

ARE THE CAVERNICOLES FOUND IN HAWAIIAN LAVA TUBES JUST VISITING ?

by

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ABSTRACT

Some Hawaiian cavernicoles appear to occupy areas of Kazumura Cave for less than two days at a time. It is thought that they appear from and disappear back into the system of cooling cracks, channels and vesicles present in the surrounding lava flows. This 'mesocavernous habitat' is thought to be extensive, to contain tree roots and detritus on which cavernicoles feed, and to provide them with a humid microclimate which is subject to fewer perturbations than the larger and draughtier caves. For these reasons it is suggested that the 'mesocavernous habitat' is the principal habitat of Hawaiian cavernicoles, though some inhabit caves where they offer a suitable microclimate, or else make periodic sorties into caves in order to exploit cave-based resources.

INTRODUCTION

The hypogean environment of Hawaii is of great interest to biologists (Howarth, 1973, 1981, etc.). The caves are developed in basaltic lava as long, slightly sinuous, gently sloping tunnels of fairly uniform diameter. They are traversed every few metres by cooling cracks, generally between 2mm and 10mm wide. These cracks admit water into the caves after rain, and also drain those parts of the caves which lie above the water table. The cracks are entered by tree roots (mainly of *Metrosideros polymorpha*) which penetrate the caves at intervals, where they may hang free, spread out on the cave floor, grow down, along, or even up the cave walls, or disappear into cooling cracks. These living roots, together with dead roots and their decomposition products, provide the food-energy base for highly specialized invertebrate communities which inhabit the hypogean world of the lava flows.

The discovery of cave-adapted (= troglomorphic) arthropods in Hawaiian lava tubes by Howarth (1972) was unexpected, as four long-held assumptions were thought to preclude the existence of a cave-adapted fauna in Hawaii. First, obligate cavernicoles were known mostly from limestone caves in temperate regions south of maximum glaciation and were considered glacial relicts, and most of the few known tropical forms are aquatic and were assumed to be relicts of changes in seawater level (Barr, 1968; Vandel, 1965). Second, lava tubes were considered too ephemeral and too often polluted with volcanic gases to allow evolution of cave faunas (Torii, 1960; Barr, 1968). Third, islands were considered unfavourable sites for the evolution of cave faunas because the pre-adapted forms (the taxa represented in continental caves) are poorly represented on oceanic islands as a result of their lack of dispersability (Peck, 1974). And finally, Hawaiian lava tubes were known to lack the two main energy

sources of continental caves: sinking streams and troglonexes, those animals that roost in caves and return to the surface to feed (Howarth, 1981).

The Hawaiian cave fauna has been described in a series of papers in the journal *Pacific Insects* since 1973. An excellent review of the biota is given by Howarth (1981), who paints a detailed picture of the functioning of the community in Kazumura cave (which was the venue for the study reported here). Howarth recognized ten categories within the spectrum of life forms in Kazumura Cave: discounting the accidentals which are mainly exotic species, the community can be split into three rhizophagous, one omnivore, three zoophagous, and two saprophagous categories. The latter, and one zoophagous category are occupied by exotics and endemic troglolithes. All the other categories are dominated by endemic obligate cavernicoles (= troglobites), which are strongly hygrophilic and anemophobic (Howarth, 1981; Hadley *et al.*, 1981; Ahearn and Howarth, 1982). This is in some ways surprising in view of Howarth's observation (1980) that tropical caves do not generally provide an optimal habitat for hygrophilic arthropods. Indeed, during a study conducted in Charcoal Cave, which runs beneath desert terrain in the rain shadow of Kilauea Volcano, Howarth (1982) found that cavernicoles avoided the 100m-long 'transition zone' of the cave (defined as that area beyond the limit of light penetration where external climate produces perturbations in cave microclimate (Barr, 1968). In the same paper, he made a most interesting suggestion: 'I believe that the major populations of cave animals live in the smaller interconnected voids within the lava below the variable temperature zone, and colonize caves only where food and evaporation rate allow. Within these smaller voids the relative humidity remains near saturation and the evaporation rate is negligible.' The 'voids' to which Howarth refers are plainly seen in recent lava flows on Kilauea volcano, where the visitor must be constantly wary of what seem to be solid lava surfaces, but which unexpectedly collapse into holes when stepped on. Howarth (1982) describes their formation thus: 'Overflows of pahoehoe spread out as thin layers. Degassing can swell the still plastic upper crust and form large gas bubbles. Also shrinkage during cooling may separate layers of lava, or cause extensive systems of cracks, creating voids. Gas vesicles form in the cooling lava from trapped bubbles. These may form extensive porous layers of vesicular basalt within a flow. Other voids such as tumuli and buried tree molds also occur.' These voids form '. . . an extensive system of interconnected channels and air spaces . . . Roots of plants colonizing these flows, utilize these voids in the same way that other plants use soil. Such an environment is a harsh or rigorous one for most terrestrial animals. It is perpetually dark, with a relatively constant temperature, with a constantly water-saturated atmosphere possibly above the limits of many terrestrial species, and without many of the environmental cues used by surface species.' It is, on the other hand, an ideal habitat for the Hawaiian cavernicoles, and is presumably far more extensive, and therefore of far more biological significance than the caves!

