HAWAII IBP SYNTHESIS:
4. THE HAWAIIAN LAVA TUBE ECOSYSTEM

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Lava Tubes as Life-Support Systems

How and why an animal would lose its eyes, color pattern, and other characters, and restrict itself perpetually to the rigorous environment of caves has long intrigued biologists. Much is known of the ecology of limestone caves in temperate regions (Vandel 1965; Barr 1968). The realization that lava tubes also harbor an analogous specialized fauna is more recent (Torii 1960). In addition to Hawai'i, significant lava tube faunas are now known from the Galapagos (Leleup 1967, 1968), Japan (Ueno 1971), and North America (Peck 1973). In Hawai'i the fact that at least seven native groups have independently evolved troglobitic species on at least two islands indicates that adaptation to lava caves is a general process.

Troglobites (obligatory cavernicoles) are restricted to the true dark zone of caves. The dark zone environment, as outlined by Howarth (1973) is similar to that described by Poulson and White (1969) for temperate limestone caves. It is a rigorous one defined by the absence of light; the relative constancy of temperature at or near the average annual temperature of the region and of relative humidity above the physiological limits of most terrestrial animals; and the absence of many environmental cues. There is generally a rocky substrate and often an illusion that food is scarce.

Lava tubes are destroyed by erosion in a relatively brief geologic time. However, they are continually being created during volcanic eruptions since oceanic volcanoes are characteristically built with vesicular basalts which often flow as pahoehoe, and such flows almost always build lava tubes (Peterson & Swanson 1974). Lava tubes are a common land form on younger oceanic islands. Further, since the voids in basaltic lavas offer some avenues for subterranean dispersal from older caves to younger caves, we can expect that a specialized cave fauna will develop wherever new basaltic lava flows continually cross older flows over a long enough period of time, and the climate allows the continuous colonization of caves.

In Hawai'i rain water percolates rapidly into the young porous basalt. Only where the water table is near the surface is significant water found in the cave. This occurs near the coast and a remarkable aquatic fauna, including many troglobites, inhabits isolated coastal pools of brackish water (anchialine habitat) in young lava flows (Holthuis 1973; Maciolek & Brock 1974).

In younger lava tubes the substrate is usually barren lava rock. However, this can vary considerably in texture, e.g., a polished glazed surface, irregular pile of breakdown blocks, highly vesicular porous lava, and even ashy rubble. The absence of organic detritus is often surprising. Lava tube slimes which represent insipient soil formation often cover large areas. In the oldest caves clay and soil have filled most smaller voids and cover the floor in many areas.

Limestone caves also have a rocky substrate, often as irregular blocks, but there is a greater variety of minerals including crystals, biogenic minerals, and alluvial sediments. A fine residual silt from solution of limestone is characteristic, and is closely associated with terrestrial troglobites (Barr & Kuehne 1971).

The main energy sources in Hawaiian lava tubes are plant roots, especially 'ohi'a (*Metrosideros collina* var. *polymorpha*), slimes deposited by organically rich percolating ground water, and accidentals which are those animals that blunder in. In contrast, the main energy sources in continental limestone caves are trogloxenes, especially bats and crickets, and debris washed in with sinking streams, especially during floods. Additional energy is supplied by accidentals, percolating ground water, autotrophic bacteria, and aerial plankton.

The greater overburden of limestone caves often precludes the importance of tree roots and, except for Paulian and Grjebine (1953) who discovered an intermediate cave-adapted cixiid in Madagascar (Synave 1954), most biospeleogists have disregarded roots in their surveys. However, the discovery in Hawai'i of a cave cixiid (Howarth 1972) stimulated other researchers to check roots in caves. Recently Fennah (1973b) described three species of troglobitic fulgoroids, two from Mexico and one from Australia, and Peck (1975) listed an undescribed species from Jamaica caves.

The absence of native trogloxenes in Hawai'i may be related to the absence of winter and of a need to hibernate, and also to the fact that the continental trogloxenic groups did not colonize Hawai'i. Hawai'i's only bat and only native land mammal (*Lasiurus cinereus semotus*) is a forest species and is not known to enter caves.

