

Final Report:
**A BIOLOGICAL ASSESSMENT OF CAVES
IN LAVA BEDS NATIONAL MONUMENT**

Steven J. Taylor¹ and Jean K. Krejca²

¹Center for Biodiversity, Illinois Natural History Survey
1816 South Oak Street, Champaign, Illinois 61820

²Zara Environmental, 118 West Goforth Rd., Buda, Texas 78610



20 April 2006

Illinois Natural History Survey, Center for Biodiversity Technical Report 2006(6)

Prepared for:
Lava Beds National Monument, Attn: David Larson, Chief of Resources
#1 Indian Well Headquarters, Tulelake, CA 96134

Summary

Lava Beds National Monument (LBE) contains more than 500 lava tube caves and features and more than 28 miles of passages. In addition to their geological, anthropological and historical interest, the caves are home to a variety of cave-adapted organisms.

Here we report on a study in which twenty-nine (29) caves were inventoried for cavernicolous invertebrates between 2 June and 4 August 2005. Environmental data collected during the study shows that most of the lava tube caves examined have a dark zone varying in temperature from just above freezing to about 12 °C, where relative humidity varies from about 85 to 100 %. In 193 samples (hand collections, Berlese funnel samples, pitfall trap samples, or sight records), we recorded 1,511 specimens. Of the animals recorded, 22.6% were flies (Insecta: Diptera), 19.3% were springtails (Insecta: Collembola), 16% were spiders (Arachnida: Araneae), 12.2% were millipedes (Diplopoda), 11.7% were mites (Arachnida: Acari), and 5.3% were diplurans (Insecta: Diplura). A variety of other animal taxa make up the remaining 12.9%.

Two large troglobitic invertebrates that were commonly encountered are the millipede *Plumatyla humerosa* and the dipluran *Haplocampa* sp. Common and nearly ubiquitous springtails of the family Tomoceridae (probably *Tomocerus* spp.) are important members of the cave community, and account for more than half of the springtails encountered. Two mammal groups, woodrats (*Neotoma* spp.) and bats (Vespertilionidae) are especially important in bringing nutrients into these caves, and bacteria and fungi growing on their feces provide energy to other cave animals.

We discovered a terrestrial troglobitic isopod of the family Trichoniscidae that may be new to science and was rarely encountered. In addition, a troglobitic pseudoscorpion (Arachnida) was also discovered, and this species is almost certainly a new to science.

Richness of the taxa showed no discernable patterns with respect to their association with different lava flows, vegetational zones, or elevation. Cave resource managers at Lava Beds National Monument should take into consideration the unique cavernicole fauna of the caves when considering impacts of cave visitors, who comprise the primary threat to these animals. Future biological monitoring efforts should include timed area searches of selected caves, and we present evidence that suggests these might best be carried out by professional biologists. Further study is needed to understand the role of several of the most important cave inhabitants, including the millipede *Plumatyla humerosa*, the dipluran *Haplocampa* sp., and the woodrats (*Neotoma* spp.).

Table of Contents

Summary	2
Table of Contents	3
List of Tables	4
List of Figures	5
List of Appendicies	9
Objectives	11
Methods	11
Transect-based quadrat data	12
Meter data	12
Data collection	15
Laboratory work	16
Results and Discussion	16
Environmental conditions	16
Transect data	20
General collecting	24
Phylum Annelida: Class Oligochaeta	40
Phylum Arthropoda: Class Crustacea: Order Isopoda: Family Trichoniscidae	40
Phylum Arthropoda: Class Arachnida	41
Order Acari: mites	41
Order Araneae: spiders	42
Order Opiliones: harvestmen	43
Order Pseudoscorpiones: pseudoscorpions	43
Phylum Arthropoda: Class Symphyla	43
Phylum Arthropoda: Class Diplopoda: millipedes	43
Phylum Arthropoda: Class Chilopoda: centipedes	55
Phylum Arthropoda: Class Insecta	55
Order Microcoryphia: bristletails	55
Order Thysanura: silverfish	55
Order Ephemeroptera: mayflies	55
Order Diplura: diplurans	57
Order Collembola: springtails	59
Order Psocoptera: book and barklice	63
Order Thysanoptera: thrips	63
Order Orthoptera: Family Rhaphidophoridae: cave and camel crickets	64
Order Homoptera: Family Cicadellidae: leafhoppers	64
Order Lepidoptera: butterflies, moths, and skippers	64
Order Coleoptera: beetles	67
Order Coleoptera: Family Tenebrionidae: darkling beetles	68
Order Coleoptera: Family Scarabaeidae: scarab beetles	68
Order Coleoptera: Family Chrysomelidae: leaf beetles	68
Order Coleoptera: Family Staphylinidae: rove beetles	68
Order Hymenoptera: Family Apidae: bees	69
Order Siphonaptera: fleas	69
Order Diptera: flies	69
Order Diptera: Family Tipulidae: crane flies	71

Order Diptera: Family Mycetophilidae: fungus gnats	71
Order Diptera: Family Psychodidae: moth flies	71
Order Diptera: Family Chironomidae: midges	71
Order Diptera: Family Sciaridae: black fungus gnats.....	71
Order Diptera: Family Culicidae: mosquitoes	71
Order Diptera: Family Bombyliidae: bee flies	74
Order Diptera: Family Scatopsidae: minute black scavenger flies.....	74
Order Diptera: Family Syrphidae: flower flies	74
Phylum Chordata: Subphylum Vertebrata	75
Class Aves: Order Passeriformes: Family Hirundinidae: swallows	75
Class Aves: Order Strigiformes: owls	75
Class Mammalia: mammals.....	75
Order Rodentia: Family Cricetidae: <i>Neotoma</i> sp.: woodrat	75
Order Rodentia: Family Erethizontidae: <i>Erethizon dorsatum</i> : porcupine	75
Order Lagomorpha: Family Ochotonidae: <i>Ochotona princeps</i> : pika	78
Order Chiroptera: Family Vespertilionidae: bats.....	78
Order Chiroptera: Family Vespertilionidae: <i>Corynorhinus townsendii</i> (Townsend's Big Eared Bat)	81
Plants.....	81
Comparison of the Fauna of Inventoried Caves	82
Cave communities at Lava Beds National Monument	90
Training of NPS staff.....	94
Future monitoring and research	94
Acknowledgements.....	96
Literature Cited.....	97

List of Tables

Table 1. Summary of caves surveyed during this study, composition of field crews, and sampling dates.....	17
Table 2. List of taxa recorded from 29 caves at Lava Beds National Monument between 2 June and 4 August, 2005.	37
Table 3. Taxon presence absence at caves inventoried between 2 June and 4 August 2005 at Lava Beds National Monument.	85
Table 4. Cave groups based on regions delineated in Figure 72.	88
Table 5. Numbers of caves by zone indicated in Figure 72 (A), and by elevation/vegetation zone (B), in which taxa of special interest were found during the 2 June – 4 August 2005 bioinventory of caves at Lava Beds National Monument, California. Coda Cave is not included in this summary because we lacked location data for this site.....	91

List of Figures

Figure 1. Using aspirators to collect in Rollercoaster Cave, Lava Beds National Monument, California	13
Figure 2. JKK collects data from a 0.1 m ² quadrat while our field assistant, JoAnn Jacoby, records the data on field sheets.	14
Figure 3. Psychro-dyne ® psychrometer (large gray box), soil temperature probe (white, on right side), and barometer (bottom) used to collect environmental data during the 2 June – 4 August 2005, lava tube bioinventory at Lava Beds National Monument, California.	15
Figure 4. Relationship between 2 cm soil temperature and light levels, with data coded by name of primary field crew responsible for data collection	18
Figure 5. Relationship between relative humidity and light levels, with data coded by name of primary field crew responsible for data collection.	19
Figure 6. Percent of meter reading data falling within different ranges of light meter readings (A, n=123) and relative humidity readings (B, n=125).	21
Figure 7. Percent of data falling within different ranges of 2 cm soil temperature (A, n=111), and relationship between air temperature near ground level, 2 cm soil temperature, and available light (B).	22
Figure 8. Relationship between 2 cm soil temperature, relative humidity, and light (A), and approximate cave zones delineated on the basis of these metrics (B).	23
Figure 9. Light (Lux, note Log ₁₀ scale) readings in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).	25
Figure 10. Soil temperature (°F) at 2 cm depth in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).	26
Figure 11. Air temperature (°F) at 2 cm above substrate in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).	27
Figure 12. Relative humidity (%) at 2 cm above substrate in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).	28
Figure 13. Transect-based quadrat substrate moisture data for Spider Cave. A. Ceiling, B. Walls (average of left and right walls), C. Floor. Data collected 14 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).	29
Figure 14. Transect-based quadrat substrate moisture data for Nirvana Cave. A. Ceiling, B. Walls (average of left and right walls), C. Floor. Data collected 4 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).	30
Figure 15. Transect-based quadrat substrate composition data for Spider Cave. A. Ceiling, B. Walls (average of left and right walls), C. Floor.	31
Figure 16. Transect-based quadrat substrate composition data for Nirvana Cave.	32
Figure 17. Transect-based quadrat-derived evidence of animal life in Spider Cave.	33
Figure 18. Transect-based quadrat-derived evidence of animal life in Nirvana Cave.	34
Figure 19. Transect-based quadrat counts of animals in Spider Cave.	35
Figure 20. Transect-based quadrat counts of animals in Nirvana Cave.	36

Figure 21. General taxonomic distribution of animals recorded from 29 caves at Lava Beds National Monument, California, based on fieldwork conducted between 2 June and 4 August, 2005.....	37
Figure 22. Trichoniscid isopod in Maze Cave, Lava Beds National Monument, California.	40
Figure 23. A probable cave-adapted mite (Acari: Rhagidiidae) in Maze Cave (3 June 2005), Lava Beds National Monument, California.....	41
Figure 24. Humidity and light associated with records of Rhagidiidae found in lava tube caves in Lava Beds National Monument, California, 2 June – 4 August, 2005.....	42
Figure 25. An adult female of a commonly encountered reddish-brown spider thought to belong to the family Nesticidae, in Valentine Cave, Lava Beds National Monument, California...	44
Figure 26. A large basket-web spider in Maze Cave, Lava Beds National Monument, California.	44
Figure 27. A large basket-web in Maze Cave, Lava Beds National Monument, California.	45
Figure 28. A spider, perhaps <i>Cybaeus</i> sp. (Cybaeidae) commonly encountered under stones in dry to normal areas of caves, especially in the entrance and twilight zones.	46
Figure 29. Typical web configuration of the spider species picture in Figure 28 (perhaps <i>Cybaeus</i> sp.), in Rollercoaster Cave, Lava Beds National Monument, California.....	47
Figure 30. An unidentified minute green-abdomened spider encountered in several of the caves, here in Boulevard Cave, Lava Beds National Monument, California.....	47
Figure 31. A sheet web thought to belong to a spider in the family Linyphiidae. Maze Cave, Lava Beds National Monument, California.....	48
Figure 32. A pseudoscorpion from a cave at Lava Beds National Monument, California.....	48
Figure 33. A troglobitic pseudoscorpion from a Lyon’s Road Cave at Lava Beds National Monument, California.....	49
Figure 34. A symphylan on moss in twilight zone of Four Star Cave, Lava Beds National Monument, California.....	49
Figure 35. An unusual looking polydesmid millipede on moss in twilight zone of Four Star Cave, Lava Beds National Monument, California.....	50
Figure 36. <i>Californiulus</i> sp. (Chordeumatida: Paeromopodidae) in Caldwell Ice Cave, Lava Beds National Monument, California.	51
Figure 37. <i>Plumatyla humerosa</i> (Chordeumatida: Conotylidae), a common inhabitant of caves at Lava Beds National Monument.	52
Figure 38. Temperature conditions under which <i>Plumatyla humerosa</i> was recorded (n=81 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.....	53
Figure 39. Light and humidity conditions under which <i>Plumatyla humerosa</i> was recorded (n=81 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.....	53
Figure 40. Substrate upon which <i>Plumatyla humerosa</i> was recorded (n=130 specimens) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.	54
Figure 41. Centipedes (Chilopoda: Lithobiomorpha) from caves at Lava Beds National Monument, California.....	56
Figure 42. <i>Haplocampa</i> sp. (Diplura: Campodeidae) in Nirvana Cave, Lava Beds National Monument, California.....	57
Figure 43. Air and 2 cm soil temperature at sites were <i>Haplocampa</i> sp. (Diplura: Campodeidae) was recorded during our survey of caves at Lava Beds National Moneument, California, 2 June – 4 August, 2005.....	58

Figure 44. Light and humidity conditions under which <i>Haplocampa</i> sp. (Diplura: Campodeidae) was recorded (n=33 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.	58
Figure 45. Substrate upon which <i>Haplocampa</i> sp. (Diplura: Campodeidae) was recorded (n=56 specimens) at caves in Lava Beds National Monument, California, during field work conducted between 2 June and 4 August, 2005.	59
Figure 46. A springtail of the family Tomoceridae (probably <i>Tomocerus</i> sp.), a common inhabitant of caves at Lava Beds National Monument.	61
Figure 47. Light and humidity conditions under which Tomoceridae were recorded (n=48 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.	62
Figure 48. Air and 2 cm soil temperature at sites where Tomoceridae were recorded (n=49 samples) during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.	62
Figure 49. Substrate upon which Tomoceridae were recorded (n=88 specimens) at caves in Lava Beds National Monument, California, during field work conducted between 2 June and 4 August, 2005.	63
Figure 50. <i>Ceuthophilus inyo</i> (Orthoptera: Rhaphidophoridae) in Maze Cave, , Lava Beds National Monument, California.	65
Figure 51. Air and 2 cm soil temperature at sites where <i>Ceuthophilus inyo</i> (Orthoptera: Rhaphidophoridae) was recorded (n=21 samples) during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.	65
Figure 52. Light and humidity conditions under which <i>Ceuthophilus inyo</i> (Orthoptera: Rhaphidophoridae) was recorded (n=21 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.	66
Figure 53. Substrate upon which <i>Ceuthophilus inyo</i> (Orthoptera: Rhaphidophoridae) was recorded (n=24 specimens) at caves in Lava Beds National Monument, California, during field work conducted between 2 June and 4 August, 2005.	66
Figure 54. A moth, perhaps a Plume Moth (Pterophoridae), in the entrance of Catacombs Cave, Lava Beds National Monument, California. Accidentals, such as this moth, commonly wander into caves.	67
Figure 55. A rove beetle (Staphylinidae), in Rollercoaster Cave, Lava Beds National Monument, California.	68
Figure 56. A small dung-fly (Sphaeroceridae), in Rollercoaster Cave, Lava Beds National Monument, California.	69
Figure 57. Flies and mite in association with decomposing <i>Neotoma</i> guano pellet, in Rollercoaster Cave, Lava Beds National Monument, California.	70
Figure 58. A fungus gnat (Mycetophilidae) pupa suspended from the ceiling deep within Lyon's Road Cave, Lava Beds National Monument, California.	72
Figure 59. Air and 2 cm soil temperature at sites where Mycetophilidae were recorded (n=11 samples) during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.	73
Figure 60. Light and humidity conditions under which Mycetophilidae were recorded (n=11 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.	73
Figure 61. A black fungus gnat (Sciaridae) in Maze Cave, Lava Beds National Monument, California.	74

Figure 62. JoAnn Jacoby traverses a ledge above a large open pit and below an owl nest (probably great-horned owl, <i>Bubo virginianus</i> [Strigidae]) in Caldwell Ice Cave, Lava Beds National Monument, California.	76
Figure 63. Fungal growth on a single pellet of <i>Neotoma</i> sp. guano in Maze Cave, Lava Beds National Monument, California.	77
Figure 64. Woodrat (<i>Neotoma</i> sp.) nest in Catacombs Cave, Lava Beds National Monument, California.	78
Figure 65. Bat skeleton in Valentine Cave, Lava Beds National Monument, California.	79
Figure 66. Bat skull from Lyon’s Road Cave, Lava Beds National Monument, California.	79
Figure 67. Air and 2 cm soil temperature at sites where evidence of bats (open circles) and living <i>Corynorhinus townsendii</i> were encountered during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.	80
Figure 68. Light and humidity conditions under which evidence of bats (open circles) and living <i>Corynorhinus townsendii</i> were encountered at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.	80
Figure 69. Jean Krejca (left) collecting in the moss-covered entrance of Four Star Cave, while JoAnn Jacoby (right) takes notes.	81
Figure 70. The fern <i>Aspidotis californica</i> in a cave entrance at Lava Beds National Monument.	82
Figure 71. View of typical terrain at Lava Beds National Monument. Note collapsed lava tube segments in foreground.	83
Figure 72. Map of Lava Beds National Park showing major flows (black), areas in which caves were sampled (gray), major buttes (stars), and elevation contours (dotted lines).	84
Figure 73. Number of taxa recorded per cave in our 2 June – 4 August 2005 bioinventory at Lava Beds National Monument.	87
Figure 74. Mean number of taxa per cave by zones indicated alphabetically in Figure 72, versus percent of caves in that zone that were sampled by SJT and/or JKK during the 2 June – 4 August 2005 bioinventory of caves at Lava Beds National Monument, California.	88
Figure 75. Mean number of taxa per cave by elevation zones (corresponding to vegetation areas delineated by Lahr [1960]), versus percent of caves in that zone that were sampled by SJT and/or JKK during the 2 June – 4 August 2005 bioinventory of caves at Lava Beds National Monument, California.	89
Figure 76. Lava tubes can appear to be only barren bedrock devoid of life, as in this section of passage in Valentine Cave, Lava Beds National Monument, California.	92
Figure 77. A diagrammatic representation of cave zones commonly found at Lava Beds National Monument, and some of the organisms which can be found in these areas.	93
Figure 78. A tree root in the ceiling of Catacombs Cave, Lava Beds National Monument, California.	93
Figure 79. NPS staff (red helmets, Sean Dunn [left] and Robert Pleszewski [right]) listen to Steve Taylor [right] as JoAnn Jacoby prepares to take notes at the entrance to Valentine Cave, Lava Beds National Monument, California.	95

List of Appendices

Appendix A. Summary of data from Crawford (1998, in litt.) resulting from his 1989 bioinventory of ten caves at Lava Beds National Monument, California.	100
Appendix B. Calculation of relative humidity using wet bulb and dry bulb temperatures in combination with barometric pressure.....	103
Appendix C. Field forms used in data collection during the 2 June – 4 August 2005 bioinventory of lava tube caves at Lava Beds National Monument, California.	104

Lava Beds National Monument (LBE) contains more than 500 lava tube caves and features and more than 28 miles of passages. In addition to their geological, anthropological and historical interest, the caves are home to a variety of cave-adapted organisms. Cave environments often harbor rare, endemic species that are specifically adapted to the predictable conditions of underground habitats. These organisms are sensitive to perturbations including thermal and moisture fluctuations, pollutants, and impacts associated with visitation (trampling, litter, introduction of exotic species, etc.). As there is no primary energy source in most caves (absence of light), the cave community is also dependent on a healthy, functioning surface community (plants and animals above ground) as a source of nutrients.