The study described in this report was conducted by M. McHale, F. G. Howarth and me over a four-week period from December 1981 to

January 1982, in Kazumura Cave and John Martin's Cave, Hawaii. During the course of a bioclimatic study (Chapman and Howarth, in press) data were collected on the time period spent in the cave by individuals of six endemic and three exotic species of cavernicolous invertebrates.

METHODS

We visited 31 study sites in Kazumura Cave, and five in John Martin's Cave at intervals of one to four days over a period of five weeks. During our early visits, attractant baits were placed on some sites. They were bread, or poi (a starchy food available in Hawaii) vividly stained using food dyes. As the study progressed, other baits were emplaced, of yeast, or a mixture of bread, yeast and syrup. These were stained with different coloured food dyes. Some raw liver baits were set in John Martin's Cave and were similarly stained. Each time we visited each site, we recorded the numbers of each cavernicolous species seen and whether they were coloured through eating bait (coloured gut contents showed through the weakly pigmented teguments of the crickets, Collembola and some millipedes). The Collembola (*Sinella* spp.) and millipedes (*Dimerogonus* sp. and *Oxidus gracilis*) tended to collect in the vicinity of the baits, moving around very little during the period of our visits. We therefore assumed that any springtail or millipede with a coloured gut seen close to a single bait consecutively on two or more of our visits was the same individual. The highly mobile crickets (*Caconemobius* spp.) differed in pigmentation and number of tarsal spines, as well as in sex and instar (stage of life). Some specimens were further distinguishable by damage to appendages (missing leg, or spines on one leg) and even more so by the colour, or colour mixture of gut contents when they had been eating the dyed baits (coloured gut contents generally persisted over several days). By a combination of these features, it was usually possible to recognize individual crickets with some confidence from one visit to the next. Large lycosid spiders (*Lycosa howarthi*) were captured, returned to the laboratory, individually marked with small, circular, numbered plastic discs attached dorsally on the carapace by means of a droplet of 'superglue', and released unharmed on our next visit at the point of collection (controls marked in this way and kept in the laboratory during the period of the study showed no apparent ill effects). Juvenile lycosids were measured in the field to aid subsequent recognition, and the position of each was noted. Nymphs of the cixiid bug *Oliarus polyphemus*, being sap-feeders, were not attracted to baits, but tended to stay on the same individual root or group of roots except when dislodged by flowing water after rain, so that it was possible to follow the movements of individuals (or groups of individuals) with some degree of confidence. Adults of *O. polyphemus* and of the mesoveliid bug *Speovelia aaa* were present periodically in very small numbers on some sites and so it was assumed that serial sightings on the same site (if of the same sex) involved the same individual.

The visual census method used in this study to record presence or absence of cavernicoles on sites could, it might be supposed, miss a substantial portion of the fauna. This would certainly be a serious problem

in limestone caves, but is less so in young lava caves, where pale, poorly pigmented cavernicoles show up well against the black rock walls which are covered with a smooth glaze which affords few hiding places. The cave floor is often uneven, rough and pitted, but still it offers few completely concealed hiding places, and most cavernicoles did not appear to any substantial degree to frequent the drier stretches of cave walls or floor between the damp root-rich patches which formed our study sites.

