Great Basin Naturalist

Volume 42 | Number 3 Article 12

9-30-1982

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INVERTEBRATE FAUNAS AND ZOOGEOGRAPHIC SIGNIFICANCE OF LAVA TUBE CAVES OF ARIZONA AND NEW MEXICO

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Abstract.— A field survey in caves near Grants, New Mexico, and Flagstaff, Arizona, found only an exceptionally poor fauna of 14 species with no strong patterns of cave restriction. The faunal poverty is judged to be correlated with and influenced by the similarly impoverished boreal forests in nearby mountains. Species of flightless arthropods, suitable for cave colonization and restricted to cool-moist litter of boreal ("Hudsonian-Canadian Life Zone") forests, are apparently not now present in suitable, nearby mountain habitats. They may not have dispersed to all available montane sites from the Southern Rocky Mountains during glacial conditions. Either the forests did not exist as continuous dispersal corridors for the litter arthropods, or the fauna could not track the rate of spread of the forests.

The lava tube caves of the Colorado Plateau of New Mexico and Arizona (Fig. 1) are still inadequately explored. Lava tubes elsewhere, such as in the Pacific Northwest, Japan, Hawaii, and the Galapagos (Peck 1973, Howarth 1973), contain a very distinctive fauna. It is therefore possible that a specialized fauna exists in some of the lava tube caves of the Colorado Plateau.

The reasoning is based on previous work in some "Canadian-Hudsonian Life Zone" forests in the mountains of the southwest indicating an unsuspected diversity of invertebrates similar to those in caves (Peck 1978, 1980). The strongest hypothesis accounting for most of the elements in the temperate terrestrial cave faunal assemblage suggests they were derived from preadapted (montane) mesic forest litter inhabitants. These species probably encountered lower elevation and lower latitude caves during glacials (pluvials) when appropriate forest "life zones" occurred at lower elevations and latitudes. These populations were then isolated in caves during interglacials (interpluvials) (Barr 1967, 1968), survived in them, and presumably underwent population evolution.

Two areas in the southwestern United States contain lava tube caves that seem to ideally fit the prerequisites of faunal establishment and evolution. Field workers in July and August of 1975, 1977, and 1979 surveyed these lava tube caves near Grants, New Mexico, and Flagstaff, Arizona, and also examined many montane litter populations.

Field Sites

New Mexico.— A large volcanic field occurs near Grants, New Mexico (Thornbury 1965, Hunt 1956, 1974). The Bandera Lava Field, or Grants Malpais, contains numerous and extensive lava tubes (Hatheway 1977) at the foot of the Zuni Mountains (9100 ft elevation) and Mount Taylor (11,300 ft), a central-type volcano. The lava field biota is discussed by Lindsay (1951). The main lava flow is of late Pleistocene age and covers about 220 square miles, from about 8300 ft down to 6200 ft. The caves, occurring in habitats of Transition down to Upper Sonoran Life Zones (Fig. 2), are indicated on the Ice Caves 7.5 minute topographic quadrangle of the U.S. Geological Survey.

Many sites were sampled: Ice Caves, and six other cave-sink segments of the same cave system in Secs. 22, 23, and 26, T9N, R11W, on the continental divide at approximately 7800 ft; eight cave sections and sinks on the northern slope of Lava Crater, Sec. 25, T9N, R11W, at approximately 7800 ft; and eight cave segments and sinks in Sec. 33, T9N, R11W, including Truckett Guano Cave (Bat Cave), at about 7300 ft. The caves were judged, based on other comparable caves, to

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Fig. 1. Map showing distribution of Cenozoic igneous rocks on the Colorado Plateau. Pleistocene and Recent basalt lava flows with lava tubes are most common near Mount Taylor, New Mexico, and the San Francisco Mountains, Arizona (after Hunt 1974).

be suitable for invertebrates. Seemingly adequate food inputs, extensive dark zones, abundant moisture, and cool to cold temperatures (several have permanent ice) also supported the supposition. Only Truckett Guano Cave (with multiple entrances at different elevations and associated continuous air currents) is too warm and dry to contain cave-restricted faunas.

Additional litter surveys were made in epigean habitats of cool, moist, forested, talus slopes on Lava Crater and on Mount Taylor at elevations of 8500, 9000, 10,500 and 11,000 ft, as well as in the Guadelupe, Sierra Blanca, Manzano, Sandia, Santa Fe, Sangre de Cristo, and Magdalena ranges.