Here we report on a study of the biota of caves in Lava Beds National Monument that provides 1) additional faunal surveys to supplement the taxon list of Crawford (in litt., 1998); 2) a collection of digital photographs of typical cave fauna which will facilitate visitor interpretation, field identifications, and future monitoring; 3) information on the distribution and abundance of cavernicoles in selected caves; and 4) recommendations for management of the cave fauna (e.g., visitation, biologically sensitive areas, etc.).

Some research has been done on the cave fauna of LBE. Sampling done in November and December of 1989 by Crawford (in litt., 1998) resulted in a preliminary list of at least 69 invertebrate taxa, including several troglobites (cave-limited species) or presumptive troglobites: 3 springtails (families Poduridae, Entomobryiidae, and Sminthuridae), 1 dipluran (*Haplocampa* sp.), 1 rhagidid mite, and 1 millipede (*Plumatyla humerosa* Loomis 1943, Chordeumatida: Conotylidae) (Appendix A). Ferguson (1992) mentions that he collected a *Haplocampa* species from Merrill Ice cave in 1982 which was a new species, but did not describe it. He (Ferguson 1992) also notes collections of campodeid diplurans from several other caves at Lava Beds National Monument (Catacombs Cave, Fern Cave, Lost Pinnacle Cave, and Merrill Ice Cave) by Rod Crawford in 1989. Holsinger (1974) described a subterranean amphipod (*Stygobromus mysticus* Holsinger 1974, Amphipoda: Crangonyctidae) from Siskiyou County at Greenview, but the habitat for this species is "possibly a well", and thus this animal might not be a part of the lava tube fauna of this area. Finally, Rudolph et al. (1985) produced an unpublished manuscript on the cave fauna of California, which also lists the troglobitic millipede *Plumatyla humerosa* as occurring in Siskiyou County, California. Crawford (in litt., 1998), reporting data from surveys of ten lava tube caves, indicates that a number of other arthropods – mainly springtails, spiders, mites, flies, and beetles – are troglaphiles in the caves of LBE. The presence of several cavernicoles within caves of LBE suggested that a more structured examination of the caves in the monument might yield valuable new information. Below, we provide additional records for many of the species previously reported from LBE, as well as more detailed information on microhabitat and substrate associations for these taxa.

Elsewhere in the United States, lava tube faunas are better studied. In New Mexico's El Malpais National Monument, a set of 6 lava tubes were sampled in each season over a period of two years to yield an extensive faunal list that included six troglobites and many other cavernicoles (including troglaxenes and troglaphiles). As a result of identifying where the most diversity of organisms occur within the cave, these areas were highlighted for conservation efforts (Northup and Welbourn, 1997). Other papers highlight specific taxa that occur in lava tubes in the western United States, including Benedict (1979), Briggs (1974) and Genter (1986). An inventory of lava tubes on Mt. St. Helens (Senger and Crawford 1984) was reported on, in addition to an earlier review of lava tube fauna of the western United States (Peck 1973). Peck

(1982) also looked at the zoogeographic significance of lava tube caves in Arizona and New Mexico.

By far, however, the most studied lava tube fauna in the United States occurs in Hawaii. Many authors cover various systematic groups in detail (Barnard 1977, Bellinger and Christiansen 1974, Brindle 1980, Bousfield and Howard 1976, Fennah 1973, Gagné and Howarth 1975a and 1975b, Gertsch 1973, Gurney and Rentz 1978, Hoch 2002, Liebherr and Samuelson 1992, Muchmore 1979, Schultz 1973, Wirth and Howarth 1982, Zacharda 1982) and Howarth (1981, 1982, 1987a, 1987b, 1991) analyzed the ecology and evolution of various taxa.

The LABE Cave Management Plan will be strengthened by the inclusion of the more detailed information about cave communities presented herein. Knowing where the rare species occur, where the greatest species diversity occurs, and the ecological relationships that characterize the community of cavernicoles can only improve the quality of decisions made about priorities for cave conservation and management. In addition, this inventory and ecological information can help direct monitoring plans that will allow the park to detect changes that may be resulting from cave usage or other surface activities. These kinds of data have been effectively incorporated in to management plans elsewhere in the National Park Service (e.g., Mammoth Cave National Park, Carlsbad Caverns National Park, Sequoia and Kings Canyon National Parks), providing land managers with important tools facilitating the long-term preservation of these fragile environs.

Objectives

The objectives of this study are to: 1) conduct a biological inventory of cave-adapted macroinvertebrate species in ten caves at LABE during a single field visit; 2) train accompanying LABE personnel in techniques for making biological collections in caves of LABE; 3) review literature pertinent to the biota of caves at LABE; 4) develop a preliminary list of taxa based on our collections; 5) create a collection of color digital images of all common cave-dwelling invertebrate taxa of LABE; 6) identify current and potential future threats to the cave invertebrate communities of the ten caves sampled in LABE; 7) suggest methods to lessen threats to the cave invertebrate communities in the ten caves; 8) recommend specific cave invertebrate monitoring techniques for the ten caves; and 9) identify areas of speleology, especially pertaining to biospeleology, needing further research at LABE. All information associated with the above objectives will be given to LABE and will be included in the Final Report

Methods

Cave maps, localities and other pertinent information were obtained from LABE personnel, and a Scientific Research and Collecting Permit was obtained prior to the initiation of field work.

A variety of field collecting techniques are available for cave macroinvertebrate studies. Sampling generally was qualitative in nature, with a focus on maximizing diversity of taxa and habitats within each cave. The primary technique was hand collecting, which was facilitated by

use of forceps, aspirator (Figure 1), or a fine paintbrush as conditions and taxa dictated (aspirator for fast-moving taxa, forceps for taxa too delicate for hand collecting, paintbrush for smallest and most delicate taxa). For aquatic habitats, a baster (used to collect larger aquatic taxa, such as amphipods and isopods) or fine mesh net (used to dip out samples of debris or larger organisms and to wash sediment in search of benthic macroinvertebrates) would have been used if these habitats had been available. The only non-frozen water we sampled were tiny drip pools on bedrock floors or breakdown – these contained only epipluestic (on top of surface film) fauna, which were collected with an aspirator. Baiting methods (with and without the use of pitfall traps) were utilized only to a limited extent. Although baiting is a very desirable method, it generally requires two visits to a cave. Samples were collected into 70% ethanol in nalgene containers. Some material was collected live for photography and was preserved later the same day or the following day.

Our sampling focused on troglobitic species, but invertebrates that are troglonexes or troglaphiles also were collected. Accidental taxa – typically most abundant in the entrance and twilight zones of caves – were not a major focus of this study. Collections of cave-adapted taxa were limited only to representatives of each taxon when additional collecting could significantly impact the cave community. Field collections focused on macroinvertebrates – no special effort was made to collect fungi, bacteria, protists, nematodes, and other microfauna. Vertebrates were not collected, except for some bones.

Transect-based quadrat data

In addition to the qualitative data collection described above, we used a quantitative quadrat sampling method in two of the caves, Nirvana Cave and Spider cave. A 0.1 m² quadrat (0.316 m x 0.316 m) was used to survey fauna along a transect starting at the cave entrances and proceeding into the dark zone, with quadrats placed at 2 meter intervals. This technique (Figure 2) provides a baseline for density estimates and microhabitat information.

Meter data

We used a temperature probe to measure soil temperature at 2 cm depth. A battery powered psychrometer was used to obtain wet bulb and dry bulb temperatures, and a barometer reading was taken in association with the psychrometer readings (Figure 3), allowing us to accurately determine relative humidity (Appendix B). Most commercially available meters, such as Kestrel ® brand RH/wind/temperature meters or Onset HOBO ® RH Temp loggers, do not provide accurate humidity measurement above 80-90% humidity. As cave humidities are often in the high 90's, we used the Psychro-dyne ® psychrometer. In addition, we used a Kestrel ® RH/wind/temperature meter to record conditions on the surface adjacent to the cave, and a light meter to measure light levels (lux) at the entrance and progressively deeper inside of the caves. The light meter sensitivity was poor at low light levels, with the lowest possible readings being “1 lux” and “<1 lux”. We coded “<1 lux” as 0.2 lux (arbitrarily, but based on the knowledge that lux functions on a log₁₀ scale). When the light meter detected no light whatsoever, we coded these data as 0 lux.



A



B

Figure 1. Using aspirators to collect in Rollercoaster Cave, Lava Beds National Monument, California. A. SJT sampling woodrat guano using a traditional aspirator (photo by Jean Krjeca). B. JKK collecting from the ceiling using an aspirator often used for collecting spiders – note lavasicles on the ceiling to the right (photo by Steve Taylor).

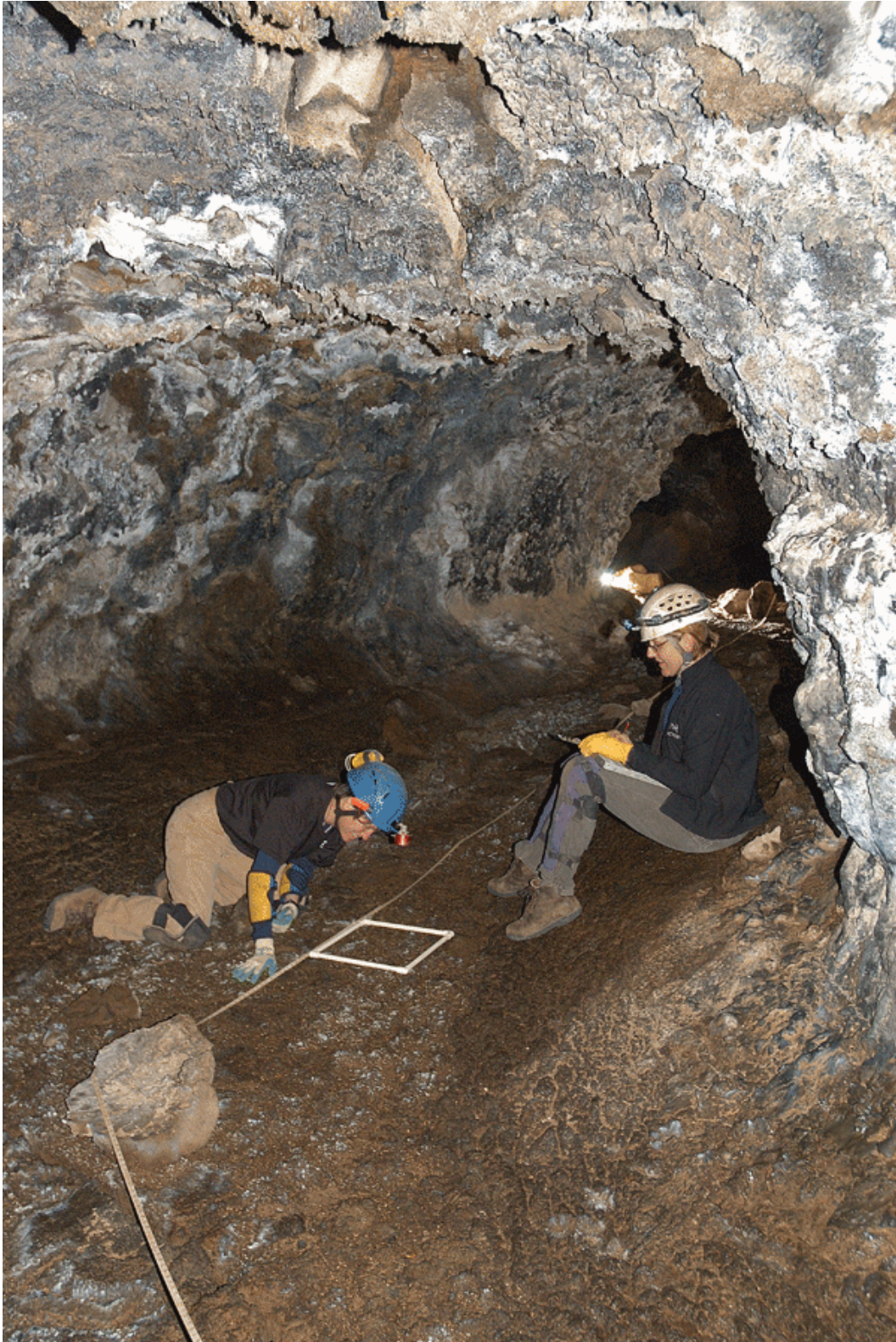


Figure 2. JKK collects data from a 0.1 m² quadrat while our field assistant, JoAnn Jacoby, records the data on field sheets. Note survey tape indicating transect line. Nirvana Cave, Lava Beds National Monument, California. Photo by Steve Taylor.



Figure 3. Psychro-dyne ® psychrometer (large gray box), soil temperature probe (white, on right side), and barometer (bottom) used to collect environmental data during the 2 June – 4 August 2005, lava tube bioinventory at Lava Beds National Monument, California. Photo by Jean Krejca.

Data collection

During our field visit (2-17 June 2005) we used standardized field forms (Appendix C) that we developed to record microhabitat association data for the collected specimens. At significant points in each cave (by zone: Entrance, Twilight, Middle+Dark), temperature and humidity measurements were recorded on the field forms. We made notes of differences in levels of human impact, presence of bats, ease of access, prior collections known from caves, and known cavernicole occurrences. Copies of the completed forms were provided to LABE at the end of the field sampling period. The field time also was used to discuss various aspects of cave biology with monument staff, including collecting techniques, general identification methods, and assessment of cave ecosystems and threats to that ecosystem. A powerpoint presentation was made to LABE staff near the end of our visit, and has been provided to the Chief of Resources at LABE. A collecting permit was obtained prior to the initiation of field studies. One volunteer field assistant, JoAnn Jacoby, assisted us with field work, as did David Larson, Robert Pleszewski, and Sean Dunn (all LABE staff). Additional specimens and meter data were collected by Robert Pleszewski and Sean Dunn between 28 June and 4 August 2005 (after our departure), and those data are included in this report. Caves visited twice include a preliminary trip by Robert Pleszewski and Sean Dunn (30 May, 1 & 2 June) to place pitfall traps. To provide a more complete synthesis of available knowledge on macroinvertebrates in lava tube caves at

LABE, we also summarize data previously reported by Crawford (in litt., 1998) from collections he made in ten caves at LABE in November and December of 1989.