The records of individual cavernicoles were sometimes continuous over two or more of our visits to the cave, and sometimes not. Individuals seen on one of our visits, but not the next, were judged to have resided in the cave for less than two days. Individuals seen consecutively on two of our visits were judged to have been resident for up to one week. Individuals seen consecutively on three or four of our visits were judged to have been resident for one to two weeks. Animals seen consecutively on more than four of our visits were judged to have been resident for more than two weeks. These duration categories are necessarily approximate, because the data are based on irregularly-spaced sightings.

RESULTS

The results of the study are presented in FIG. 1. The four columns represent different time-spans of residence in the cave by individuals of a particular species-stage. The column heights in each case represent the number of visits of a particular time-span as a proportion of the total number of recorded visits for that species-stage. The numbers in each left hand column give the total number of individual visits by each species-stage recorded over all the sites in Kazumura and John Martin's caves during the four week period of the study.

DISCUSSION

As has been suggested in the introduction to this account, lava caves of a diameter sufficient to admit cave biologists almost certainly represent a minor portion of the total hypogean habitat of recent lava flows. Moreover, substantial portions of lava caves may from time to time represent a climatically hostile environment for invertebrate cavernicoles which are physiologically specialized in a way which renders them dependent on a saturated, or near-saturated, atmosphere (Howarth, 1980). This discussion will therefore take as its starting point Howarth's (1982) hypothesis that the major populations of the Hawaiian cavernicoles live in what he later termed 'mesocavernous' habitats (Howarth, 1983), that is the extensive system of vesicles, channels, and cooling cracks present in young lava flows.

If the cavernicoles are mainly based outside the caves and are entering them from time to time via the cooling cracks, to opportunistically exploit cave-based resources, then it would seem probable that the more vagile species (those which move around a lot) will appear in the cave more frequently and will leave more quickly, while less vagile species will appear

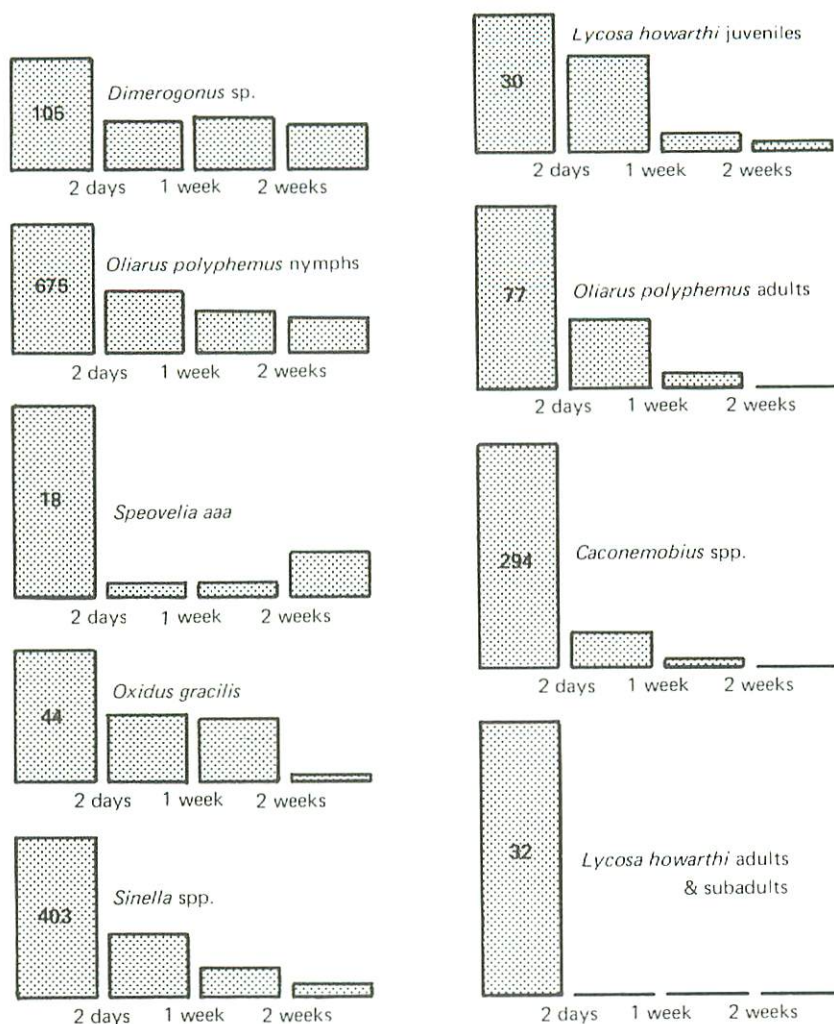


FIG. 1 — TURNOVER OF CAVERNICOLES IN KAZUMURA AND JOHN MARTIN'S CAVES. SEE TEXT FOR EXPLANATION.

