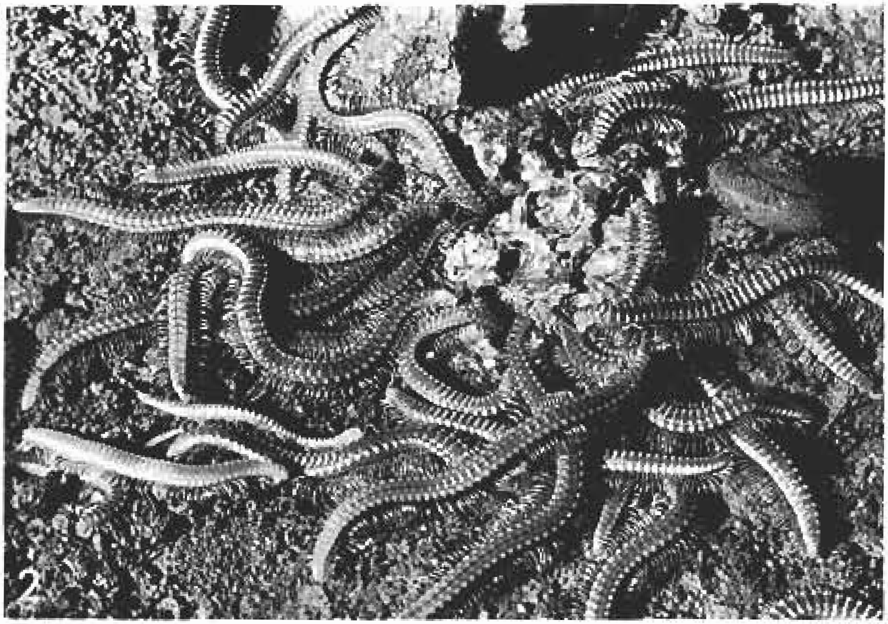


Figure 2. An aggregation of *Tetracion jonesi*, a troglobitic lysiopetalid milliped, and one *Mesodon* snail clustered around rotted pig liver bait in Crossings Cave. The milliped is the most significant member of the Crossings Cave scavenger community in terms of both individual size and total species biomass. It might also be a predator, perhaps on *Hadenoecus* cricket eggs or nymphs.

The other species that were caught in the traps in either one or both years occurred in significantly lower numbers. These then do not represent a large component of the community, but since so little is known on the subject of cave community composition, it is worth noting their presence. Species found only just inside the cave entrance at 3 m are a ptiliid beetle; one each of the phorid flies *Dorniphora perplexa* (Brues), *Spiniphora slossonae* (Malloch), and *Puliciphora suavis* Borgmeier; three nymphal gryllacridid cave cricket *Ceuthophilus* sp.; a lepismatid thysanuran; and a trombidiid mite. The troglophilic clubionid spider *Leiocranoides unicolor* Keyserling occurred with four individuals from 3 to 10 m in the cave, and two snails, *Mesodon* sp., were taken from 10 to 23 m. The troglobitic carabid beetle, *Pseudanophthalmus loedingi* Valentine, was represented by six individuals from 23 to 78 m. Four individuals of an aleocharine staphylinid beetle, *Atheta* sp., were taken from 3 to 78 m. Four tineid moths, *Amydria arizonella* Dietz, occurred from 3 to 182 m. Twenty-two sminthurid collembola, *Arrhopalites* sp., were found in 1968 only, from 23 to 78 m. One each of an ant, a pseudoscorpion, a trichoniscid isopod, and the psocopteran *Psyllipsocus ramburii* Selys-Longchamps were taken from 156 to 182 m in 1968.