Laboratory work

In the lab, material was sorted by taxon and curated in glass museum vials with Nalgene stoppers or screw-cap lids, with internal labels containing locality and habitat data. Vouchers of duplicate materials will be deposited in the collections of the Illinois Natural History Survey and the Texas Memorial Museum – both institutions have large, well-curated permanent research collections. Material that is currently being sent out to taxonomic experts should ultimately be deposited in one or both of these collections, except for limited material retained by specialists (a common practice among taxonomists). Vouchers of common cavernicoles will also be provided to LABE as a reference collection for the cave fauna of the park. Some taxa may be too rare to be provided for such a collection, but digital photographs of these taxa will be made available whenever possible. All material collected remains property of the monument, and thus museum specimens and material to be sent to appropriate specialists will be "on loan". All material collected will be identified as far as is feasible, to family for most insects, and at least to order for most arthropods. Identification of other phyla will generally be at least to the class level. All taxa photographs were made with a digital camera, and in most cases the photographer was Jean Krejca. These digital images will be provided to LABE with this Final Report.

Results and Discussion

Twenty-nine (29) caves were inventoried for cavernicolous invertebrates during the course of our field work (Table 1). For 18 of these caves, generally the longest caves we sampled, cave length data were available, and these averaged 1874.5 feet in length, ranging from just over 500 feet long to over 7,500 feet in length (the longest cave at Lava Beds National Monument). At least 8 of the caves we sampled are among the 20 longest at LABE, and all 18 of the caves for which we have length data are among the 64 longest lava tube caves at LABE. Thus, our study emphasized caves with significant length.

Environmental conditions

All of the caves sampled are lava tube caves, but environmental conditions in the caves varied from warm and dry in caves with multiple entrances and airflow, to cold and humid in caves with single entrances and a configuration that facilitated the accumulation of cold air and moisture at low spots in the cave. We collected data on temperature, humidity, and light at more than 120 locations throughout the 29 caves, and also collected these data at 20 stations at 2 meter intervals along a transect beginning at the entrance of two caves of quite different environmental conditions.

Both soil temperature (Figure 4) and relative humidity (Figure 5) were correlated with light meter data. However, when we examine data collected during the first part of the field work, when we (SJT, JKK, JJ) were present, and compare this to the data collected later, when RP and SD were collecting data, there is a distinct difference (Figures 4, 5), with the latter generally recording higher light levels, lower humidity, and warmer soil temperatures. These

Table 1. Summary of caves surveyed during this study, composition of field crews, and sampling dates.

Cave Name	Field Crew	Date
Big Painted Cave	Robert Pleszewski, Sean Dunn	1-Jun-05
	Jean Krejca, Steve Taylor, JoAnn Jacoby	5-Jun-05
Bulevard Cave	Robert Pleszewski, Sean Dunn	30-May-05
	Jean Krejca, Steve Taylor, JoAnn Jacoby	4-Jun-05
Caldwell Ice Cave	Jean Krejca, Steve Taylor, JoAnn Jacoby	12-Jun-05
Catacombs Cave	Robert Pleszewski, Sean Dunn	30-May-05
	Jean Krejca, Steve Taylor, JoAnn Jacoby	4-Jun-05
Coda Cave	Robert Pleszewski, Sean Dunn	7-Jun-05
Coral Reef Cave	Jean Krejca, Steve Taylor, JoAnn Jacoby	12-Jun-05
Cox Ice Cave	Robert Pleszewski, Sean Dunn	1-Aug-05
Craig Cave	Robert Pleszewski, Sean Dunn	27-Jul-05
Crazy Cave	Robert Pleszewski, Sean Dunn	28-Jun-05
Crystal Cave	Robert Pleszewski, Sean Dunn	2-Aug-05
Deep Cavern Cave	Robert Pleszewski, Sean Dunn	15-Jul-05
Fossil Cave	Jean Krejca, Dave Larson, Robert Pleszewski	17-Jun-05
Four Star Cave	Jean Krejca, Steve Taylor, JoAnn Jacoby	11-Jun-05
Lazaroff's Hole	Robert Pleszewski, Sean Dunn	20-Jul-05
Lyon's Road Cave	Jean Krejca, Steve Taylor, JoAnn Jacoby	13-Jun-05
Maze Cave	Robert Pleszewski, Sean Dunn	30-May-05
	Jean Krejca, Steve Taylor, JoAnn Jacoby, Robert Pleszewski, Sean Dunn	3-Jun-05
Merrill Ice Cave	Robert Pleszewski, Sean Dunn	1-Jun-05
	Jean Krejca, Steve Taylor, JoAnn Jacoby	5-Jun-05
Nirvana Cave	Robert Pleszewski, Sean Dunn	2-Jun-05
	Jean Krejca, Steve Taylor, JoAnn Jacoby	4-Jun-05
NSS #8851	Robert Pleszewski, Sean Dunn	19-Jul-05
Pearl Cave	Jean Krejca, Steve Taylor, JoAnn Jacoby	11-Jun-05
Post Office Cave	Robert Pleszewski, Sean Dunn	28-Jul-05
Rollercoaster Cave	Jean Krejca, Steve Taylor	10-Jun-05
Spider Cave	Jean Krejca, Steve Taylor, JoAnn Jacoby, Robert Pleszewski, Sean Dunn	14-Jun-05
	Robert Pleszewski, Sean Dunn	14-Jul-05
Township Cave	Robert Pleszewski, Sean Dunn	25-Jul-05
Upper Heppe Cave	Jean Krejca, Robert Pleszewski	16-Jun-05
Upper Thicket Cave	Robert Pleszewski, Sean Dunn, David Larson	4-Aug-05
Valentine Cave	Robert Pleszewski, Sean Dunn	30-May-05
	Jean Krejca, Steve Taylor, JoAnn Jacoby, Robert Pleszewski, Sean Dunn	2-Jun-05
Willy's Pipe Dream Cave	Robert Pleszewski, Sean Dunn	14-Jul-05

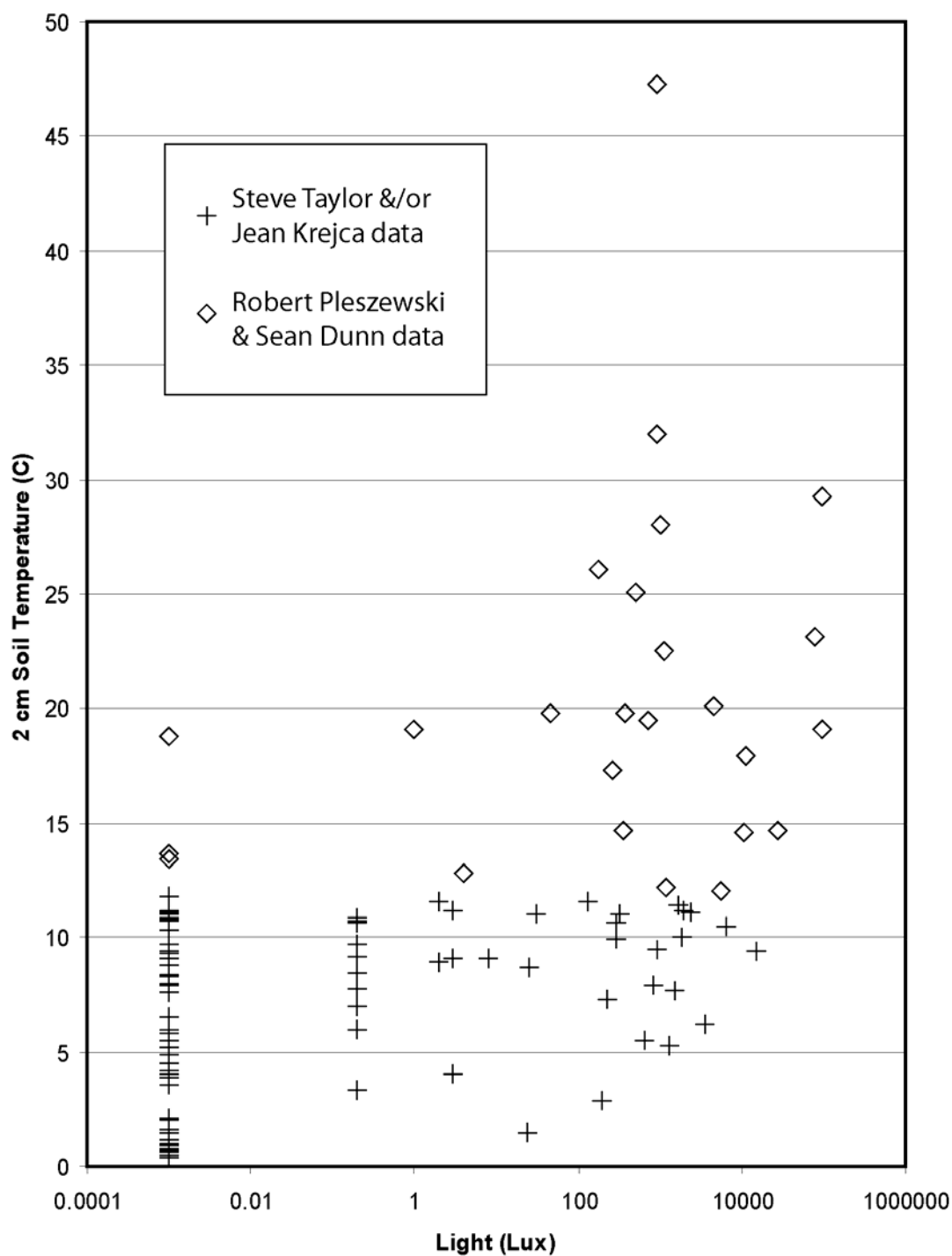


Figure 4. Relationship between 2 cm soil temperature and light levels, with data coded by name of primary field crew responsible for data collection. Data comprise all available sample meter readings, except transect data, obtained between 2 – 17 June (Taylor & Krejca) and between 28 June – 4 August (Pleszewski & Dunn) in 2005 sampling at lava tube caves in Lava Beds National Monument, California. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.

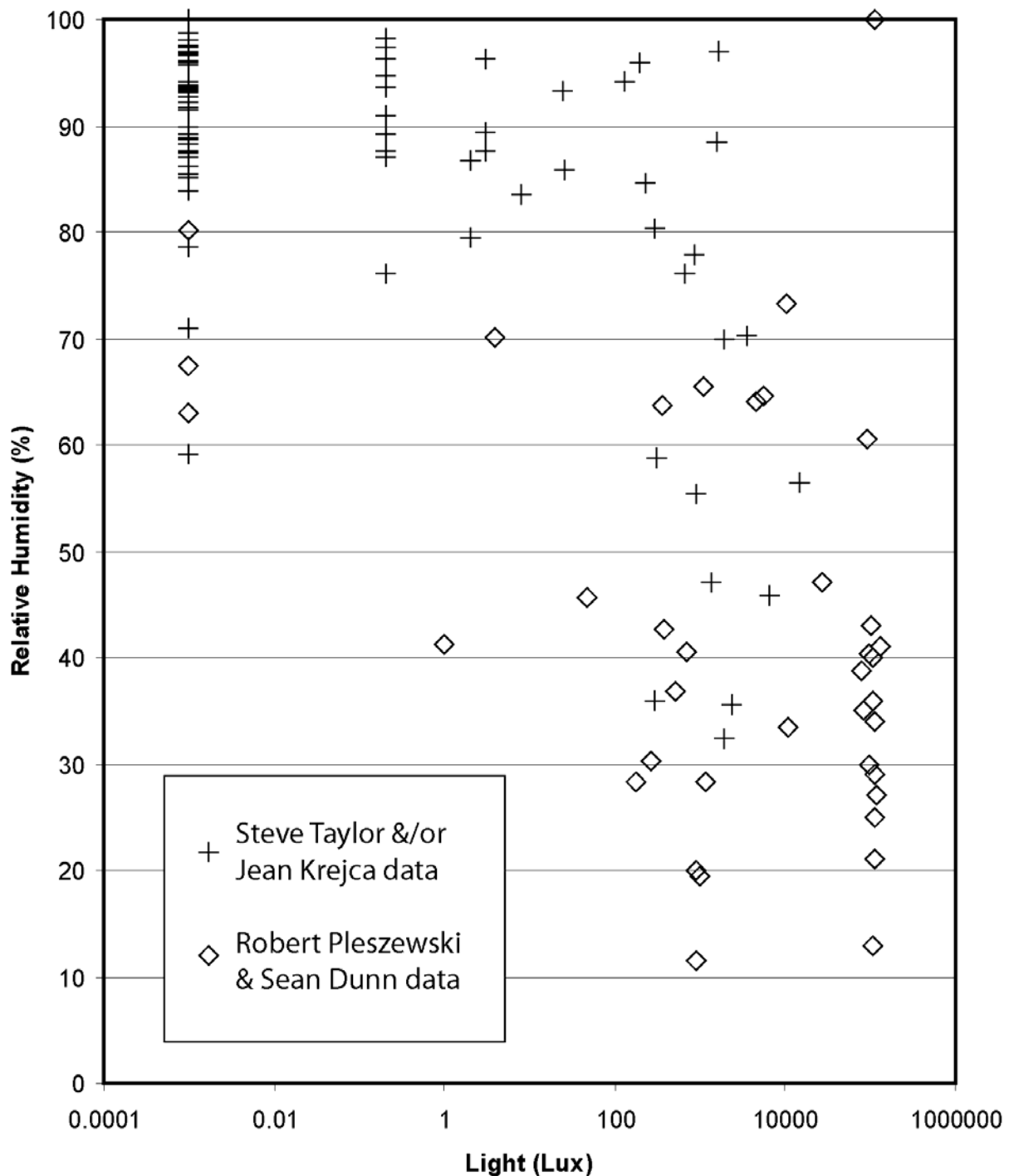


Figure 5. Relationship between relative humidity and light levels, with data coded by name of primary field crew responsible for data collection. Data comprise all available sample meter readings, except transect data, obtained between 2 – 17 June (Taylor & Krejca) and between 28 June – 4 August (Pleszewski & Dunn) in 2005 sampling at lava tube caves in Lava Beds National Monument, California. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log10 scale.

differences could result from 1) changes in seasonal conditions, with a warming and drying trend as one progresses further into the summer months; 2) a difference in familiarity with the equipment [the relative humidity meter is sensitive, and requires regular moistening of the wick and removal of dust accumulations]; and/or 3) a difference in the average distance into the caves the researchers sampling efforts extended, resulting in fewer deep-cave samples in the later part of the field collection period. As we have no real reason to attribute the observed differences to any one of these three options, and because we suspect all three may have come into play, we are retaining both sets of meter data for analysis.

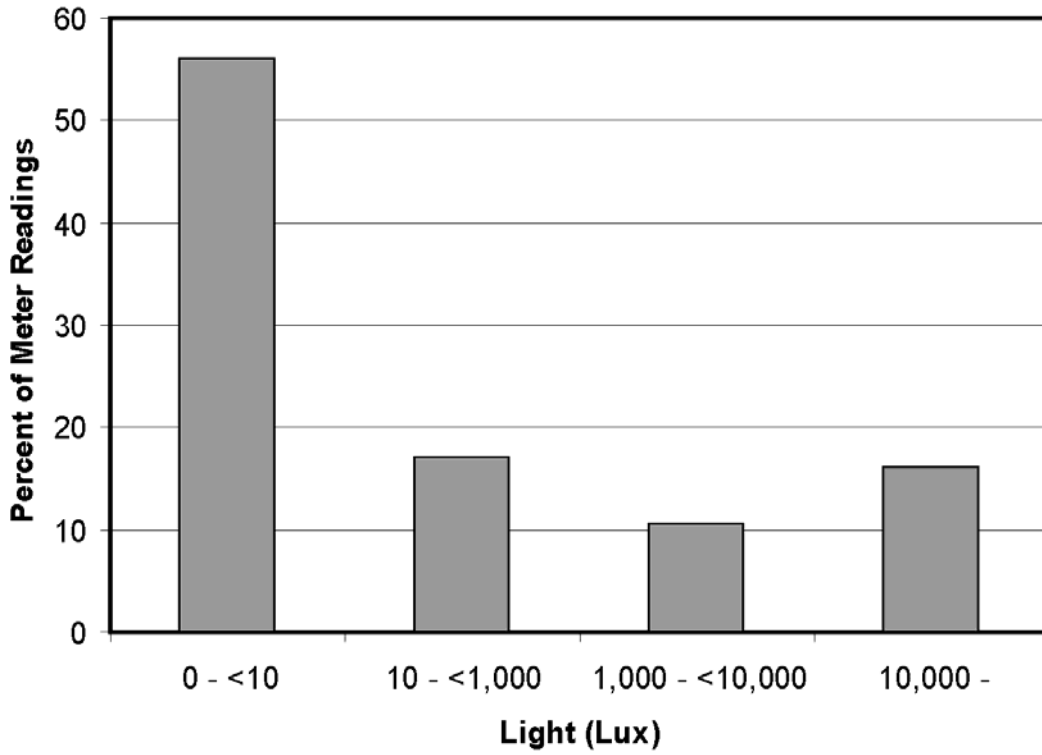
Figures 4 & 5 also show expected patterns, with deep caves generally being characterized by temperatures below 12 °C and relative humidities above 82%. In many parts of the world, deep-cave temperatures correspond to the average yearly temperature. LABE is unusual in that there is a range of deep-cave 2 cm soil temperatures, which range from the average yearly temperature (somewhere around 10-12 °C) down to nearly freezing (our lowest temperature recorded was 0.4 °C) to freezing, where year-round ice accumulates in the caves. Variation in deep-cave relative humidity and air temperatures among caves is related to air flow, often tied to the number and configuration of the entrances in the caves. Some of the caves with larger and multiple entrances do not achieve the extremely high humidities seen in some of the single-entrance caves, because of the drying influence of the air being transported into the cave from outside.