less frequently and will leave more slowly. This suggestion is entirely compatible with the data. Less vagile species such as the millipedes and collembola appeared at baits much later than crickets, but remained longer. This was particularly evident in the millipede *Dimerogonus* sp., a conspicuous pale-coloured species which appeared at baits in ever-increasing numbers during the course of the study. The exotic entomobryid Collembola *Sinella yosiia* and *S. caeca*, and the exotic millipede *Oxidus gracilis* reacted to baits in a similar manner, but were less inclined to stay put.

Most highly vagile cavernicoles (such as *Lycosa howarthi* and *Caconemobius* spp. crickets) must inevitably wander into caves from time

to time as they move about the labyrinth of cooling cracks and other mesocavernous spaces in which they live. The results of this study suggest that, having done so, they do not generally remain in the cave for periods of more than a couple of days at a time, even when a plentiful supply of food is present in the form of attractive baits, although the crickets did make use of this food source while resident in the cave. It should be noted that the mean length of residence in the caves may have been considerably less than two days for *Caconemobius* and *L. howarthi*, as the shortest duration category in FIG. 1 is a maximum of two days. It seems likely that residence would be prolonged rather than shortened by the presence of baits in the caves, so that large spiders and crickets are, under natural conditions, perhaps even more transient visitors to the caves than the data suggest. I suggest that juvenile spiders, *L. howarthi*, though able to move quickly, may have remained on sites for longer periods than adults of the species, because they may take smaller and less vagile prey, such as Collembola, which were present on sites in increasing concentrations as a result of our baiting programme. The cryptic behaviour of juvenile *L. howarthi* suggested that their normal habitat is in mesocavernous spaces: they were generally found under rocks or in narrow crevices in the cave floor, as indeed were adults of this species, though the latter could also be found wandering in more open situations from time to time.

The cixiid bugs *Oliarus polyphemus* showed the greatest contrast in juvenile/adult behaviour. This is easily explained, as the nymph is the feeding stage, while the adult is a highly vagile dispersal stage (Howarth, 1981). The nymphs are largely sedentary on tree roots, on whose sap they feed. They surround themselves with a fragile wax cocoon and move only when disturbed by excessive water flow along their root, or by visiting cave biologists! The former was a common cause of their removal from vertically hanging roots in the cave, but might be less of a problem in mesocavernous habitats. On the other hand, caves may afford greater safety from predators such as *Caconemobius* crickets and *L. howarthi*, which were both observed carrying *O. polyphemus* bugs in their jaws during this study. It is presumably more difficult for predators to capture the bugs on free-hanging tree roots in the cave than on tree roots in the narrow confines of mesocavernous habitats.

The mesoveliid bug *Speovelia aaa* appears to be fairly territorial. Some specimens were seen almost every time we visited a particular site, slowly patrolling an area of wall bench. These individuals were almost certainly resident in the cave. At other sites, an individual would be seen during one of our visits, and be gone the next.

One species not included in FIG. 1., because it was recorded in too low numbers, is the exotic nesticid spider *Nesticus mogera*. This species, a snare builder, is perhaps the most sedentary of all the Kazumura cavernicoles, and the few individuals seen in the cave were resident throughout the study period.