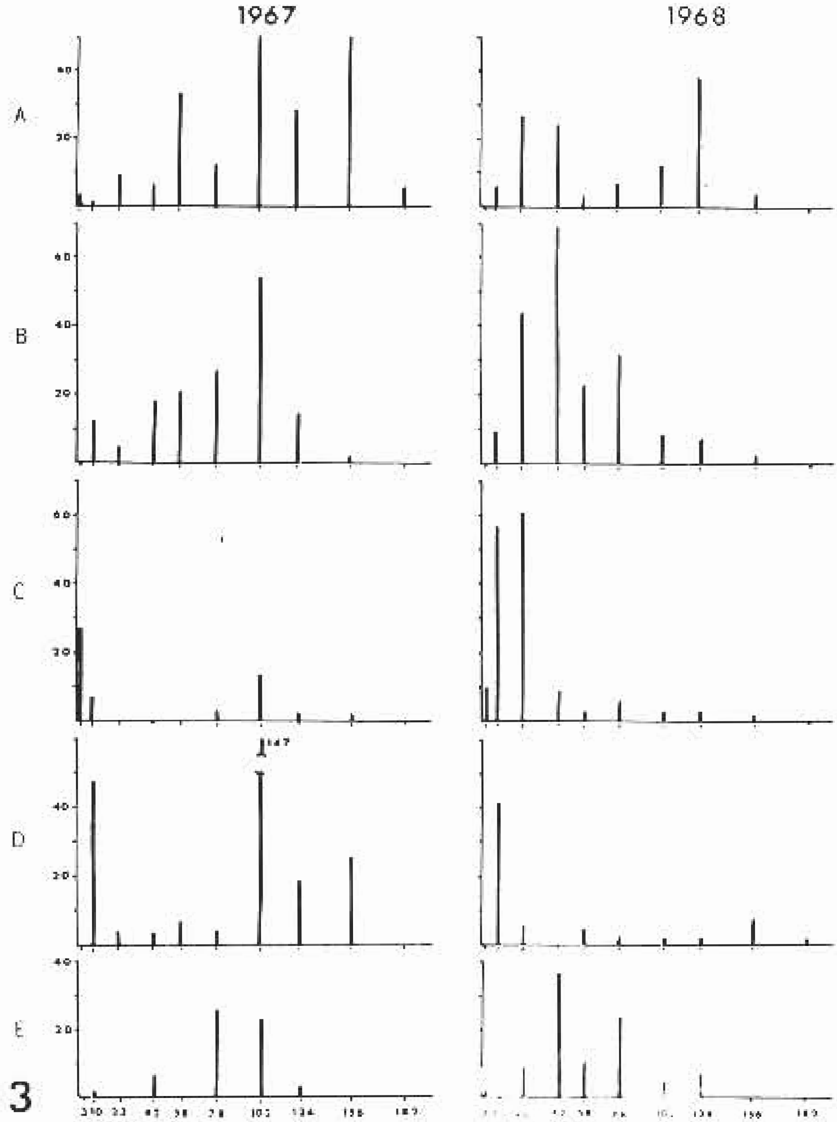


Figure 3. Numbers of organisms (ordinate) caught in August in 1967 and 1968 (columns down) in carrion-baited pitfall traps in a seven day interval in Crossings Cave, Jackson County, Alabama, at stations progressively deeper in the cave (abcissa). The ordinate and abcissa scales are the same for all graphs. The same trap sites were used both years. A. Crickets (Gryllacrididae, *Hadenoecus*). B. Beetles (Leiodidae, Catopinae, *Ptomaphagus loedingi longicornis*). C. Flies (mostly Phoridae, especially *Megaselia cavernicola*, but including some Sciaridae, and Sphaeroceridae). D. Millipedes (Lysiopetalidae, *Tetracion jonesi*). E. Collembola (*Pseudosinella hirsuta*).

The relationships of total numbers of all the trapped fauna to the depth inside the cave in each year are shown in figures 4A and 4B; the relationships of the live weight biomass of the catch to the depth inside the cave in each year, in figures 4C and 4D.

The results for 1967 show a bimodal distributional tendency for faunal abundances in terms of both total numbers of individuals and total biomass. The first peak is just inside the dark zone of the cave, at 10 m. The second and higher peak is at 102 m, and corresponds to the region of the cave with heavy *Hadenoecus* cricket guano deposition. However, in 1968 the faunal abundance in terms of numbers of individuals is unimodal with a broad peak from 10 to 42 m, and this fluctuates with a general downward trend for progressively deeper sites. The biomass picture for 1968 is one of a bimodal distribution with the major peak at 10 m and with a broad but lower peak from 124 to 156 m.