As most of our sampling focused on the dark zone of the caves, light meter readings reflected the scarcity of available light at most sample sites (Figure 6A). Deep-cave (dark zone) relative humidity was generally above 80%, while surface – and some entrance and twilight zone readings – ranged mostly from 40 to 70% relative humidity (Figure 6B). Similarly, 2 cm soil temperatures were low (0.4 -12 °C) for most collections (Figure 7A), corresponding to our emphasis on dark zone sampling. The 2 cm soil temperature was highly correlated with the air temperature, especially in deep-cave habitats (Figure 7B), with more variability in entrance, twilight, and surface readings.

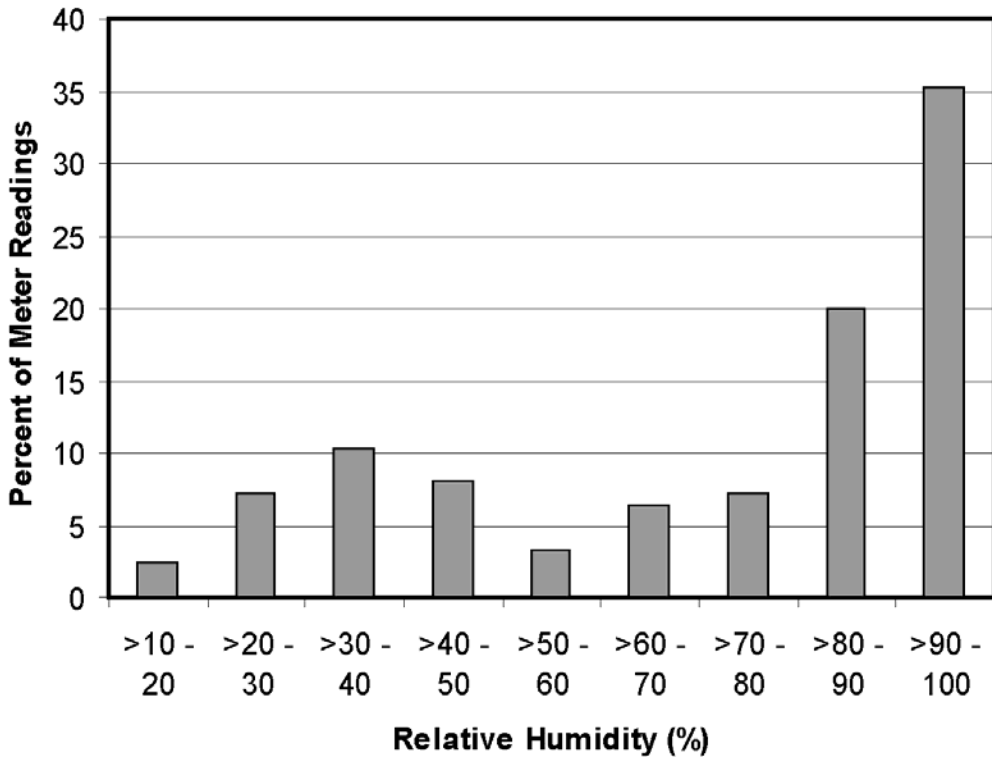
Relative humidity and 2 cm soil temperature also were well correlated (Figure 8A), and when we examine these data in relation to light levels, it is possible to roughly define ranges of these environmental variables that one might expect during June in the different cave zones (Figure 8B). Figure 8B also draws attention to the fact that entrance, twilight, and dark zones are, in fact, artificial constructs for our convenience which merely describe regions along a continuum. We expect that dark-zone temperatures remain relatively constant throughout the year, especially in longer caves with only a single, small entrance.

Transect data

Examination of the environmental metrics collected along the transects in two caves further highlights the transition from entrance to dark zone, as well as the considerable differences between individual caves in the temperature, humidity, and light levels. Nirvana Cave has a single entrance and a characteristically cool and very humid dark zone (most of which was beyond the end of the transect, deeper into the cave), while Spider Cave has 3 entrances and is very dry and warm. Several other caves at LABE have even more entrances (caves with 21, 15, 11, 9, 8, 7, 7, and 7 entrances, and many with fewer entrances), and such

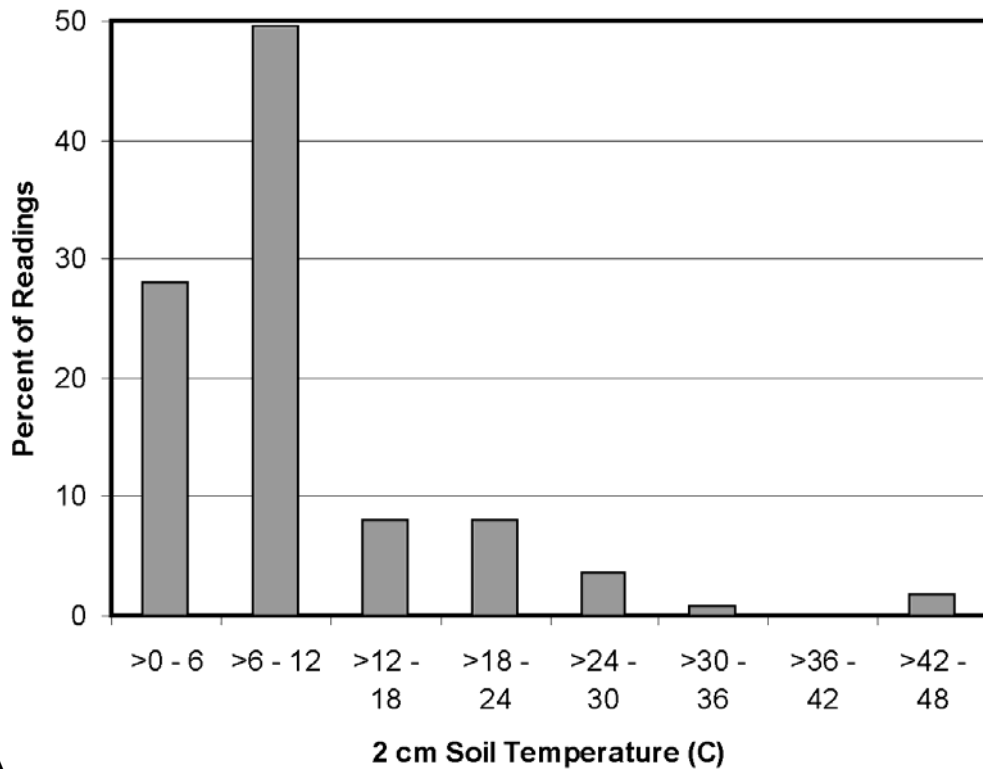


A

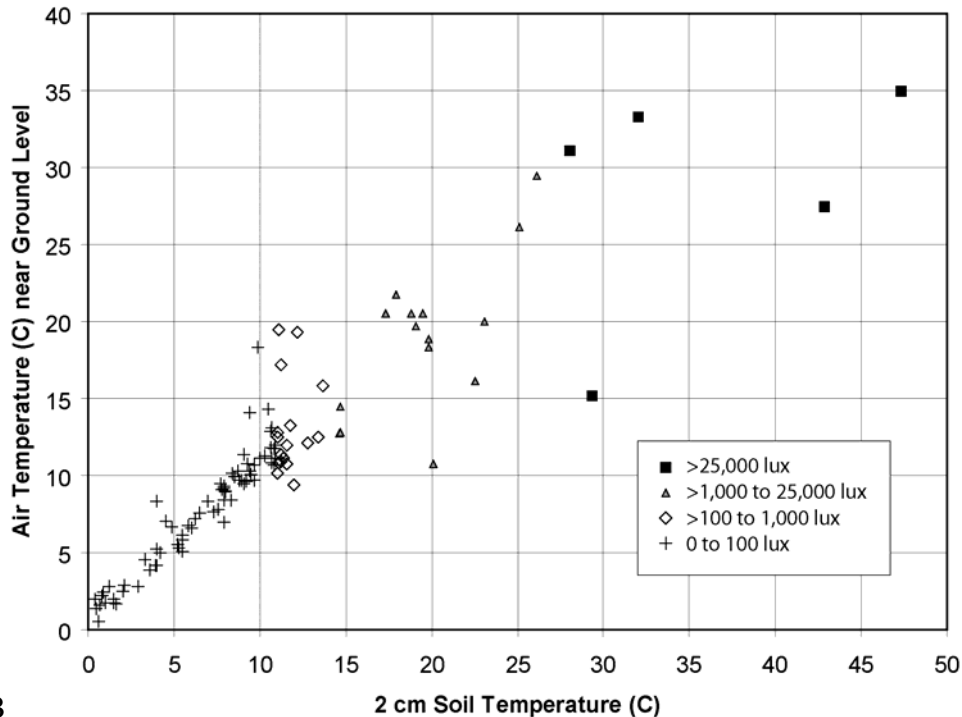


B

Figure 6. Percent of meter reading data falling within different ranges of light meter readings (A, n=123) and relative humidity readings (B, n=125). Data comprise all available sample meter readings, except transect data, obtained during 2 June – 4 August 2005 sampling period at lava tube caves in Lava Beds National Monument, California.

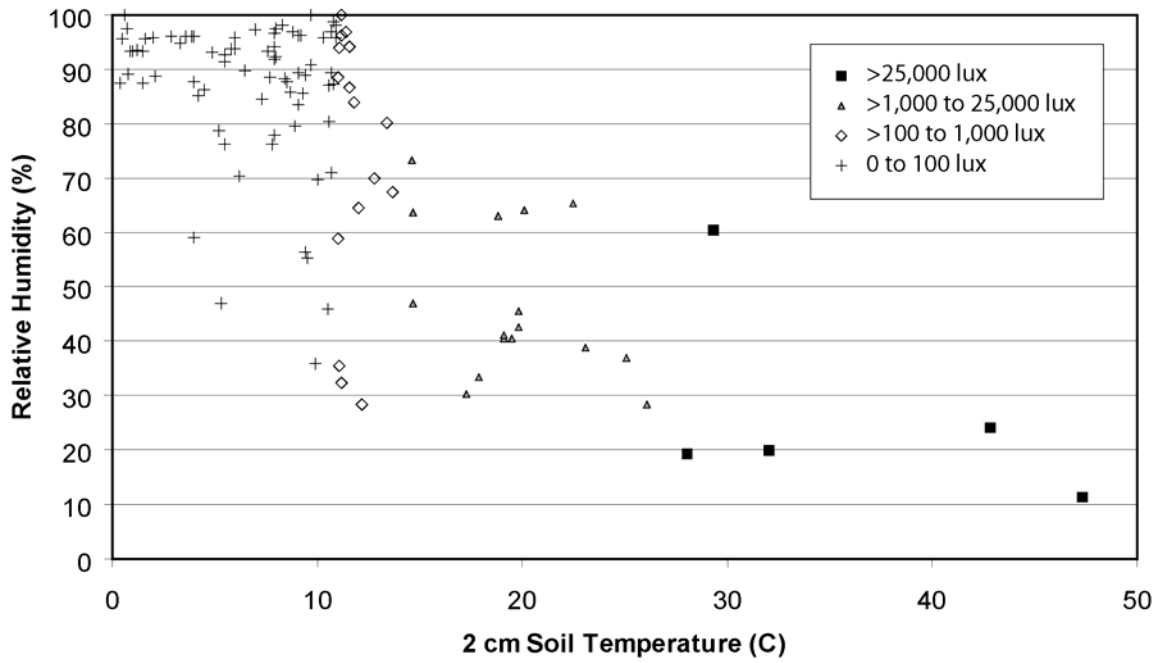


A

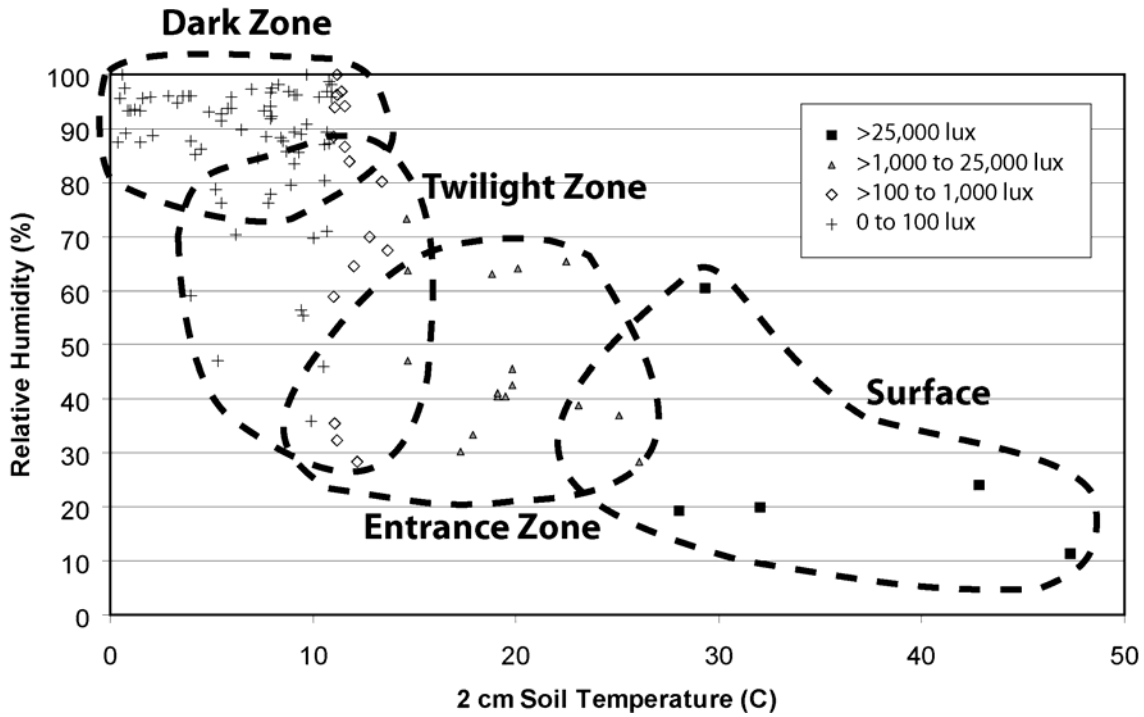


B

Figure 7. Percent of data falling within different ranges of 2 cm soil temperature (A, n=111), and relationship between air temperature near ground level, 2 cm soil temperature, and available light (B). Data comprise all available sample meter readings, except transect data, obtained during 2 June – 4 August 2005 sampling period at lava tube caves in Lava Beds National Monument, California.



A



B

Figure 8. Relationship between 2 cm soil temperature, relative humidity, and light (A), and approximate cave zones delineated on the basis of these metrics (B). Data comprise all available sample meter readings, except transect data, obtained during 2 June – 4 August 2005 sampling period at lava tube caves in Lava Beds National Monument, California.

caves, or at least portions of such caves, are expected to be relatively dry, with temperatures tending towards current surface conditions.

While Spider Cave and Nirvana Cave show similar patterns in reduction of available light as one proceeds deeper into the caves (Figure 9), the similarity ends there. Soil (Figure 10) and Air (Figure 11) temperatures are much higher in the dark zone of Spider Cave – more influenced by surface conditions – than in Nirvana Cave, and the relative humidity deep within Spider Cave (Figure 12) is much lower than the typical deep-cave moisture levels (Figure 8B) seen in the Nirvana Cave transect (Figure 12). We also characterized substrate moisture subjectively as dry, normal (damp to touch, but moisture not visible), and wet (glistening wet, hand placed on surface will have moisture apparent on it when removed), and the relative moisture levels on the floor, walls, and ceiling in Spider Cave (Figure 13) is much drier than the typical pattern we observed, which is characterized by that seen in the transect for Nirvana Cave (Figure 14).