The picture which emerges from this study is that highly vagile cavernicoles appear and disappear rapidly in the cave, while some of the more sedentary species congregate in ever increasing numbers in the cave if lured there by an unusually rich supply of food. This in itself does not

CAVERNICOLES IN HAWAII

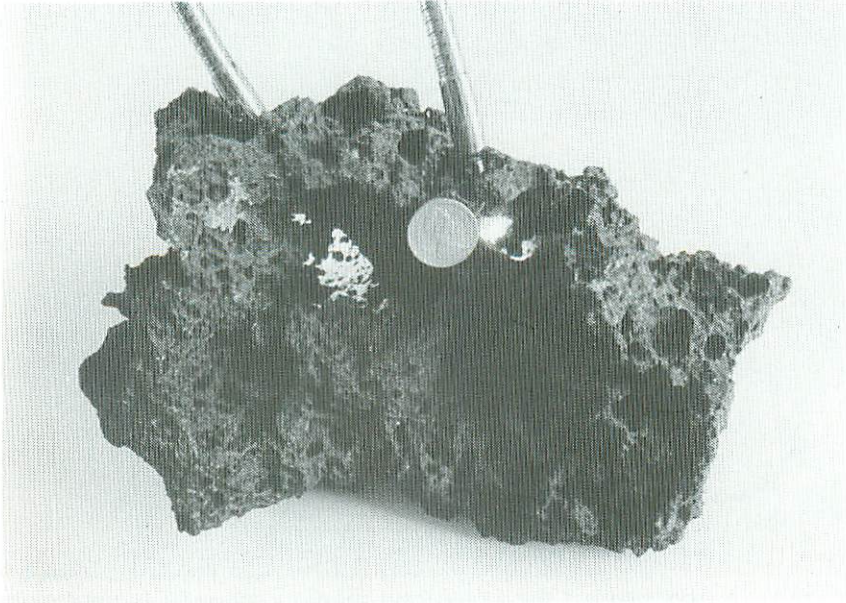


PLATE 1 — A PIECE OF VESICULAR BASALT. THE PATCHES OF BRIGHT LIGHT WHICH ILLUMINATE POCKETS IN THE ROCK TO EITHER SIDE OF THE COIN EMANATE FROM THE TWO FIBRE-OPTICS LIGHT SOURCES AT THE TOP OF THE SPECIMEN. THEY ILLUSTRATE HOW VESICLES IN LAVA FLOWS MAY INTERCONNECT AND SO ALLOW PENETRATION BY GROWING TREE ROOTS AND PROVIDE A HABITAT FOR SMALL INVERTEBRATES. THIS IS ONE OF THE 'MESO-CAVERNOUS' HABITATS REFERRED TO IN THE TEXT.

Phot.: P. R. J. Chapman

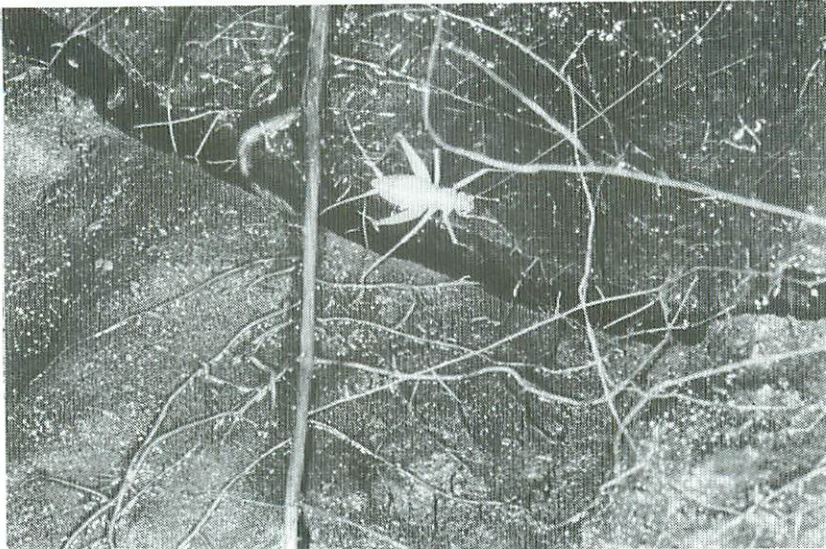


PLATE 2 — A *CACONEMOBIUS* CAVE CRICKET STRADDLING A COOLING CRACK FROM WHICH IT HAS JUST EMERGED ON TO THE WALL OF KAZUMURA CAVE. TREE ROOTS CAN BE SEEN CRISS-CROSSING THE CAVE WALL AND ENTERING AND EMERGING FROM THE CRACK.