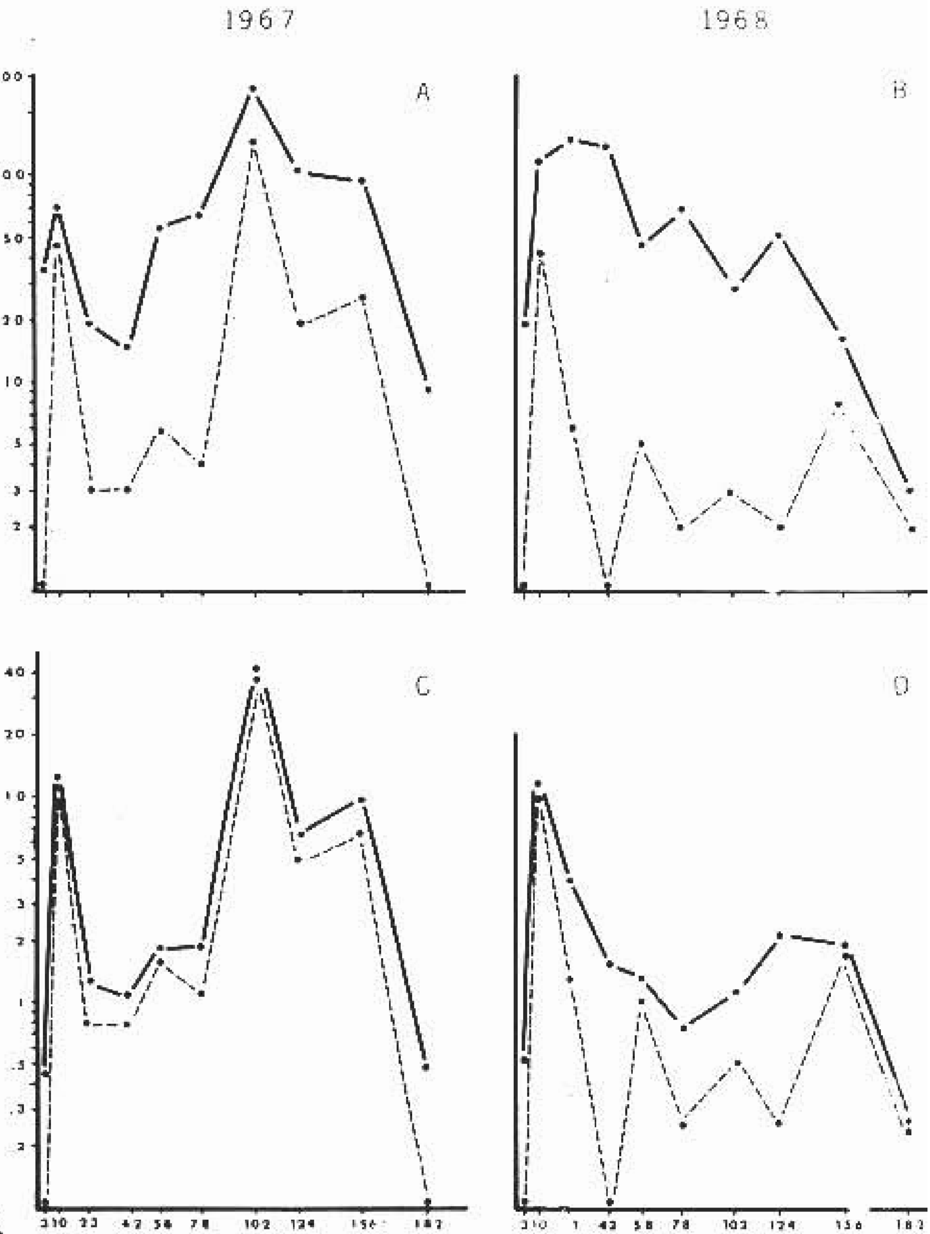
DISCUSSION

The first year: An equilibrium community

As expected, the 1967 results show a population peak in terms of both individual numbers and biomass just inside the entrance dark zone. The peak occurs at the overlap of the region of high food infall from the entrance with the beginning of the cave region of cool, dark, and moist microclimatic conditions that are stable throughout the summer.

Similarly, the population peak at about 100 m reflects the location of the scavenger community at the position of *Hadenöecus* cricket concentration on the cave ceiling, and the region of greatest cricket guano availability. *Ptomaphagus*, flies, *Tetracion*, and *Pseudosinella* are thus shown to correspond in their abundances to that of the cricket guano, and this demonstrates the importance of cricket guano in supporting this fauna. This dependency of the scavengers on the crickets is to be expected in the parts of the cave away from the entrance food input. It is inknown whether or not the regions under the cricket roosts are the locations of the first or second largest quantities of food input into the cave in the form of guano and occasional dead crickets, but larger scavenger populations are supported here than at the entrance where physical environmental factors are seasonally more variable.

The distribution of captured crickets (figure 3A) does not fully coincide with the abundance of the scavenger fauna because guano deposition, which attracts the scavengers, results from the aggregations of mature and near-mature crickets on the cave ceiling. None of these larger crickets were captured in the traps on the cave floor. Only small nymphs, judged to be first to fourth instar were caught. If the nymphs do not feed as scavengers below the adults, they need not congregate in the same areas as adults, but may rather be more abundant in other regions for other reasons, such as remaining near the substrates that were suitable for the laying of the eggs from which they hatched. Thus, cricket nymph abundances need not correspond to sites of adult concentration and defecation.