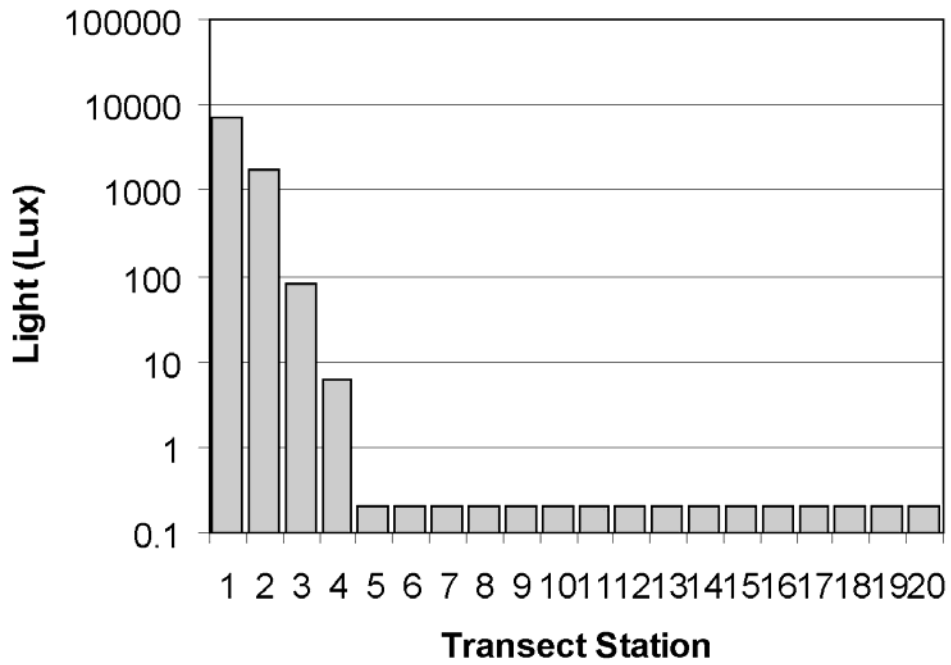
The nature of the substrate in the two transect caves was typical of that we encountered in most of the caves during our bioinventory. Both Spider Cave (Figure 15) and Nirvana Cave (Figure 16) had walls and ceilings composed almost entirely of bedrock. The floor of these caves was also mostly bedrock, breakdown, or rocks, with somewhat more variability than the walls and ceilings – soil, accumulations of guano, and other substrates were occasionally recorded.

Caves are notable in the absence of primary producers, and the general low levels of nutrients available in the caves. The rarity of organic deposits enumerated in our quadrat data (Figures 17,18) reflects the corresponding rarity of organisms encountered during the quadrat surveys in the two caves (Figures 19,20), and corresponds well (subjectively) with the conditions we observed in the other caves we sampled. In general, energy sources were rare and accumulated in discreet areas (i.e., near woodrat middens, by organic debris near pools of water, etc.), making the transect approach to bioinventory and future monitoring an ineffective approach. Searching preferentially in suitable habitat and collecting by hand yielded much better results.

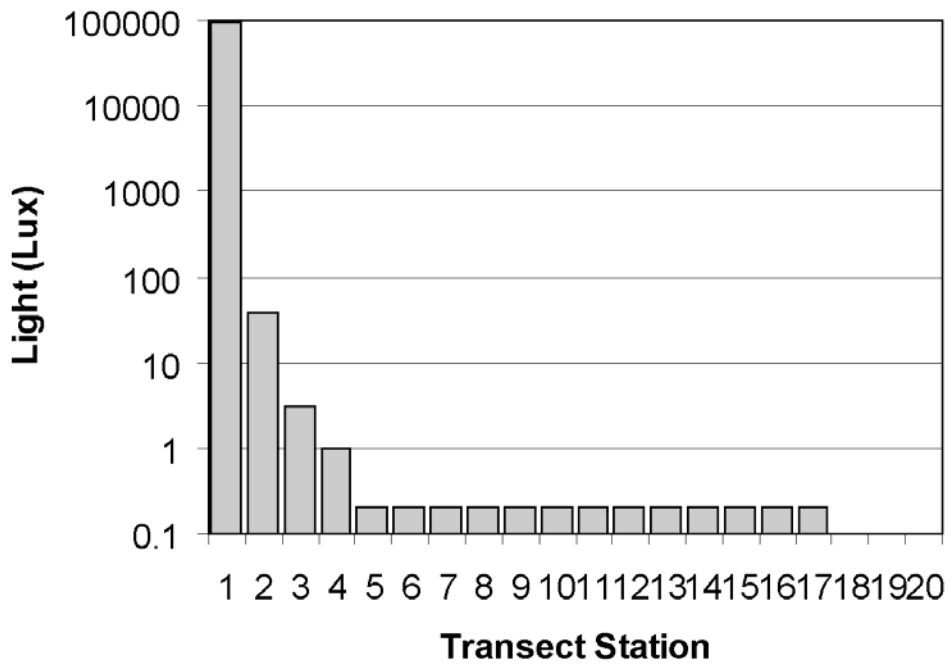
General collecting

We recorded about 155 samples (hand collections, Berlese funnel samples, pitfall trap samples, or sight records) through 17 June 2005, with an additional 38 samples obtained by Robert Pleszewski & Sean Dunn between 28 June and 4 August 2005. These records account for approximately 1,511 specimens for which we have data. Most of this material is only partially identified, and some of the most important material is currently being sent out to taxonomic experts for further identification.

Of the animals recorded, 22.6% were flies (Insecta: Diptera) and 19.3% were springtails (Insecta: Collembola), of which about 57% are in the family Tomoceridae (probably *Tomocerus* spp.) (Figure 21). Spiders (Arachnida: Araneae), millipedes (Diplopoda), mites (Arachnida: Acari), and diplurans (Insecta: Diplura) made up 16, 12.2, 11.7, and 5.3 % of the animals recorded, respectively (Figure 21). All of the diplurans are an undescribed species of *Haplocampa* (Campodeidae), and 92.9% of the millipedes are the locally common troglobite,

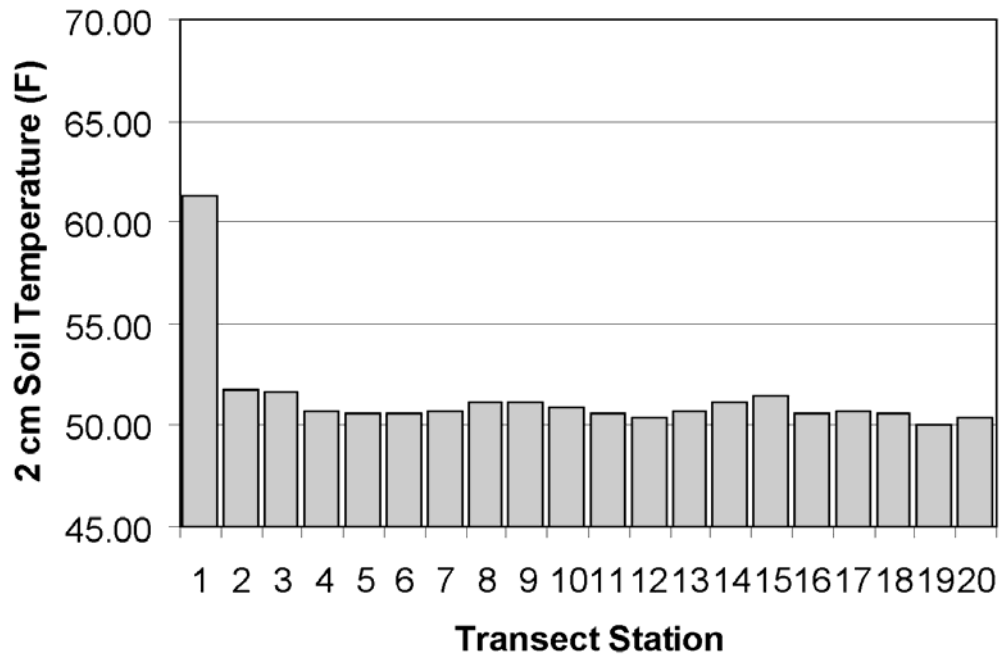


A

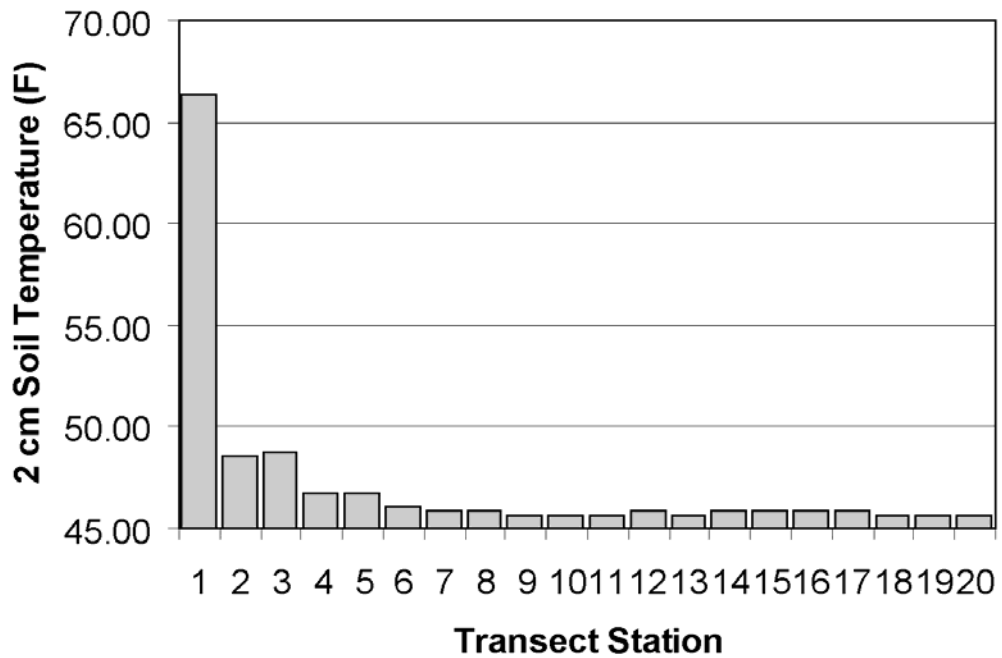


B

Figure 9. Light (Lux, note Log_{10} scale) readings in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).

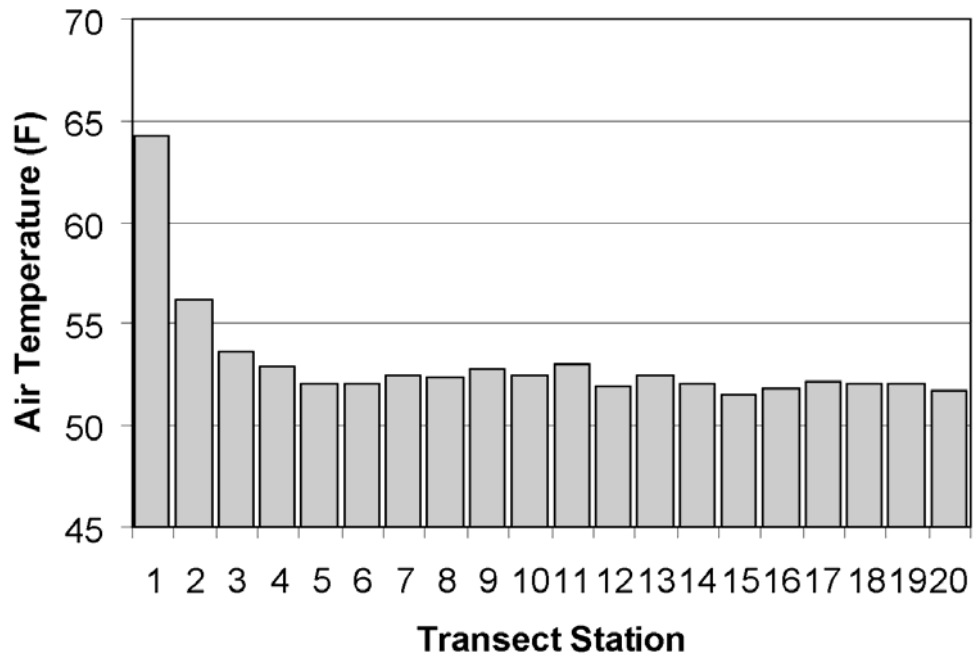


A

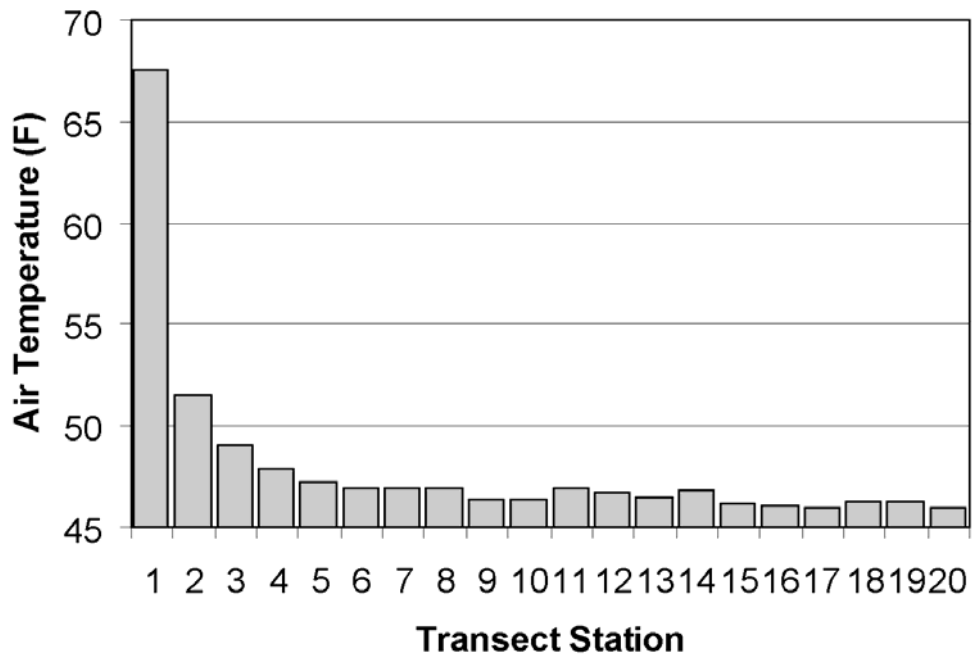


B

Figure 10. Soil temperature (°F) at 2 cm depth in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).

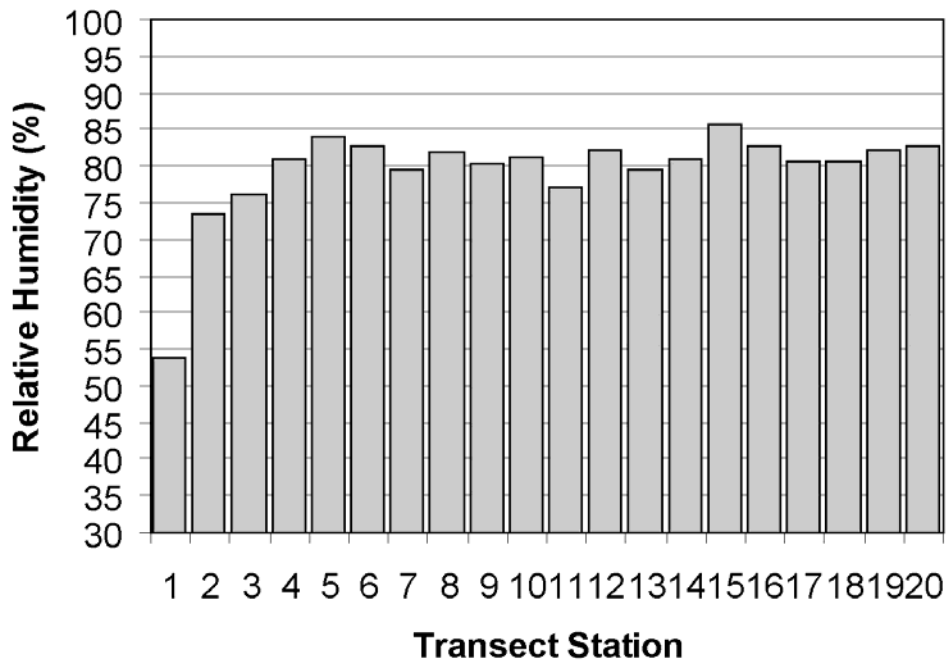


A

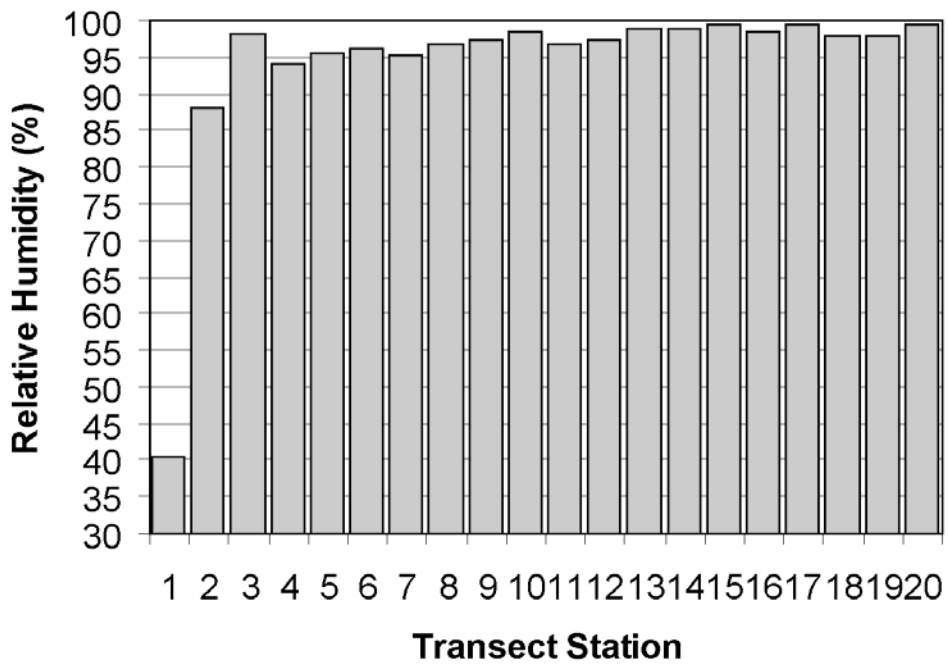


B

Figure 11. Air temperature (°F) at 2 cm above substrate in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).