Sinking streams are not important energy sources in Hawaiian lava tubes. It is unusual for a stream to enlarge a lava tube; rather, it speeds the siltation and erosion processes. The few lava tubes visited that had captured a temporary stream were shortly blocked with silt, had signs of periodic flooding, and had a poor fauna.

Cave Fauna

Native cavernicolous animals are predominantly arthropods. In Kazumura Lava Tube, 10 troglobitic and seven native troglophilic (facultative cavernicoles) species occupy nine general niches: three primary consumer niches, feeding on living and dead roots; one omnivore; two predatory niches differing in strategies (i.e., with and without snares); one sarcophagous niche; and two saprophagous niches, one feeding on fungus and one generalist. There is broad niche overlap as underscored by omnivore niche occupied by the troglobitic cricket.

Only one species of root penetrates into Kazumura Lava Tube to any great extent, and five native and four exotic arthropods feed on it. The troglobitic cixiid which is probably the most abundant arthropod in the cave is a sapsucker. The living root chewers are represented by three species of moths of the genus *Schrankia*. One of these is a weak flier and appears to be troglobitic. An undescribed troglobitic millepede occupies the living and dead root feeding niche.

At the top of the food chain is a large striking troglobitic wolf spider which stalks its prey and does not build a web. The other five native predators are less well known and probably live in cracks and rarely enter larger passages. A troglobitic terrestrial water treader scavenges on dead arthropods. The two saprophagous niches are occupied by four troglophilic taxa.

To date no native organisms have been found boring into or specifically feeding on large diameter roots, and this is possibly an empty niche. However, in arthropod surveys it is difficult to generalize on negative evidence, i.e., I can only say I have not found it, not that it does not exist. As explained by Janzen (1977) natural functioning ecosystems have few if any empty niches unless there is a major new disturbance, such as that created by an exotic species.

Even though 15 exotic species have colonized Kazumura Lava Tube, with one exception (snare building predators) they do not appear to have invaded the niches to a great extent.

On the younger flows on Hawai'i Island the troglobites have a wide distribution, but many lowland troglobites have not been found above 1000 to 1500 m where other species often occur. Roots are more important in higher caves. The few lava tubes on Maui are significant because their fauna provides a control group for Hawai'i Island studies. At least six native groups have independently evolved troglobitic species on the two islands.

Most continental troglobites are considered relicts of past climatic changes, especially glaciation and changes in sea level (Vandel 1965; Barr 1968; Mitchell 1969). However, many of the Hawaiian troglobites have close surface relatives still extant. Three such species pairs, Caconemobius varius--C. fori; Oliarius polyphemus --O. inaequalis; and Nesidiolestes ana--N. selium have been recognized (Fennah 1973a; Gagné & Howarth 1975; Gurney & Rentz 1978; Howarth 1979). This strongly suggests that troglobites are relicts only if the surface species have become extinct, not that they become caveadapted after extinction of the surface population. There are many examples of adaptive radiation among continental cave animals, but most apparently are true relicts due to the more complex geological history of the continents.

Cave Perturbations and Maintenance Trends

Continental caves are often viewed as islands and their ecosystems share an apparent fragility in response to perturbations. Cave ecosystems on islands may be in double jeopardy and several of the newly discovered arthropods are candidates for endangered species status. What then is the future of this unique ecosystem, not even recognized before 1971? If perturbations had caused its demise sometime during the last 200 years, biologists would have continued to believe no such fauna had ever existed in Hawai'i.

On Hawai'i Island there are still many avenues of dispersal between lava tubes and continual new flows can be expected; therefore, one can expect the survival of the cave fauna, barring any major catastrophies. On the older islands of Maui and Kaua'i the caves are eroded remnants, many of the avenues of dispersal are closed through erosion, and the cave animals lead a tenuous, threatened, or endangered existence.

The major perturbations facing the Hawaiian cave ecosystems are as follows: (1) destruction of the forest by grazing animals, fire, exotic plants, agriculture, and urbanization; (2) creation of new entrances and increased siltation and filling of caves by the erosion resulting from the above activities; (3) colonization by exotic animals; (4) use of caves for refuse disposal; and (5) direct disturbance by human visitation.