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Lastly, at 156 m, there is a coincidence of a high population of cricket nymphs and of *Tetracion* millipeds, but not of other scavengers and not of guano. Since *Abacion*, an epigean lysiopetalid relative of *Tetracion*, is known to be an omnivore and perhaps a carnivore (Hoffman and Payne, 1969), the 156 m abundance of *Tetracion* may be due to its functioning in a predatory role in a *Hadenoecus* oviposition site. The possibility of *Tetracion* acting in a predatory manner in cave systems should be investigated. If the milliped is a cricket egg predator, a competitive exclusion possibility will thus help to explain why beetle predators on cricket eggs do not exist in caves of the southern Cumberland Plateau of Tennessee and Alabama, while they do exist in caves in Texas and in northern Tennessee and Kentucky (Barr, 1967, 1968; Kane, Norton, and Poulson, 1975; Norton, Kane, and Poulson, 1975; Mitchell, 1971).

The second year: A disturbed community

Although a similarity exists in the structure of the populations in the first 50 m of the cave in both 1967 and 1968, all the populations in the deep cave in 1968 were very different. An inspection of the graphs in figure 3 and 4B shows that the population numbers decreased in the deep cave and appeared to be displaced towards the entrance, into the zone from 23 to 78 m. This may represent an actual movement of the populations, but is more probably a reflection of a deep disturbance caused by the 1967 trapping and the subsequent removal of part of the community.

For instance, the large milliped *Tetracion* is not as important in the cave in terms of numbers of individuals (figure 4A, dashed line) as it is in terms of community biomass (figure 4C, dashed line). But as a simple consequence of removing this one species in 1967, the 1968 community picture became very different in terms of both numbers and biomass.

Neither the milliped population nor the entire community in 1968 had regained a structure and composition similar to that of the previous year. It is obvious that more than a year is needed for the recruitment, replacement, and stabilization of the populations, especially of this large milliped scavenger. Since a average milliped individual has a volume of about .2 ml and a mass of about .25 gm, the 1967 removal of 147 individuals at the 102 m station alone represented the removal of about 37 grams of living biomass from the cave

Figure 4. Semilog plots of the scavenger community taken in pitfall traps (solid lines, total community; dashed lines, *Tetracion* millipeds) at stations progressively deeper in Crossing Cave. A and B are numbers of individuals in 1967 and 1968 (as ordinate, Pn+.1) respectively. C and D are biomass in grams (as ordinate, Pn+.1) in 1967 and 1968 respectively. Abcissa units, the same for all plots, are trap distances from the cave entrance. The space between the dashed and solid line represents the relative importance of all other scavenger species compared to that of *Tetracion*. In terms of numbers in 1967, this milliped generally accounts for about half the fauna (A), but makes up most of the fauna in terms of biomass (C). In 1968, the year after the initial disturbance of the community, the milliped population had not recovered. The other species, released from competition with the milliped, expanded to a greater proportion of total community individual numbers (B) and biomass (D).

system. Conclusions are that the cave cannot provide enough food, and/or the reproduction and growth rates of the milliped are too slow for the replacement of this biomass in a year. Either of these reflects a direct or indirect control of the population by food abundance in the deep cave.

Predators and scavengers

In both years, many species known to inhabit the cave were not collected. These are mostly rare in the cave, or are predators such as web-spinning spiders that are generally not taken at carrion baits. However, it would be expected that predator abundance would be high where prey abundance is high. This is often seen in caves where predatory beetles congregate near dung or carrion baits, supposedly because of the concentration of scavenging prey. The catch of predators (*Pseudanophthalmus*, *Atheta*, and *Leiocraniodes*) do not strongly suggest that this congregation effect was operating in Crossings Cave.

Competition between scavengers

The *Tetracion* millipeds were more abundant closer to the entrance in both years than were the *Ptomaphagus* and *Pseudosinella*. In morphology (the number of ocelli and amount of pigmentation), *Tetracion* is not highly cave-specialized, and it thus may be more tolerant of entrance environmental conditions than *Ptomaphagus* or *Pseudosinella*. This possibly greater tolerance may then allow the milliped to scavenge more successfully on the leaf debris input in the twilight zone at the entrance.