ARIZONA.— The San Francisco Volcanic Field, near Flagstaff, covers about 3000 square miles and is the second largest in the contiguous United States (Hunt 1956, 1974, Robinson 1913, Thornbury 1956). The oldest flows are 6.2 ± 1.2 million years by K-Ar dating (Colton 1967). The field is topped by Humphreys Peak (12,680 ft), which experienced extensive Pleistocene glaciation (Péwé and Updike 1976, Sharp 1942).

Fig. 2. Sink entrance to segment of lava tube system near Truckett Guano Cave, near Ice Caves, New Mexico, at 7300 ft elevation, in a pinyon-juniper-grassland community. During full glacial climatic conditions the area may have been covered by a boreal forest of spruce and fir.

The caves lie in extensive sheets of third-period eruptive basaltic lava (late Pleistocene to Recent). These sheets cover about 1200 square miles and are situated in a ponderosa pine-grassland (Transition Life Zone) at about 7000 ft (Fig. 3). The environmentally varied caves are described by Forney (1971), Hassemer (1962), and Ingold (1964). I found the following: Slate Lakes Cave had a temperature of 7 C. Kana-a Cave is too small, close to the surface, and warm (15 C) to contain a significant fauna. Sunset Crater Ice Cave, with permanent ice (air temp 1 C) and abundant organic matter, is heavily visited by tourists to Sunset Crater National Monument. Lava River Cave, also called Government Cave, is the largest, with about 3600 feet of passage. It seems well suited to contain a cave fauna. Some ice was present near the entrance talus slope, and the air temperature was 4 C and the relative humidity 94 percent 1000 feet inside. At the cave end the air temperature was 6 C and the relative humidity was 97 percent. Scattered thin accumulations of bat guano yielded no fauna in Berlese extraction nor did pack-rat fecal piles. Porcupine fecal piles are abundant and extensive, but, again, Berlese extraction yielded no fauna. Numerous small cheese and carrion baits along the length of the cave yielded no fauna in either 1977 or 1979. Lange (1956) found the remains of woodchucks (*Marmota flaventris*) in Lava River Cave. This species presently occurs no nearer than Kane County, Utah, across the Colorado River. This represents a postglacial regional extinction.

Mountain litter was sampled for fauna on Humphreys Peak, the Chuska Mountains, Mogollon Rim and the White Mountains, and the Kaibab Plateau.

Annotated Faunal List

Some New Mexican cave faunas are reported in Welbourne (1978), who is also preparing a report on the cave faunas of the limestone caves of New Mexico. The only Arizona caves to be fully surveyed for invertebrates are in the Grand Canyon (Peck 1980). In many of the collections reported below, species level determinations are not now possible. The following contains the standard terminology for cavernicolous animals (Barr 1968): troglobitic is obligately cavernicolous; troglophilic is facultatively cavernicolous.

Phylum Arthropoda

Class Arachnida

Order Acarina

Family Rhagidiidae

Undetermined genus and species. One specimen from Truckett Guano Cave. These are often found in cool and wet situations in forests and caves. Most species are troglophiles and have very wide ranges, but two troglobitic genera occur in Idaho and Washington (Elliott 1976, Zacharda 1981).

Family undetermined; mites in three families occur in guano in Truckett Guano Cave. These are currently under study by W. C. Welbourne.

Order Pseudoscorpionida

Undetermined species (immatures, possibly *Dinocheirus astutus* Hoff, Chernetidae); collected from sinkhole debris of a cave near Ice Caves. Commonly present in bat guano in Truckett Guano Cave.

Class Diplopoda

Order Julida

Family Nemasomidae

"Nemasoma" uta Chamberlin, W. Shear det. One specimen in caves near Ice Caves. Although certain species of millipeds are frequent cave inhabitants, this species is considered accidental.

Class Collembola

Order Entomobryomorpha

Family Entomobryidae

Tomocerus flavescens (Tullberg), K. Christiansen det. Several specimens were taken in caves near Ice Caves. The species is widespread across most of North America and is a common cave inhabitant (Christiansen 1964, Christiansen and Bellinger 1980).