(1) Since the main energy source is plant roots, the destruction of the overlying forest removes this energy source. The obligatory primary consumers die off rapidly and the food web shrinks to a few scavengers and predators feeding on accidentals. A few primary consumers, notably Schrankia and the millepede, can switch to some exotic root species.

(2) Troglobites are restricted to the true dark zone where the relatively constant environmental conditions are maintained. New entrances introduce surface climatic influences and the cave

fauna is destroyed. Further, the erosion of the surface causes rapid filling of the voids in the lava and eventually the cave itself.

(3) The introduction of exotic species, or biological pollution, is perhaps the most insidious perturbation because it is normally irreversible and it often pervades the ecosystem in unforeseen ways. The impact of exotic species will be discussed below.

(4) Using caves for refuse dumps hastens the filling of the cave and introduces large amounts of food that alters the cave food web in several ways. (a) In relatively closed caves it can foul the air and kill the inhabitants. (b) By composting it can raise the cave temperature and dry the cave. (c) Most importantly, it often allows the colonization of the cave by opportunistic scavengers and predators. The high populations of these being supported on refuse can swamp the endemic biota.

Kaua'i has few extant lava tubes and the two known troglobites are among the most bizarre discoveries to date. Regrettably, the fields with the largest caves known on Kaua'i were covered by 5 m of sugarcane bagasse shortly before I visited the area. The caves are now gone, the fauna extinct, and no one will ever guess what that fauna might have been!

The entrance to Offal Cave, a relatively large lava tube on Haleakala Volcano, Maui, was used as an offal pit by the local slaughterhouse, and the tallow, rotting bones, and other garbage are piled high near the entrance and scattered throughout the downslope portion of the cave. The cave is no longer used for this purpose, but even now the cave ecosystem approaches that reported for large bat caves in tropical continental areas, where a huge amount of animal matter is introduced into the cave and supports a large population of many troglophiles. In Offal Cave these troglophiles are almost all exotic carrion feeders, scavengers, and predators, including such groups as cockroaches, earwigs, ants, moths, spiders, millepedes, and isopods. This is the only cave where many of these organisms have invaded any significant distance from the entrance, and it is assumed that it is the rich, novel food supply that allows them to colonize the cave environment. Only one endemic troglobite, the omnivorous cricket <u>Caconemobius howarthi</u>, occurs in this section of the cave.

Unfortunately, grazing has destroyed all native trees over Offal Cave and no roots now penetrate into the deep cave, so that it remains hypothetical whether other troglobites may have survived the influx of offal and associated biota if the rest of the ecosystem were intact. I believe most would not have survived, as such a large amount of organic matter would have heated the cave and dried or otherwise affected the environment. Such a large influx of exotic predators, sustained by the high population of exotic scavengers, also would have preyed on any cave species so that few endemics would have survived.

(5) Caves are fragile ecosystems and, like other discrete geologically defined habitats such as montane bogs and sand dunes, are easily disturbed by human visitation. Normal weathering processes are so changed and attenuated that even footprints can remain for centuries. In Hawai'i careless or destructive visitors kill or break tree roots, mark walls, litter the cave, and trample animals and their habitats. Tobacco smoke is a strong insecticide and smoking in the enclosed cave environment may be lethal to the fauna. The heat from both the body and a torch, if used, can dry the cave. Any smoke also introduces a large number of condensation nuclei to the saturated cave atmosphere. Littering is related to the using of caves as refuse dumps as discussed above. Cave visitation by the public should be discouraged until adequate protection of sample caves and ecosystems is assured.

Impact of Exotics

Many of the arthropods recently introduced by man, especially household pests and soil forms coming in with plant materials, have successfully colonized certain Hawaiian lava tubes. Such animals as the cockroaches, centipedes, millepedes, isopods, spiders, and other groups have been successful in lowland caves. Some of these exotics have surely altered the ecology of the caves, but it is unknown whether any replaced native species in the cave ecosystem. This is the region most disturbed by man. Many exotic species of roots penetrate these caves and mostly exotic species occupy these exotic niches. These are also the caves littered by visitors and used for dumps, as explained above.

