A COMPARISON OF VOLCANIC AND KARSTIC CAVE COMMUNITIES

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ABSTRACT

The communities of cave-adapted animals recently discovered in lava tubes and tropical caves rovide systems to independently test evolutionary theories developed from historic biospeleological studies in temperate limestone caves. Limestone caves are usually old, deep, large, three-dimensional mazes, with few mesocaverns and subject to complex geological history often including uplift, folding, and subsidence. Compared to limestone caves, lava caves are usually younger, shallower, smaller, less complex mazes, with more abundant mesocaverns and with a simpler history. In spite of these major contrasts resulting from differences in parent rock and mode of formation, specialized subterranean animals living in both lava and karstic caves display remarkably similar adaptations, indicating that selection pressures and ecology must be similar. Indeed, there are important ecological similarities. Once beyond the influence of entrances, the physical environment in subterranean habitats is perpetually dark, humid, and nearly isothermal; lacks most environmental cues; and often contains lethal or sublethal gas mixtures and wet barren rocky substrates. Even though the types and sources of food vary among regions and caves, the difficulties of finding food resources as well as finding mates in dark three-dimensional mazes are similar. For both rock types, numerous cave-sized and smaller passages exist that have no entrance allowing access to humans, and also at least some of the surface over both is often barren with food resources sinking into subterranean voids out of the reach of surface species. Troglobites evolved to exploit these resources in the harsh subterranean environment. Because of their different geological histories, lava and limestone cave communities may accumulate and lose species differently over time. In limestone caves, succession progresses downward, with younger habitats deeper below the surface. Succession in lava tubes is opposite, with younger habitats near the surface and older habitats deeper. New lava flows continually rejuvenate aging cave habitats in volcanically active areas, allowing for specialized species to occur in exceptionally young caves.

INTRODUCTION

These are exciting times in biospeleology, as the discoveries of specialized cave animals in lava tubes are expanding our understanding of cave biology. The studies being conducted in the caves of the Canary Islands are at the cutting edge of this research. Thus, it was especially fitting that the 7th International Vulcanospeleological Symposium was held there.

I am often asked to contrast the ecology and evolution of cave faunas in limestone and lava caves. Of course, our understanding of lava tube biology has only recently begun to catch up to what's known for limestone caves, but some differences and similarities have emerged that could shed light on the question. Certainly, the striking similarity of morphological features among obligate cave animals, no matter what the parent rock, indicates that some fundamental evolutionary principles must be involved in their origin. In this paper, I compare the ecology of obligate cave species in limestone and lava caves, focusing especially on terrestrial systems.

HISTORY

Obligate cave animals were known to the ancients and to science very early. Formal cave biology studies began in Europe more than a century ago following the discovery of underground lakes in caves.

Since limited water resources in karst terrains restrict economic development, cave hydrology became an important science. The subsequent discovery of many bizarre cave-adapted animals spurred ecological and evolutionary studies. Cave animals were also found during explorations and efforts to convert caves to tourist attractions.

Until recently, most underground biological studies were done in temperate limestone caves (Vandel 1965, Barr 1968, Culver 1982). The reasons for the early exclusion of lava tubes are probably complex but relate more to the relative proximity of karst areas to urban scientific centers in Eastern North America and Europe and to preconceptions and fears of volcanoes than to real biological differences. A few obviously cave-adapted animals were known from lava caves and other rock types, but they were considered exceptional phenomena and not indicative of general principles (e.g., Barr 1968). Interestingly in Japan, where limestone and lava caves both occur near science centers, remarkable cave animals were found in lava tubes beginning in the late 1930s (Torii, 1960; Ueno, 1971). However, even these discoveries by Japanese biologists were largely discounted by most mainstream cave biologists.

This parochial view of nature still plagues science. The maxim «If I didn't believe it, I wouldn't have seen it» is still all too true. Thetake home message from this paper can be summarized as: «Assume nothing in evolutionary biology»!

Since the early 1970s, there has been a revolution in cave biology following the rediscovery of the lava tube fauna in Japan; the discovery of lava cave faunas in Hawaii, Galapagos, Canary Islands, North America, and elsewhere; and the discovery of similar faunas in fractured rock terrains of diverse types, and of course in the tropics (Ueno, 1971; Howarth, 1983; Juberthie, 1983). These faunas provide systems to independently test the evolutionary theories developed from the marvelous and pioneering historic biospeleological studies done in temperate limestone caves.