The trap at 3 m and the trap at 10 m caught the greatest diversity of species. This may be interpreted as an increased species diversity at the ecotone of the cave and the forest. However, the fact that usually only one individual of each forest taxon was caught shows that even though the diversity is high, the additional species are not an important part of the entrance community in terms of biomass or energy flow, and that these species are not significant competitors with the cave species.

Since all the scavenging flies, *Tetracion*, Collembola, and *Ptomaphagus* seem to depend largely if not exclusively on cricket guano in the deep cave, they obviously are all in potential food competition with each other. The competitive limiting effects of one species population on the other are not known. Because *Tetracion* seems better able to withstand the physical conditions nearer the entrance as well as those in the deep cave, and has the largest standing-crop biomass in the cave (excluding perhaps that of the crickets), it is ecologically the most important member of the deep cave terrestrial community (again excluding the crickets). It must have a competitive superiority over the other scavengers in Crossings Cave. At present there are no clues as to how or if the guano resource is partitioned or utilized so that the other scavengers are able to support themselves in the face of competition with *Tetracion*. In size alone, one average 0.25 g *Tetracion* is the biomass equivalent (but perhaps not the food consumption equivalent) of about 160 *Ptomaphagus* (a weighed sample of 91 adult beetles gave a mean weight of 0.0016 g beetle). Individual flies and collembola are about 1/2 to 1/10 the size of a

Ptomaphagus. Consequently, the role of the milliped in energy flow in the cave probably greatly surpassess that of all the rest of the scavengers combined.

In a community dominated by these millipeds, population sizes of other species are suppressed. When large numbers of the millipeds were removed from the community in 1967, the other species populations were released from this competitive pressure, and responded by spatial expansion and population size increase. Since the other species require less than a year to reach maturity and are smaller in body size, they were able in one year to dramatically increase the number of individuals in their populations in relation to those of the milliped (figure 4B) but were not able to accumulate a proportional increase in total community biomass (figure 4D).

SUMMARY AND CONCLUSIONS

One prime effect of a cave entrance is that it is an input site of food for the cave community. With this input, it is expected that summertime cave faunas are comparatively more abundant near cave entrances, just inside the dark zone. A test of this expectation was performed by pitfall trapping at progressively deeper stations in Crossings Cave, Alabama, in the southern Cumberland Plateau of the southeastern United States.

The effect of the entrance on the undisturbed community of terrestrial scavenging intertebrates was as expected, with a bimodal distribution of numbers of individuals and of biomass with (1) a peak just inside the dark zone at about 10 m and (2) with the highest peak at about 100 m from the entrance. These regions coincide respectively with (1) where the cave dark zone overlaps with the region of highest detritus infall from the entrance, and (2) with the region of greatest adult *Hadenoecus* cricket concentration on the cave ceiling and consequently the region of greatest cricket guano abundance on the cave floor.

Following the food input importance of the *Hadenoecus* crickets, *Tetracion* millipeds are the most significant species in the cave scavenging community in terms of biomass and probably of energy flow. They are followed by *Ptomaphagus* catopid beetles, *Megaselia* phoid flies, and *Pseudosinella* collembola.

When the trapping was repeated a year later, the effects of the previous faunal removal were still evident. The community structure had not returned to its former equilibrium conditions. The distribution of population numbers in the deep cave was reduced by more than an order of magnitude even though the scavenger populations increased in response to release from competition with the milliped.

As previously concluded (Peck, 1975), severe community disturbance results from indiscriminatate and massive trapping of terrestrial cave populations. Future studies of this sort should use only baits or traps which release the fauna unharmed after the census has been performed. Study of community response to the removal of a predator or competitor should only remove one species as an experimental variable, not the entire study site community as did the traps used in this study. Even then, if baits or live traps are used, recognition must be made of the possibility of inducing an unnatural situation or of creating the ecological equivalent of a "Heisenberg uncertainty" in any census through sponsoring the first concentration of the fauna, and by enriching the community through feeding by baits and by encouraging reproduction. This criticism has been applied to studies where the use of baits have tended to obscure rather than clarify *Drosophila* habitat-dispersal relationships (Johnston and Heed, 1975).

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SUMMARY

Populations of cave invertebrates are generally considered to be food-limited. The cave entrance is a major source of food input into the community in the form of decaying organic matter. Thus, the densities of scavenging terrestrial cave invertabrates should be related to the distance from the cave entrance because this represents a measure of food abundance. A test showed this expectation to be true in Crossings Cave, Alabama. A population density peak occurred 10 m inside the cave where the dark zone and detritus infall regions meet. The greatest population peak occurred at 100 m where densities of crickets and their guano are highest. The pattern should hold for most caves, but the actual distances will vary in each site depending on its circumstances. When the fauna was removed from the cave, the remnant had not regained community equilibrium a year later. Removal of the dominant scavenger, a milliped, allowed other species populations to expand because of decreased competitions.