Class Insecta

Order Diplura

Family Campodeidae

Metriocampa sp., L. Ferguson det. Four specimens of this troglophilic species were found in litter in caves near Ice Caves and in sink debris near Lava Crater. These are widespread soil inhabitants and are occasionally found in caves. Some species are troglobitic. Some generic distributions show east-west disjunctions.

Order Orthoptera

Family Rhaphidophoridae

Ceuthophilus sp. A few immature individuals were found in Truckett Guano Cave, Kana-a Cave, and Ice Cave. The genus is a common trogloxenic inhabitant of caves, which are used as daytime refuges or as hibernacula.

Order Coleoptera

Family Staphylinidae

Atheta sp. Several specimens were in moist litter in Truckett Guano Cave. This commonly troglophilic genus is often found in caves, but the species are wide ranging.

Family Lathridiidae

Enicmus sp. One specimen was taken from pack-rat dung in Slate Lake Cave entrance talus. These are scavengers on fungi and are often in decaying and moldy materials.

Order Siphonaptera

Undetermined fleas (possibly *Sternopsylla texana* [Fox]) were extremely abundant in guano in Truckett Guano Cave.

Order Diptera

Family Mycetophilidae

Mycetophila fungorum (DeGeer), R. Vockeroth det. Seven specimens were captured from the ceiling near the entrance of Slate Lake Cave. The species is widespread from Quebec to Alaska and south to Mexico.

Family Sphaeroceridae

Leptocera sp. A few specimens were in Truckett Guano Cave. These flies are commonly scavengers in caves and forest litter.

Family Ephydridae

A few undetermined specimens were found in Truckett Guano Cave. Flies in this family are occasionally scavengers on guano.

Discussion

The caves were initially judged to have good potential for harboring a community of cavernicolous invertebrates. Lava tubes in Oregon, Washington, and Idaho have a rich and highly evolved cave fauna, and a cave-evolved fauna exists in caves near the bottom of the nearby Grand Canyon (Peck 1973, 1980). Although the caves were found to appear to be environmentally suitable, how-

Fig. 3. Sink entrance to Lava River Cave, NW of Flagstaff at 7700 ft elevation, in a ponderosa pine parkland. During full glacial conditions the region may have been covered by a boreal forest of spruce and fir, but a diverse litter fauna may not have been present to occupy the subterranean habitats of the lava flows.

ever, the fauna was exceedingly impoverished and contained solely species that have peripheral ecological associations with caves. This raises the problem of explaining the lack of a fauna.

A number of possible reasons are suggested and discussed. These are: (1) Inadequate field work. This seems unlikely because of the number of sites visited, the time spent in searching, and the variety of sampling techniques used that have been productive elsewhere. Future work in the caves can test this supposition. (2) Present environmental unsuitability. This seems unlikely, judging from inspection of the habitats. No differences in the lava tube caves between the survey areas and those of the Pacific Northwest, with a rich fauna, are apparent. (3) Past environmental unsuitability of the caves. The caves, some now containing permanent ice, may have been even colder, more ice filled, and uninhabitable during the changed climates of the glacials (pluvials). If so, earlier occupations may have been pushed to extinction, so that only modern colonists are present. Periglacial climatic unsuitability of caves at certain times has been suggested for Illinois (Peck and Lewis 1977), Canada (Peck and Fenton 1977), and the Uinta Mountains of Utah (Peck 1981). Nevertheless, the presence of the well-developed cave faunas in Idaho and Washington, which also experienced equal or greater glacial rigors, does not support this idea. (4) Inadequate age of the caves. This is unlikely. All specialized lava tube faunas exist in caves of mid- and late Pleistocene age, and of even Recent age. It is obvious that the faunas have used the abundant cracks and crevices of the basalt flows to continually move into progressively younger caves (Howarth 1973). (5) Inadequate climatic change as a stimulus for biotic movement. This must be rejected. Abundant data on biotic elevational and latitudinal shifts are available (reviewed in Martin and Mehringer 1965, Van Devender and Spaulding 1979, Wells 1979). Pollen from lake cores (Whiteside 1965) and packrat midden analyses (Van Devender and Spaulding 1979) are but two analytical methods of documenting this in the southwest. (6) The absence of a suitable ancestral litter fauna. This seems the most likely remaining cause for a lack of cavernicolous species and is supported by my empirical field observations. The diverse, rich, and balanced fauna of many taxa of flightless litter arthropods, composed of harvestmen, spiders, pseudoscorpions, millipeds, mites, diplurans, camel crickets, beetles, etc., of many southwestern montane forests seems to be impoverished or has many taxa missing on Mount Taylor and the San Francisco Mountains. Quantitative field survey work in spring and fall field seasons (more appropriate for litter faunas than my midsummer sampling) can test this impression. Data are now too few to otherwise test this idea. The only distributional analysis of southwestern forest litter vertebrates is that of pseudoscorpions by Hoff (1959). The lack of epigean survivors of close ancestors of the rich invertebrate fauna of Texas caves (Mitchell and Reddell 1971) might seem to argue against this observation. The mesic forest connections of the past from central Texas to the southeastern United States, however, are well documented (Martin and Harrell 1957), and the present aridity must be considered to be too intense to have allowed epigean survival of most ancestral stocks in the cavernous regions of central Texas.