FORMATION

Limestone

The cave ecosystem is rigidly defined by its geologic setting; thus, if we understand the formation of caves and associated subterranean voids, we can better understand the origin and ecology of cave communities. Limestone cave formation can be complex and related to chemical, climatic, geologic, and hydrologic forces, acting over very long time scales (White et al., 1995). Limestone is generally a mechanically durable rock; however, calcium carbonate, its principal component, dissolves in acidified water.

In near surface environments, this acidity is usually derived from dissolved carbon dioxide. In limestone areas, caves and karst landforms result from the interplay between the strength of limestone, which resists mechanical erosion, and its solubility, which allows groundwater to excavate the rock from within. Tectonic uplift and downcutting by erosion expose progressively deeper deposits to solution. This solution enlarges the larger developing passages since they can carry increasing amounts of water in a positive feedback system. Thus, voids enlarge and remain open as solution and erosion progress; but smaller passages often become plugged as groundwater uses the more efficient larger channels. Limestone is rarely pure calcium carbonate, and its solution usually leaves behind a sticky clay (affectionately called «slimestone»), which tends to fill the mesocavernous voids.

Limestone caves also tend to deepen with time due to erosion and downcutting, which lowers the water table, while remnant sections of older caves are abandoned as upper level passages, which collapse and eventually erode away. Thus, cave habitats in limestone are usually continuously available for colonization by cave animals, but these habitats become progressively deeper with time. Active passages can be 5 or more million years old, but the habitat can be available for much longer. During their long existence, they can be modified by geologic processes, such as tectonics and climatic change, which may alter their habitability (Barr, 1968; Ford, 1978; Culver, 1982).

Limestone caves can have complex shapes with deep shaft entrances, that allow food energy to reach deeper passages quickly. Dissolved limestone can reprecipitate, creating the well-known, spectacular formations. This dual edged sword of solution and reprecipitation can change the shape of a passage and thereby the air flow within it, so that passages once open to desiccation can be isolated from external climatic conditions and vice versa.

Local climate greatly affects cave formation. Limestone solution is orders of magnitude faster in the tropics than in temperate regions, so that cave passages there may not be continuously available for

Active lava tubes are remarkably efficient insulators; at Mauna Ulu, they carried lava over 12 km from the vent to the ocean with only a 10° C loss of temperature (Peterson and Swanson, 1974). Thus, pahoehoe lava flows build and repair their own conduits or lava tubes, that then transport the lava great distances from the vent. This mechanism is now recognized as the major factor in building shield volcanoes (Peterson and Swanson, 1974; Peterson et al., 1994). It also means that pahoehoe flows can cover large areas and create abundant underground habitats for cave animals.

There are six major geologic differences between limestone and lava caves: age, size of voids, shape, aspect, role of water, and direction of development (Table I). These have different effects on cave communities. Age is one of the most conspicuous differences between limestone and lava caves. Thus, one would expect there to be significant differences in the degree of cave-adaptation among troglobites from different caves (Vandel, 1965; Barr, 1968), but such is not the case (Hoch and Howarth, 1989). Cave species can migrate from older to younger caves in both systems, so that their age may be much older than the cave in which they are found (Howarth, 1983). Hoch and Howarth (1989) found a much better correlation with the cave environment rather than with cave age for cave planthoppers in limestone and lava caves in Australia.

Voids:

Both limestone and lava contain extensive systems of interconnected voids, but initially lava usually has a much better developed system of shallow intermediate sized voids than limestone. These voids provide ideal habitats for obligate cave species, and colonization and evolution may be rapid in young lava flows (Howarth, 1993).

Shape and aspect:

Lava flows are roughly linear, running downslope from a fixed vent. Lava caves may be long and sinuous and have a great altitudinal gradient, but they are rarely more than a few tens of meters from the surface. The shallow nature means that plant roots and other organic material from the surface may grow or be transported into them. Young to intermediate aged lava tubes (that is, from 500 to 5,000 years old) often have relatively abundant food resources. Limestone caves are often more vertical with deep shafts. Food resources concentrate in deeper voids. Thus, cave communities may be deeper below the surface in limestone.