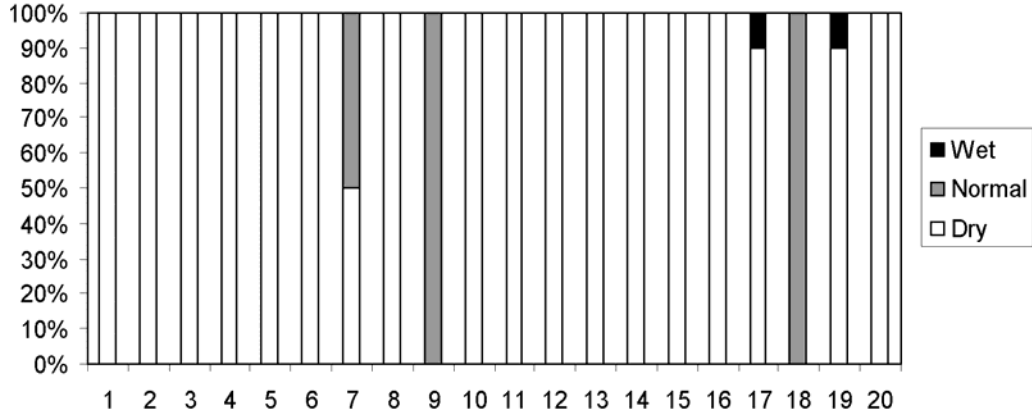


A

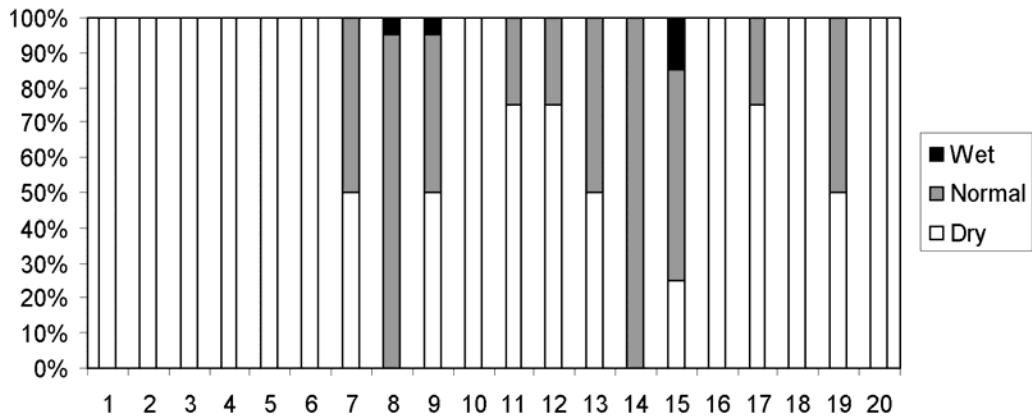


B

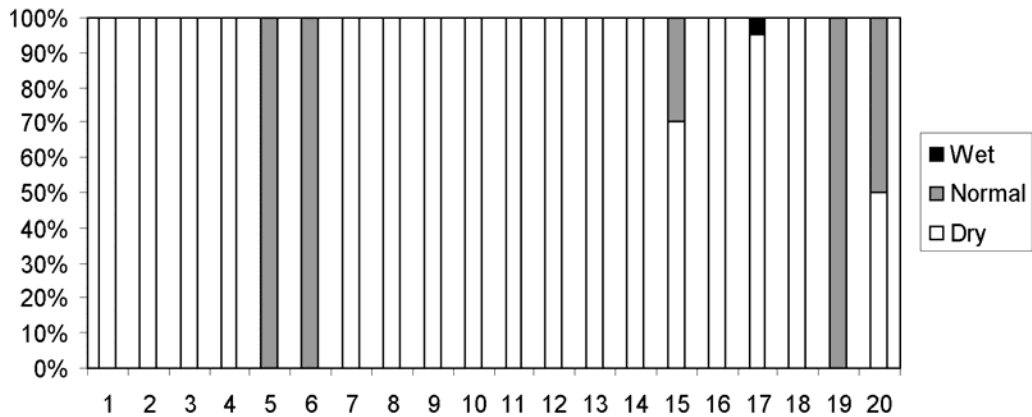
Figure 12. Relative humidity (%) at 2 cm above substrate in Spider Cave (A, 14 June 2005) and Nirvana Cave (B, 4 June 2005), Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A

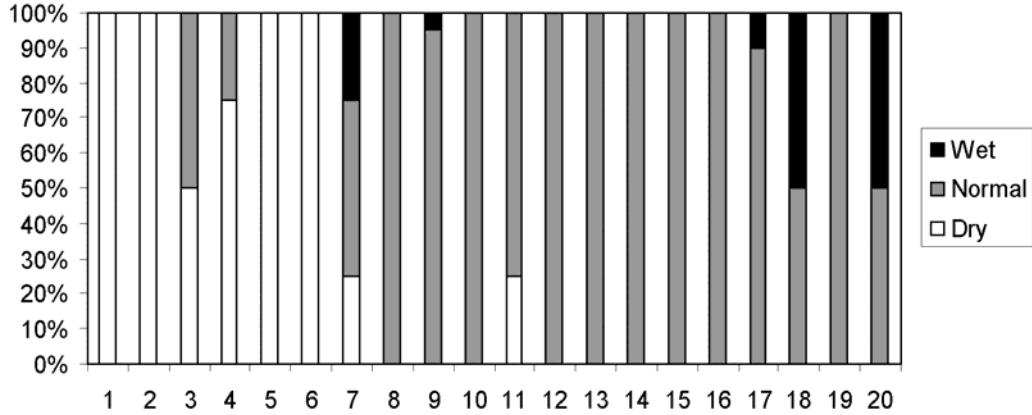


B

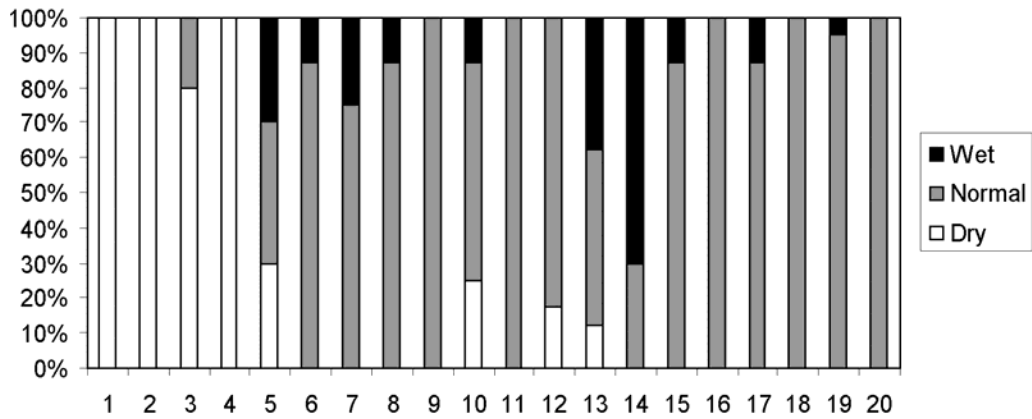


C

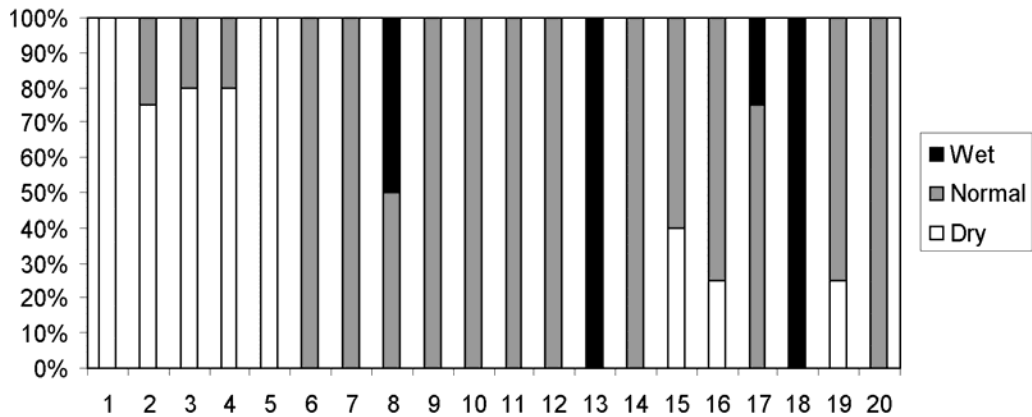
Figure 13. Transect-based quadrat substrate moisture data for Spider Cave. A. Ceiling, B. Walls (average of left and right walls), C. Floor. Data collected 14 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A

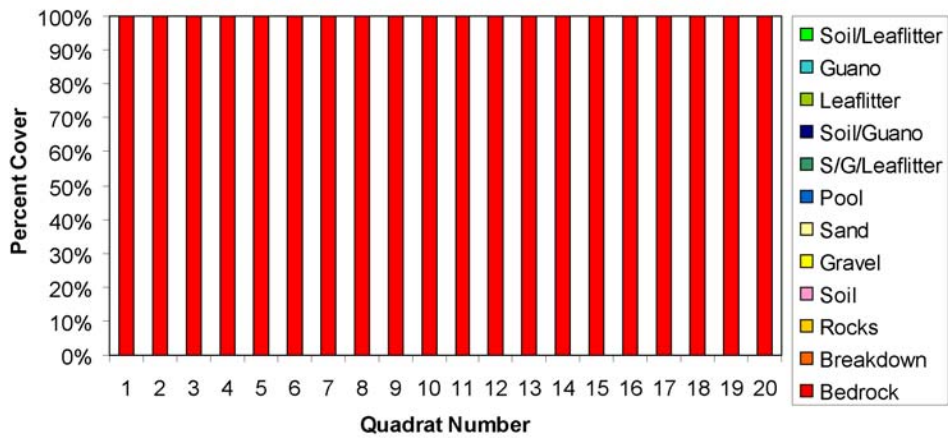


B

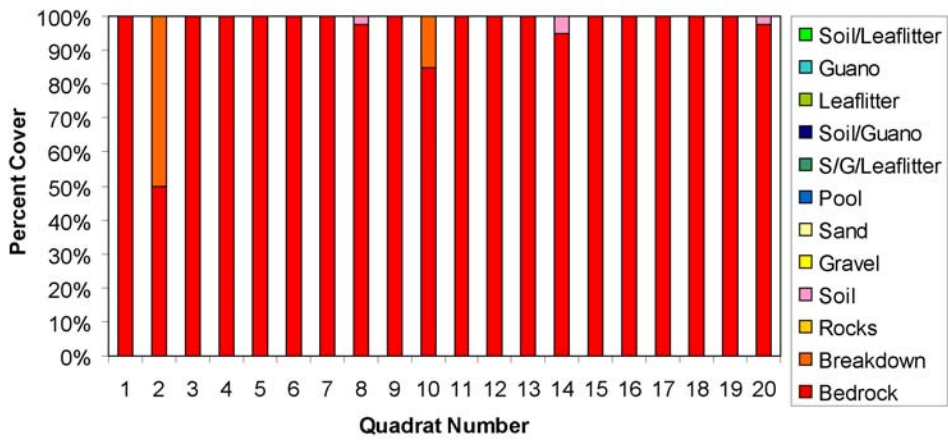


C

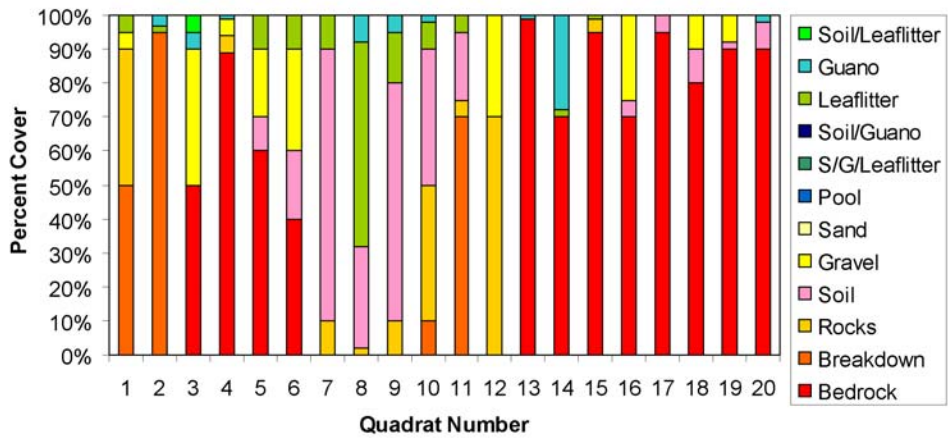
Figure 14. Transect-based quadrat substrate moisture data for Nirvana Cave. A. Ceiling, B. Walls (average of left and right walls), C. Floor. Data collected 4 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A