Exotic scavengers also exploit the dead accidental exotic mammals (roof rat and mongoose) in Kazumura Cave. Barr and Kuehne (1971) reported a similar phenomenon in Mammoth Cave, Kentucky. They felt that litter from human activities has allowed the colonization of the cave by troglophiles that would not otherwise be able to do so.

Of the nine niches found in Kazumura Lava Tube the two predatory niches showed the greatest intrusion by exotics, followed by the saprophagous niches. In this cave only one species of root is present and so restricts potential phytophagous invaders. With an increase in species diversity there is a greater chance of an exotic or native species finding a suitable niche.

Thus those secondary and tertiary consumers that are generalists have the highest diversity of prey or food to choose from, and it follows that these niches would have the most species, both native and exotic, in most habitats. The invasion by an exotic does not imply that there had been an empty niche but that the invader was able to create one.

One exotic spider, *Nesticus mogera* from Japan, is common in mid- to high elevation caves on Hawai'i Island where its sloppy inverted webs are found between adjacent protuberances and in cracks in the walls in nearly the same situation as one sometimes finds the rare troglobite Erigone stygius. Both species are about the same size and both build similar sized webs. Although their webs are quite different, they probably capture similar prey. Even though N. mogera may not be as well adapted to the cave environment as E. stygius its cave population is constantly being augmented by individuals from surface habitats. As the prey is depleted the native spider loses. This circumstantial evidence implies that N. mogera is replacing the endemic species.

Other exotic troglophiles have not colonized Hawai'i's caves. For example, the predatory snail Euglandina rosea is a common troglophile in its home region in Florida. In Hawai'i its shells are common in low to mid-elevation caves but apparently the absence of both calcium for its shells and suitable prey have prevented this species from colonizing island caves. Other examples from Offal Cave are discussed above.

With one exception exotic trogloxenes have not yet become established. Attempts to introduce cave bats to Hawai'i in the 1920's were unsuccessful (Tomich 1969). The Edible Nest Swiftlet was released in 1962 and is now established in a small area on O'ahu (Shallenberger 1976).

Five main groups of trogloxenes exist in the world. Bats and rhaphidophorine crickets are nearly worldwide in caves except at high latitudes and on a few oceanic islands. Cave rats (Neotoma spp.) are widespread in North America. The Oilbird (Steatornis caripensis) inhabits some Neotropical caves, and certain Swifts (family Apodidae) nest in caves of the Old World tropics. These groups carry in organic matter as food, excrement, nesting material, and dead bodies.

The advent of trogloxenes in Hawai'i will result in a major new energy source in the caves and the establishment of a new food web, drawing almost entirely on exotic organisms for its cycle.

Had a trogloxene colonized Hawai'i naturally before man, the cave ecosystem would certainly have been greatly altered, but native species would have eventually adapted to exploit the new niches. The present situation is quite different, as a great many potential exotic troglophiles that live in guano caves elsewhere are already established as inquilines of man or his domestic animals or as soil animals. These species will be able to invade and flourish in Hawai'i's caves when a food source is there, and few native animals will have a chance to adapt to the new conditions. A preview of this phenomenon was described above for a cave that was used for an offal dump, and the ecosystem was drastically altered with only one native species surviving.

I suggest that the apparent fragility and instability of island ecosystems when compared to continental ecosystems is more related to the degree, type, or harshness of the perturbation, than to some inherant weakness in the workings of the system. Evolution dictated that island ecosystems functioned well before the current onslaught. It is true that given the disharmonic nature of island biota, those missing groups that exploit their environment in an innovative way will drastically alter the island ecosystem when they are introduced. Examples are troglo-xenes in Hawai'i's caves and grazing mammals which convert forest to grassland. But these groups were missing once on the conti-nents, too. Did not the forests of the eastern great plains of North America give way to the bison and man, as did the eastern Mediterranean forests to the goat? Most examples on the conti-nents have been obscured because of the complex geological and evolutionary history there.

One of the reasons islands are so interesting biologically is that they have not had as complex a biological and geological history as the continents. Islands can be studied as experi-mental controls for the evolutionary and ecological processes which are occurring but are obscured on the continents.

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