For both limestone and lava, where erosion is mostly vertical, a significant amount of food energy in surface environments over caves is transported into subterranean voids out of reach of surface organisms. Evidence for this loss is the presence in both terrains of barren rocky habitats with islands of vegetation, or vice versa. This food energy is concentrated by the terrain. Most leaf litter and organic material falls into cracks and pits; thus, litter and soil accumulate only slowly over areas with extensive underground voids.

Food resources:

Food energy enters caves in five ways: carried in by animals, plants, water, and gravity, and produced autochthonously by chemoautotrophs. The importance of each of these varies regionally, and is mostly similar in limestone and lava caves, except in two important aspects: transport by plants and water. Because lava tubes are often shallow, plant roots are often the most important food resource. Young lava has little soil, and pioneering geophilic plants must send their roots deep for water and nutrients. Plant roots are also much more important energy sources in most tropical cave ecosystems (in both lava and limestone) than in most temperate caves, but their importance in temperate caves may have been overlooked during the early biological studies there (e.g., see Vandel,1965; Barr, 1968).

Since sinking streams are a major factor in the formation and evolution of limestone caves and since they can carry large amounts of detritus, they are a major food provider in most karst areas. Sinking streams are rare in lava tubes, since detritus laden streams quickly fill and erode lava tubes. Streams occasionally occur in lava tubes, such as when a tube intersects a water table. Diffuse infiltration of rain water is important in both lava and limestone caves, and colloidal oozes from organic material deposited by percolating water can be common in young lava tubes.

Table I.- Comparison of Volcanic and Karstic Cave Habitats.

FACTOR	LAVA	LIMESTONE
*Cave Formation	Brief	Long-term & dynamic
*Geological History	Relatively simple	Often complex
Surface Environment		
Exposed barren rock	Often present	Often present
Surficial area	Variable	Variable
*Size of caves	Small to large	Small to very large
*Aspect of caves	Mostly horizontal	Horizontal to vertical
*Depth of caves	Mostly shallow	Shallow to very deep
*Medium-sized voids fill with time	Initially very abundant, Fewer than in young lava	
*Age	Older habitats deeper	Older habitats on top
*Individual cave	Young (1 a - < 500 ka)	Old (100 ka - > 10 ma)
*Habitat	Young to old	Usually old
*Succession	Usually upwards	Usually downwards
Food Sources		
*Plant roots	Often most important	Locally important
Trogloxenes	Important	Important
*Water transport	Limited importance	Often most important
*Acidentals	Probably important	Probably important
Gravity transport	Locally important	Locally important
Chemoautotrophs	Locally important	Locally important
*Location of food	Mostly shallow	Often deep
Environment		
Substrate	Wet rock	Wet rock
Humidity	High	High
Carbon dioxide	Sometimes high	Sometimes high
Temperature	Nearly isothermal	Nearly isothermal
Light	Dark	Dark
Form	3-D maze	3-D maze
Zones	Five zones	Five zones
*Water	Streams rare	Streams common
*Aquatic habitats	Relatively limited	Often abundant
Terrestrial troglobite adaptations		
Morphology	Similar in both lava and limestone	
Behavior	Similar in both lava and limestone	
Physiology	Similar in both lava and limestone	

Succession:

The different geology, food resources, and environment interact to affect succession in cave communities. In limestone caves, erosion and downcutting create newer cave habitats ever deeper within the limestone deposit, while older caves degrade and no longer contain deep zone environments. Water-transported food is also carried to the deepest passages. Thus, the cave community moves deeper with time (White et al., 1995). The situation is the reverse in lava.

New lava flows undergo succession as a mature forest develops on the surface. Pioneer plants arrive, and leaflitter and wind-borne debris slowly build a soil layer. Over time the geophilic pioneers drop out in favor of soil-loving species. This succession affects cave communities. As the pioneering vegetation establishes, a greater amount of food enters cave habitats, and the most diverse cave communities occur in young vegetated lava flows. Large deep passages are often wet with abundant dripping water, while shallow passages just below the surface are often dry because the abundant cracks allow airflow and evaporation to take place.