Phot.: P. R. J. Chapman

CAVERNICOLES IN HAWAII

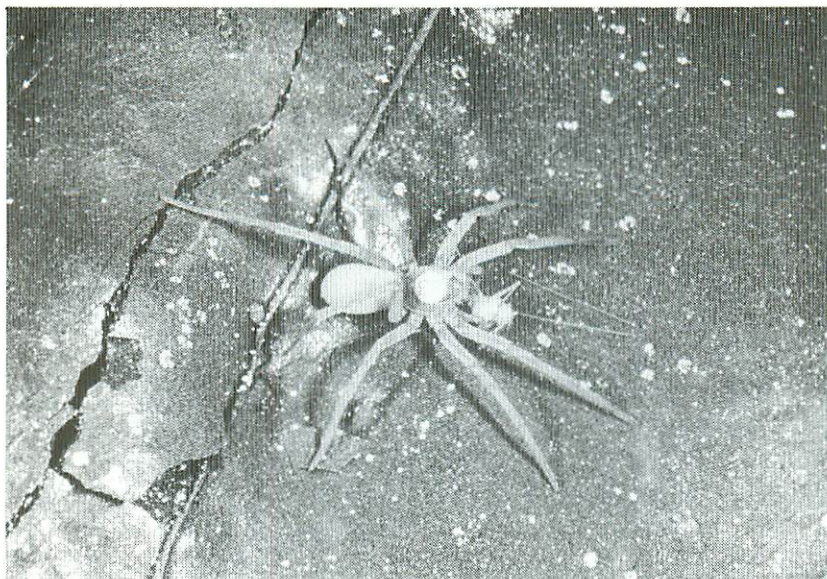


PLATE 3 — A CAVE SPIDER, *LYCOSA HOWARTHII*, EATING A FRESHLY-CAUGHT *CACONEMOBIUS* CAVE CRICKET. IN THE ABSENCE OF LIGHT, THE SPIDER'S HUNTING TECHNIQUE RELIES ON SENSING MINUTE AIR TURBULENCE CAUSED BY ITS MOVING PREY. PREY CAPTURE IS THEREFORE EASIER IN THE STILL AIR OF SMALL 'MESOCAVERNOUS' SPACES THAN IN THE MOVING AIR IN LARGE DRAUGHTY CAVE PASSAGES.

Phot.: P. R. J. Chapman



PLATE 4 — MICK MCHALE MEASURING AIR HUMIDITY AT A STUDY SITE IN JOHN MARTIN'S CAVE. CAVERNICOLES FREQUENT BENCHES ALONG CAVE WALLS SUCH AS THE ONE ON WHICH HE IS SEATED WHERE TREE ROOTS (VERTICAL LINES IN THE PICTURE) SPREAD OUT ALONG THE GLAZED BASALT SURFACE.

Phot.: P. R. J. Chapman

suggest that the cave is a less suitable habitat for cavernicoles than the 'mesocavernous' habitat, though it does support Howarth's (1982) suggestion that the latter is more populated with cavernicolous species.

Tuttle and Stevenson (1978), and Howarth (1980) have argued that large passage size, numerous entrances admitting powerful airflows, and a high ambient temperature, all conspire to produce high rates of evaporation in tropical caves. Howarth (1982) has shown that the Hawaiian cavernicoles avoid such conditions, and other studies (e.g. Hadley *et al.*, 1981) have shown that this is because cavernicoles are physiologically adapted to hydrating atmospheres. These are characteristic of mesocavernous habitats (Howarth, 1983) rather than cave habitats. Even Kazumura Cave, which runs beneath rainforest and might therefore be expected to have a permanently saturated atmosphere away from the proximity of entrances, would seem to suffer measurable evaporation throughout its length (Chapman and Howarth, in press).

Surprisingly, Chapman and Howarth (in press) found little correlation between microclimate conditions in Kazumura Cave and the recorded abundance of cavernicoles (the exception was *Lycosa howarthi*, whose abundance correlated with high atmospheric humidity). This finding may be interpreted as supporting the suggestion that cavernicoles visiting the cave from the adjacent mesocavernous habitats are able to exploit cave-based resources even when microclimatic conditions are unfavourable, provided that such excursions are of brief duration. As soon as physiological stress is felt by the cavernicole, it can return to the optimal conditions of its mesocavernous habitat, via the nearest cooling crack.

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