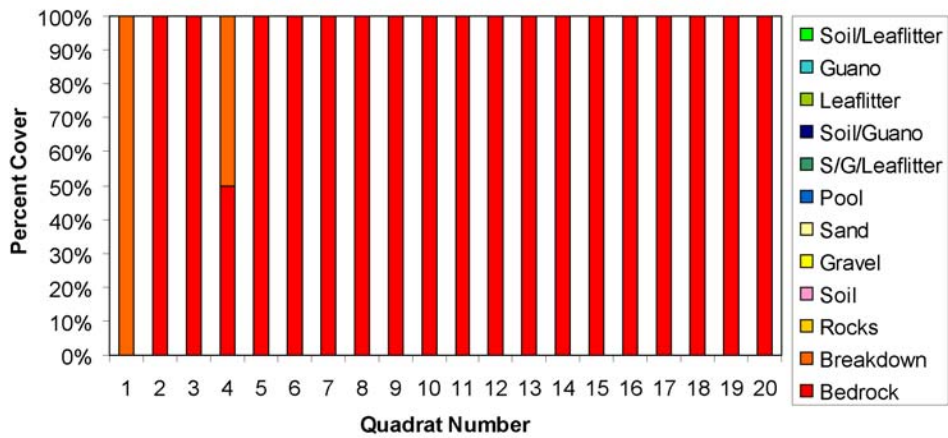


B

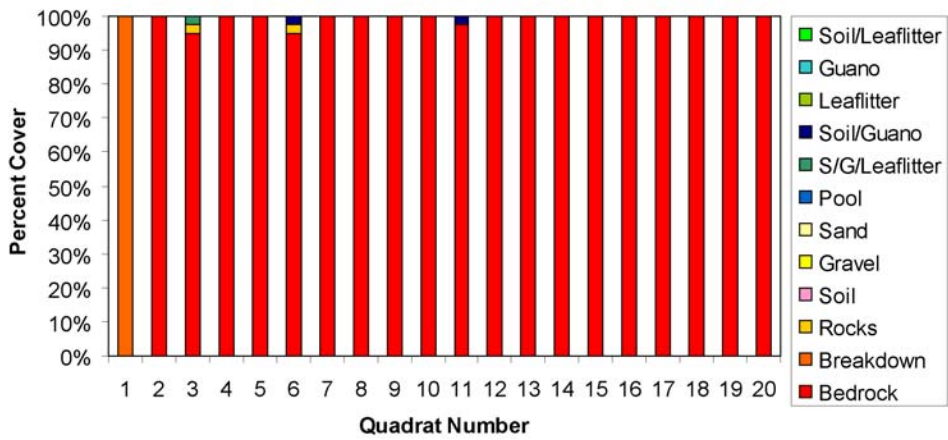


C

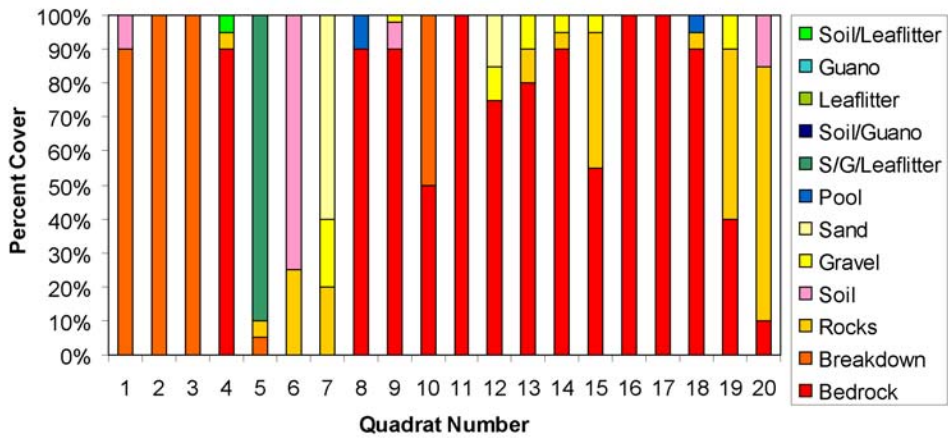
Figure 15. Transect-based quadrat substrate composition data for Spider Cave. A. Ceiling, B. Walls (average of left and right walls), C. Floor. Data collected 14 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A

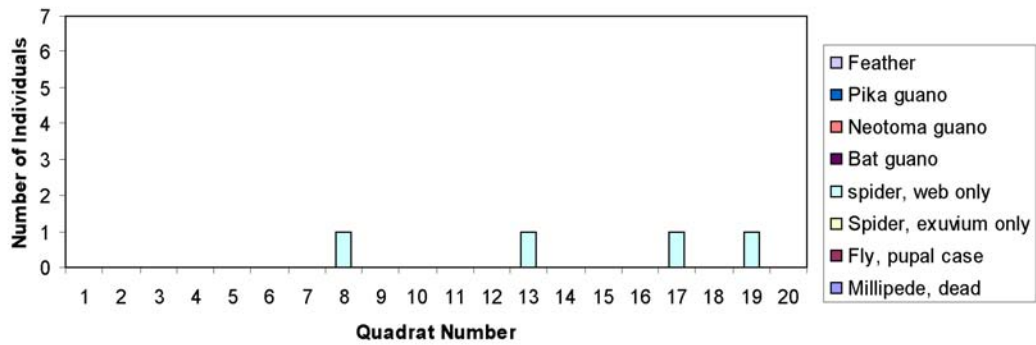


B

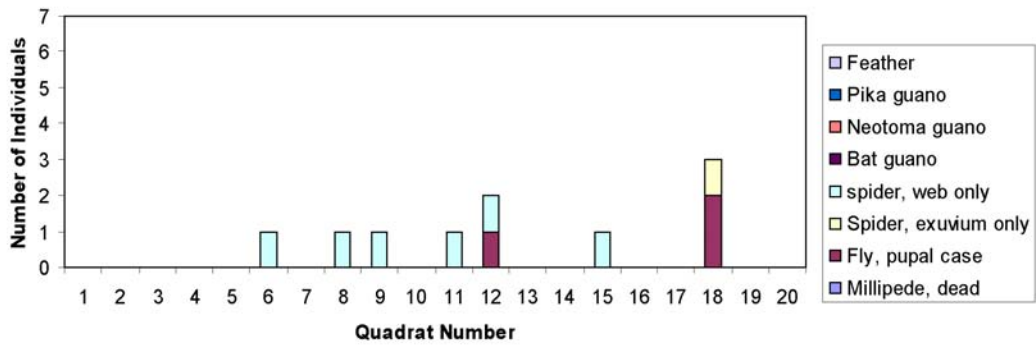


C

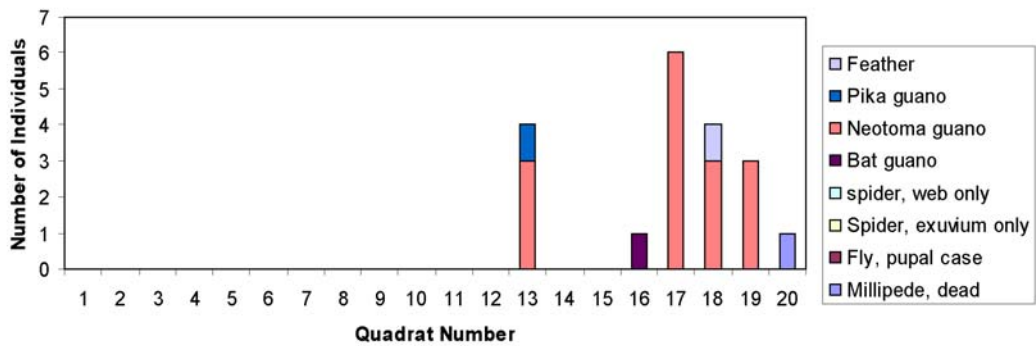
Figure 16. Transect-based quadrat substrate composition data for Nirvana Cave. A. Ceiling, B. Walls (average of left and right walls), C. Floor. Data collected 4 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A

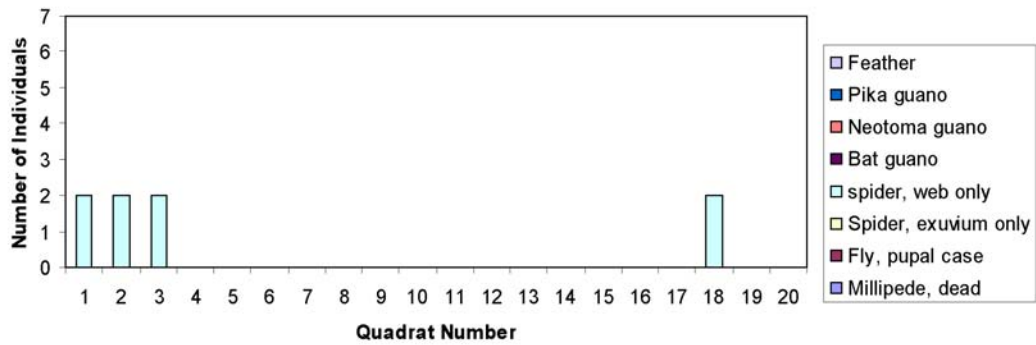


B

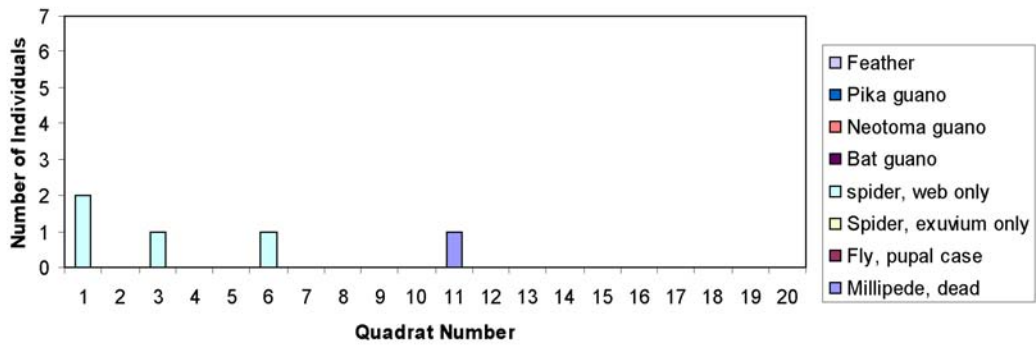


C

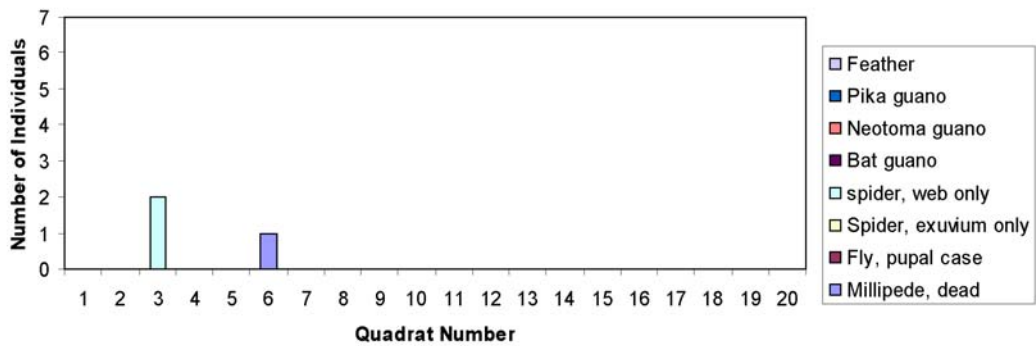
Figure 17. Transect-based quadrat-derived evidence of animal life in Spider Cave. A. Ceiling, B. Walls (sum of left and right walls), C. Floor. Data collected 14 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A

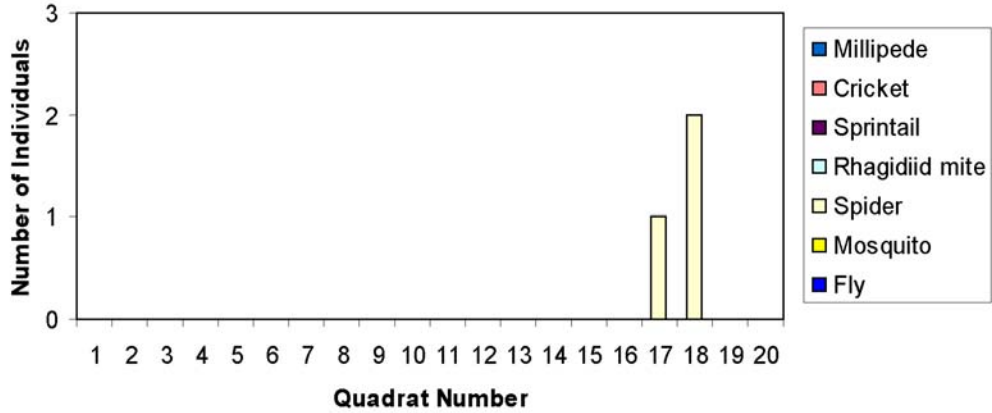


B

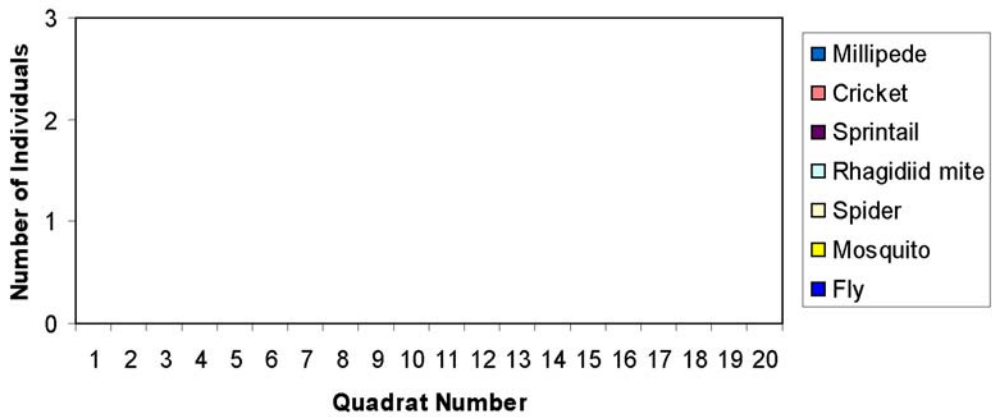


C

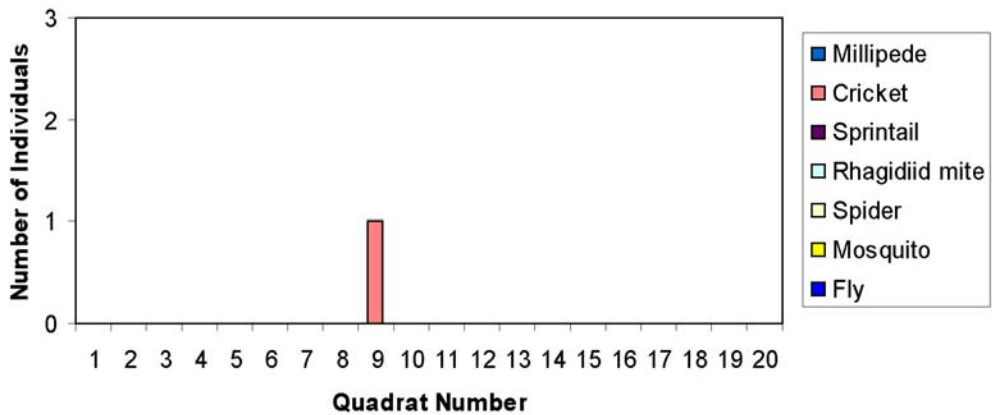
Figure 18. Transect-based quadrat-derived evidence of animal life in Nirvana Cave. A. Ceiling, B. Walls (sum of left and right walls), C. Floor. Data collected 4 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A

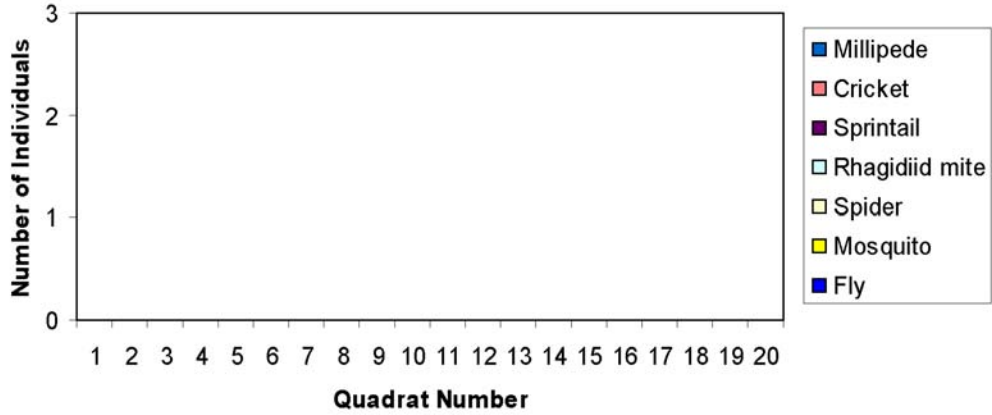


B

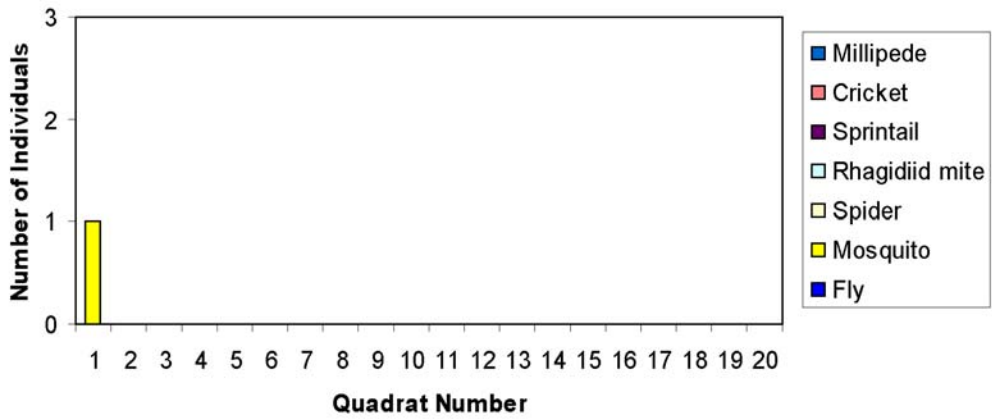


C

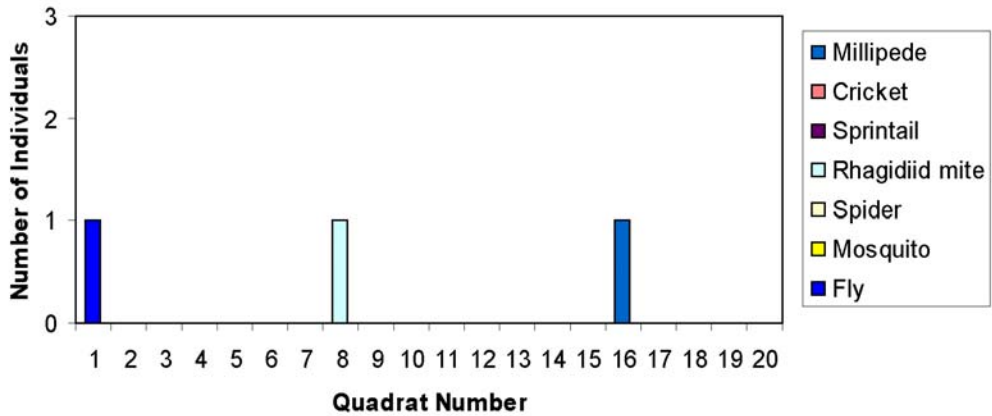
Figure 19. Transect-based quadrat counts of animals in Spider Cave. A. Ceiling, B. Walls (sum of left and right walls), C. Floor. Data collected 14 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).