Accumulating soil slowly fills surface cracks and voids, limiting root penetration by the pioneering trees. The soil also captures and holds both nutrients and water, so that plants capable of growing in soil eventually replace the pioneering species. Much less water reaches deeper cave environments, and the larger cave-sized passages, especially those connecting directly to the surface, dry out. Much less food also enters the deeper caves, and the animals retreat further from entrances and into passages that still receive food. Curiously, the soil seals the surface, so that shallower cave passages now retain moisture. Some soil inhabiting roots can grow into these shallow voids. Thus, cave animals move with their environment upwards into shallower passages as succession progresses.

The rate of succession is related to the surface climate and floristic diversity. In dry and mesic habitats on Hawaii Island, the stages can be observed in flows from 100 to 10,000 years old. In rain forest climates, succession progresses very fast, so that some of the stages are obscured, with some cave species arriving within a decade after the flow, while caves less than 10,000 years old may appear barren. Older cave habitats in active volcanic areas, can be rejuvenated by later flows that cover part of the cave and reset both surface and cave succession to their beginning stages. Recent radiocarbon dating of lava flows on Hawaii confirm that young active volcanoes are extremely dynamic environments: the total surface area of Mauna Loa has been renewed at a rate of about 40% per 1000 years, while the renewal rate for Kilauea has been even faster, at nearly 90% per 1000 years (Holcomb, 1987; Lockwood and Lipman, 1987).

Environment:

The physical environment is similar in both limestone and lava caves; they are dark, three-dimensional mazes. In addition, caves are strongly zonal habitats. Five zones can be characterized by their abiotic and biotic environments: Entrance, Twilight, Transition, Deep Cave and Stagnant Air Zones (Howarth, 1993). The extent of each zone is governed by the location, size, and shape of the entrances and passages; however, the boundaries between the zones are dynamic. The deep cave and stagnant air zones usually occur only deep within caves or beyond a passage constriction such as an n-or u-shaped deadend passage, which trap water vapor and carbon dioxide. Only a few caves extend into the stagnant air zone, but it is hypothesized that this is the environment characteristic of the mesocaverns (Howarth and Stone, 1990). In both limestone and lava caves, obligate cave species are almost universally restricted to the two deeper zones, where the air remains saturated with water vapor. Many are found only in deadend passages beyond tortuous crawlways.

Synthesis:

In spite of the great contrasts in parent rock and mode of formation, specialized subterranean animals living in both lava and karstic caves display remarkably similar adaptations, indicating that selection pressures and ecology must be similar (Howarth, 1983; Huppop, 1986). For both rock types, numerous cave-sized and smaller passages exist that have restricted contact with the surface, and also the surface over both often has barren areas with food resources sinking into subterranean voids out of reach of surface species. Troglobites evolved to exploit these resources in the harsh subterranean environment; that is, they appear to be adapted to exploit medium sized subterranean voids — mesocaverns. Limestone caves are continuously present for long periods of time, and the cave habitat deepens with age. In limestone, whenever active cracks begin to plug from soil formation, litter, and vegetation, descending water will either keep them open or enlarge others to maintain the flow of water and food energy into ever deeper caves. In Hawaii, younger lava tubes only 500 to 1000 years old appear to harbor the most diverse faunas. Tree roots dangle into caves and supply food energy directly, as well as provide avenues for other food to enter deep caves. As the lava surface ages, the cracks fill with soil, roots, and litter, which prevents food and water from entering deep caves. Simultaneously, however, shallow cave passages become more sealed from the surface climate. Troglobites track their changing environment and move closer to the surface as the lava ages.

There are exceptions; where food does enter older caves such as in 600,000 year old Koloa Cave on Kauai and in 190,000 year old Bayliss Cave in Australia, cave animals can be found. While deep young passages that receive little food input, such as parts of 500-year old Kazumura Lava Tube on Hawaii, support few animals. Barr (1968) described a similar situation in Mammoth Cave, Kentucky, in which cave species were rare in the larger main passages but more common at the ends of truncated passages where food and moisture entered the passage.

Most of the world's cave species remain unknown to science. Recent discoveries show that significant faunas can be expected wherever a system of interconnected subterranean voids have been available with food for long enough time.

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