If the lack of litter-inhabiting ancestors is real, then there are interesting implications. These are based on the assumption that the now-disjunct distributions of many taxa of flightless forest-litter arthropods with narrow ecological preferences or tolerances are indicators of past forest connections or continuity (discussed in Lawrence 1953). My preliminary findings are that present-day litter arthropod distributions indicate that continuous boreal forests, suitable as dispersal avenues during full glacials (pluvials), existed from the southern Rocky Mountains of Colorado down both sides of the Rio Grande depression to at least Sierra Blanca and the Magdalena Mountains. Mount Taylor should have been on this corridor, but the lack of many litter invertebrates suggest that it wasn't.

The San Francisco Mountains of Arizona are isolated from the Kaibab Plateau and other forest faunal source areas in the north by the Grand Canyon and lowlands of the Colorado, Little Colorado, and San Juan rivers. Nevertheless they too should have been connected by the highlands of the Mogollon Rim and White Mountains through the Datil Section to the mountains (including Mount Taylor) on the west side of the Rio Grande in New Mexico.

Problems of water loss from cuticular abrasion in volcanic soils can severely restrict the diversity of arthropods that can live in it (Edwards and Schwartz 1981). I have not subjectively noticed this in the soil and litter faunas of many volcanic areas in which I have worked, however. Also, both volcanoes (but not their basal vents and flows) have been inactive since the mid-Pleistocene, and more than enough time has since elapsed for subsequent faunal and floral occupation.

The poorer faunas of Mount Taylor and the San Francisco Mountains may be indicators that there have been persistent and significant barriers between them and the more northerly faunal source areas. Present-day southwestern boreal forests are discontinuous in distribution. This is caused by intervening lowland regions with unsuitable temperatures and inadequate rainfall. Past glacial-pluvial temperatures and rainfall in the southwest are known to have been suitable for more widespread coverage by woodlands and other forest types at lower elevations than at present (Van Devender and Spaulding 1979, Wells 1979). The boreal forests were probably not all in continuous contact (in contrast to Martin and Mehringer 1965), however. The gaps may have been more easily crossed by boreal-forest plants than by litter invertebrates with lower dispersal abilities. Thus, the plants may have spread farther and faster than the invertebrates. For instance, long-distance dispersal (probably of seeds) has allowed an impoverished and disjunct boreal and tundra flora to reach the San Francisco Peaks (Moore 1965).

In conclusion, further survey work of the taxa and distribution of montane forest litter and cave-inhabiting invertebrates of the San Francisco Mountains, Zuni Mountains, Mount Taylor, and others may contribute to understanding questions of cave colonization. More importantly, they should contribute to more general questions of Pleistocene biogeography and the historical dynamics of the still poorly understood boreal forest "communities" of the southwest (see Harper and Reveal 1978).

Acknowledgments

Hana Kukal, Olga Kukal, Morag McPherson, and Jarmila Peck helped with the collecting in caves and mountain forests, thereby greatly increasing the efficiency and accuracy of the faunal surveys. Gerald G. Forney and Glenda Rhodes provided information on cave locations. Arthur M. Phillips III provided data on montane floras and Pleistocene vegetational changes. The Museum of Northern Arizona, Flagstaff, provided space for a field camp and Berlese extractions of litter samples. The manuscript was read by Andy Grubbs, William R. Elliott, Peter Price, Paul S. Martin, and three anonymous reviewers. Field support was from operating grants of the Canadian Natural Sciences and Engineering Research Council for work on the systematics and distribution of cave and litter faunas.

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