RESUME

Les populations d'invertébrés cavernicoles sont généralement considérées comme étant limitées par la nourriture disponible. L'entrée de la grotte est la source principale d'apport de nourriture à la communauté, sous forme de matière organique en décomposition. Ainsi, les densités d'Invertébrés terrestres cavernicoles et nécrophages seraient en rapport avec la distance les séparant de l'entrée de la grotte, car celle-ci représente une mesure de l'abondance de nourriture. Une expérience a montré l'exactitude de cette prévision, dans les grottes Crossings en Alabama. La densité de population présente un pic à 10 m à l'intérieur de la grotte, là où se rencontrent la zone d'ombre et celle des détritus. Le pic correspondant à la plus grande population se trouve à 100 m à l'intérieur de la grotte, là où les densités de grillons at de leur guano sont les plus fortes. Cet exemple pourrait être valable pour la plupart des grottes, mais les distances réelles varieront dans chaque site, selon les circonstances. Lorsque la faune est retirée de la grotte par suite des piégeages, ce qui reste n'a pas retrouvé un équilibre de communauté au bout d'un an. Le retrait du nécrophage dominant, un mille-pattes, a permis à des populations d'autres espèces de s'étendre, par suite de la diminution de la compétition.

LITERATURE

BARR, T. C. 1967. Observations on the ecology of caves. Amer. Nat., 101 (922): 475—492.

BARR, T. C. 1968. Cave ecology and the evolution of troglobites. *in:* T. Dobzhansky, M. Hecht, W. Steere eds., Evolutionary Biology 2: 35—102. Appleton-Century-Crofts, New York.

BARR, T. C., Jr. and R. A. KUEHNE. 1971. Ecological studies in the Mammoth Cave system of Kentucky. II. The ecosystem. Ann. Spéléol., 26: 47—96.

CULVER, D. C. and T. L. POULSON. 1970. Community boundaries: Faunal diversity around a cave entrance. Ann. Spéléol., 25: 853—860.

DELEURANCE-GLAÇON, S. 1963. Recherches sur les coléoptères troblobies de la sous-famille des Bathysciinae. Ann. Sci. Nat. (Zool.), sér. 12, 5 (1): 1—172.

HOFFMAN, R. L. and J. A. PAYNE. 1969. Diplopods as carnivores. Ecology, 50: 1096—1098.

JOHNSTON, J. S. and W. B. HEED. 1975. Dispersal of *Drosophila*: The effects of baiting on the behavior and distribution of natural populations. Amer. Nat., 109: 207—216.

KANE, T. C., R. M. NORTON, and T. L. POULSON. 1975. The ecology of a predaceous troglobitic beetle, *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae). I. Seasonality of food input and early life history stages. Int. J. Speleol. 7: 45—54.

MITCHELL, R. W. 1971. Food and feeding habits of the troglobitic carabid beetle *Rhadine subterranea*. Int. J. Speleol., 3: 249—270, plates 83—87.

NEWTON, A. and S. B. PECK. 1975. Baited pitfall traps for beetles. Coleopterists Bull., 29: 45—46.

NORTON, R. M., T. C. KANE, and T. L. POULSON. 1975. The ecology of a predaceous troglobitic beetle, *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae). II. Adult seasonality, feeding and recruitment. Int. J. Speleol. 7: 55—64.

PECK, S. B. 1973. A systematic revision and the evolutionary biology of the *Ptomaphagus (Adelops)* beetles of North America (Coleoptera; Leiodidae; Catopinae) with emphasis on cave-inhabiting species. Bull. Mus. Comp. Zool. (Harvard University), 145: 29—161.

PECK, S. B. 1975. A population study of the cave beetle *Ptomaphagus loedingi* (Coleoptera: Leiodidae; Catopinae). Int. J. Speleol., 7: 19—32.

POULSON, T. L. and DAVID C. CULVER. 1969. Diversity in terrestrial cave communities. Ecology, 50: 153—158.

POULSON, T. L. and W. B. WHITE. 1969. The cave environment. Science, 165 (3897): 971—981.

VANDEL, A. 1965. Biospeleology. Pergamon Press inc., New York. 524 pp.