A



B



C

Figure 20. Transect-based quadrat counts of animals in Nirvana Cave. A. Ceiling, B. Walls (sum of left and right walls), C. Floor. Data collected 4 June 2005, Lava Beds National Monument, California, at transect stations placed at 2 meter intervals beginning at the cave entrance dripline (Station 1).

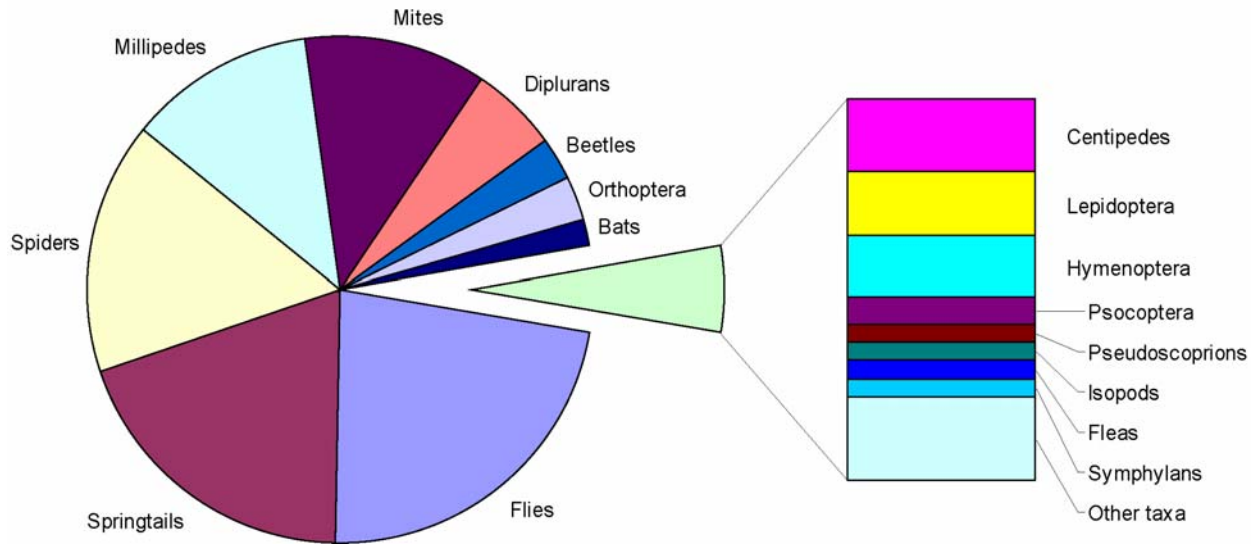


Figure 21. General taxonomic distribution of animals recorded from 29 caves at Lava Beds National Monument, California, based on fieldwork conducted between 2 June and 4 August, 2005.

Table 2. List of taxa recorded from 29 caves at Lava Beds National Monument between 2 June and 4 August, 2005.

Class	Order	Family	Species
Oligochaeta			
Crustacea	Isopoda	Trichoniscidae	
Arachnida	Acari	Unidentified mites	
		Rhagidiidae	
	Superfamily Oribatoidea	Unidentified oribatid mites	
	Araneae	Unidentified spiders	
		Nesticidae	
	Opiliones		
	SubOrder Palpatores	prob. Phalangidae	
	Pseudoscorpiones		
Symphyla			
Diplopoda	Chordeumatida		

Table 2. Continued.

Class	Order	Family	Species	
		Conotylidae?		
		Conotylidae	<i>Plumatyla humerosa</i>	
		Paeromopodidae	<i>Californiulus</i> sp.	
Chilopoda	Julida			
	Polydesmida			
	Spirobolida			
	Unidentified centipedes			
	Geophilomorpha Lithobiomorpha	Unidentified lithobiomorphs Lithobiidae		
Insecta	Microcoryphia			
	Thysanura			
	Ephemeroptera	Baetidae	Unidentified mayfly <i>Callibaetis</i> sp.	
	Diplura	Campodeidae	<i>Haplocampa</i> sp.	
	Collembola	Unidentified springtails		
		Arrhopalitidae		
		Entomobryiidae		
		Hypogastruridae		
		Onychiuridae Tomoceridae		
	Psocoptera			
Thysanoptera				
Orthoptera	Rhaphidophoridae	<i>Ceuthophilus inyo</i>		
Homoptera	Cicadellidae Cicadidae			
Lepidoptera	Unidentified adults, larvae, and scattered wings Hesperiidae			

Table 2. Continued.

Class	Order	Family	Species
	Coleoptera	Unidentified adults and larvae Tenebrionidae Scarabaeidae Staphylinidae Chrysomelidae	
	Hymenoptera	Formicidae Apidae	
	Siphonaptera Diptera	Unidentified adults, larvae and pupae Tipulidae Mycetophilidae Psychodidae Chironomidae Sciaridae Culicidae Bombyliidae Scatopsidae Syrphidae	
Aves	Passeriformes	Hirundinidae	
	Strigiformes	Undetermined (owl pellets)	
Mammalia	Undetermined (bones) Rodentia	Undetermined (bones) Cricetidae	<i>Neotoma</i> sp.
		Erethizontidae	<i>Erethizon dorsatum</i>
	Lagomorpha	Ochotonidae	<i>Ochotona princeps</i>
	Chiroptera	Vespertilionidae	Undetermined bats <i>Corynorhinus townsendii</i>
	Carnivora	Undetermined (bones)	

Plumatyla humerosa, both of which have previously been reported from LABE. A variety of other animal taxa make up the remaining 12.9% of the recorded animals. A list of the taxa recorded during our study is provided in Table 2. Because much of this material still awaits further identification (e.g., multiple spider taxa are expected), this list should be considered only provisional. Below we discuss individual taxa recorded during this study.

Phylum Annelida: Class Oligochaeta

An earthworm was recorded on only a single occasion during our study, a sight record at Lyon's Road Cave in the dark/twilight zone (<1 lux) under relatively cold conditions (soil 6.0 °C, air 6.6 °C). It was found dead on wet breakdown. This species is probably an edaphobite (soil inhabitant). The limited occurrence of soil habitats in LABE caves probably accounts for the shortage of earthworms in our samples, as these animals are relatively commonly encountered in caves in other regions.

Phylum Arthropoda: Class Crustacea: Order Isopoda: Family Trichoniscidae

This terrestrial isopod (Figure 22) is one of the two most exciting finds during this study. It appears to be a troglobite, and may represent an undescribed species. They are being examined by a taxonomic expert. This animal, possibly belonging to the genus *Brackenridgia*, was hand collected, but only rarely (3 occasions). It was recorded from Catacombs, Coral Reef, and Maze caves, where it occurred only in the dark zone (0 lux), where substrate temperatures



Figure 22. Trichoniscid isopod in Maze Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

ranged from 7.8 to 9.1 °C, air temperatures ranged from 8.9-9.2 °C, and relative humidity was very high (92.2-96.2 %). Specific habitats included: underside of rock on normal [moisture] dirt floor, wet floor on rock on edge of drip pool, and normal [moisture] bedrock wall.

Phylum Arthropoda: Class Arachnida

Arachnids, primarily mites and spiders of varying degrees of cave-adaptation, comprise an important component of cave communities at Lava Best National Monument, and are represented by a number of species.

Order Acari: mites

Our material contains numerous small mites which we have not identified. Crawford (in litt., 1998) reported several phoretic gamasoid mites, as well as pygmephorid, actenedid, trombidoid, acariform, and glycyphagid -like mites, and our material likely contains many of the same groups. In addition, we collected mites of the family Rhagidiidae (Figure 23) and orobatid mites, both groups also picked up in Crawford's 1989 collection.

The rhagidiid mites likely include troglobitic taxa, and our material has been sent to the appropriate taxonomic expert for identification and, if appropriate, description of new species. Rhagidiid mites were generally found at cave temperatures (Soil, range 2.9-13.7 °C, average 7.9 °C; Air, range 2.8-15.8 °C, average 9.2 °C), and at relatively high relative humidities (average 84.9 %) in the dark or twilight zones (Figure 24). Most collections were hand collections (2 from Berlese samples), taken on the cave floor under usually (8 collections) under normal moisture conditions (plus two 2 wet, 1 dry). Four collections were associated with *Neotoma* middens or guano, two were from the surface of small drip-pools, and four were from the underside of rocks. Rhagidiidae were recorded from Bulevard, Caldwell Ice, Lyon's Road, Maze, Nirvana, Pearl, Post Office, Rollercoaster, Township, and Upper Heppe caves.



Figure 23. A probable cave-adapted mite (Acari: Rhagidiidae) in Maze Cave (3 June 2005), Lava Beds National Monument, California. Photo by Jean Krejca.

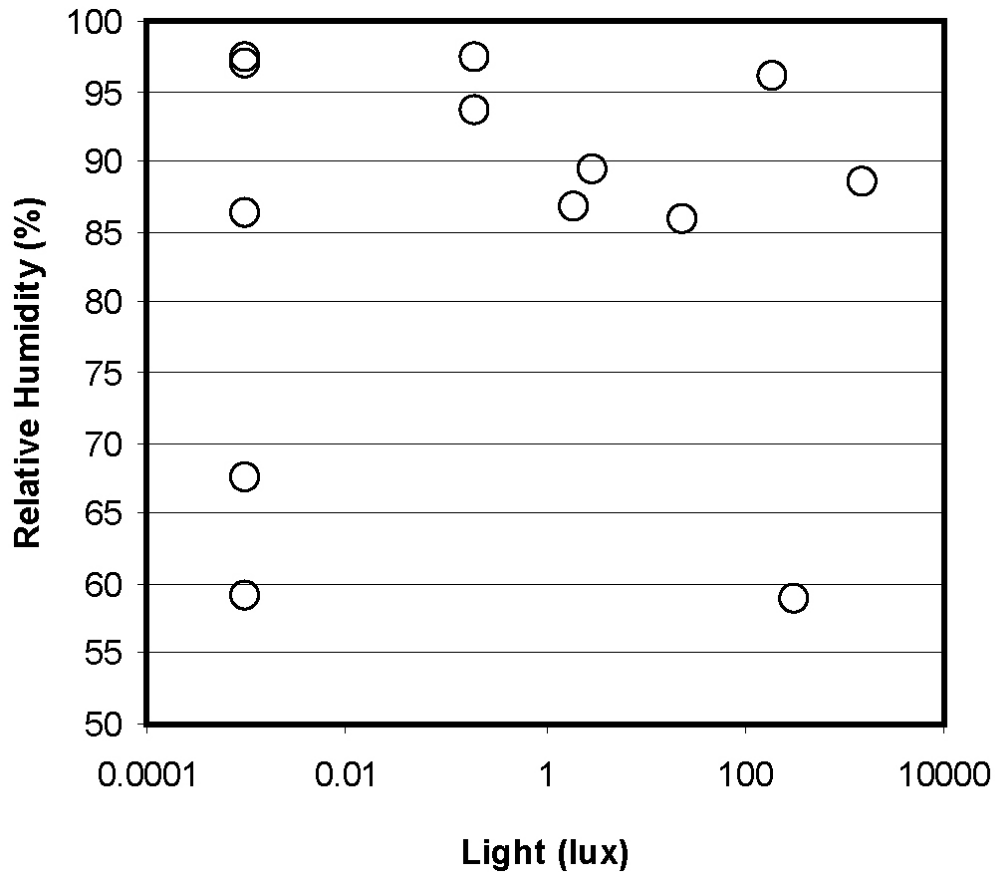


Figure 24. Humidity and light associated with records of Rhagidiidae found in lava tube caves in Lava Beds National Monument, California, 2 June – 4 August, 2005. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.

Six collections of Oribatoidea, a superfamily of beetle-like mites, were made, mostly from Berlese litter samples, which sometimes yielded higher numbers of these mites than other methods. Specimens were recorded from normal to dry floors, mostly (73 of 76 specimens) in association with *Neotoma* middens. These mites were collected at normal cave temperatures (air, 6.9-10.1 °C; soil, 7.9-9.5 °C) either in complete darkness at high humidities (96.7 % RH) or in twilight (844,914 lux) at moderate humidities (55.4, 78.0 % RH). Oribatids were recorded from Caldwell Ice, Coda, Rollercoaster, and Upper Heppe caves.

Order Araneae: spiders

Spiders comprise one of the most readily encountered groups of cavernicoles in Lava Beds National Monument caves. They were recorded from 25 of the 28 caves, and occurred in a wide variety of habitats and environmental conditions and were recorded as hand collections (81%) or sight records (19%). Unfortunately, spider identifications were not available in time

for inclusion in this report. We anticipate at least 8-10 species will be recorded once identifications are complete. We identified some spiders in the field as belonging to the family Nesticidae (Figure 25), but these identifications are tentative. In some caves, we encountered a basket-web spider (Figure 26), which spins a distinctive form of web (Figure 27), often deep within the caves. Another common spider was a ground-dwelling species that may be *Cybaeus* sp. (Cybaeidae) (Figure 28) that was commonly encountered on dry floors under stones or debris, where it spins a sloppy web extending out from its lair (Figure 29). A less obvious, but still widespread spider was a minute spider with a greenish abdomen (Figure 30), which was found in several caves. Finally, we noted distinctive mesh-like webs that may belong to a spider in the family Linyphiidae (Figure 31).

Order Opiliones: harvestmen

No cave-adapted harvestmen were encountered during this study. The only two specimens recorded were accidentals, probably of the family Phalangidae (suborder Palpatores), hand collected from the floor of the twilight zone in Lazaroff's Hole and Township Cave.

Order Pseudoscorpiones: pseudoscorpions

Four Pseudoscorpions were hand collected, one each in Caldwell Ice Cave, Deep Cavern Cave, Rollercoaster Cave, and Lyon's Road Cave. The specimens from the first three sites could be accidentals or trogloliths (Figure 32), but the specimen from the last cave is, along with the trichoniscid isopod discussed earlier, one of the most interesting animals found during our bioinventory. This pseudoscorpion appears to be a troglolithic species (Figure 33), and is probably new to science. It was found in complete darkness in the back of the cave at a humidity of 86.2% and normal deep-cave temperatures (air, 7.1 °C; soil 4.5 °C) on the underside of a breakdown rock on the floor with normal moisture.

Phylum Arthropoda: Class Symphyla

We found specimens (Figure 34) in Four Star Cave under rocks. Collections were in twilight, and probably represent the accidental occurrence of an edaphobite (soil inhabitant) in the caves. The Symphyla are a relatively obscure class of myriopods that are typically edaphobitic. At least one species, *Scutigereilla immaculata*, is a widespread pest species occurring in Europe, North America, South America, Australia, and New Zealand (Halliday 2004), where it damages the roots of various crops. Other species in the two families of Symphyla are normal components of the soil fauna.

Phylum Arthropoda: Class Diplopoda: millipedes

Four orders (Julida, Polydesmida, Spirobolida, and Chordeumatida) of millipedes (or millipeds, according to some) were recorded from caves at Lava Beds National Monument. Most of the species encountered are accidentals, but one is an important troglolith.

One millipede belonging to the order Julida was collected via Berlese sample of *Neotoma* midden material in Rollercoaster Cave. This sample was taken in the dark zone of the cave (0 lux) at a very high humidity (96.7%) and typical deep cave temperatures (air, 8.4 °C; soil 7.9 °C). One polydesmid millipede was hand collected from mossy bedrock on a normal [moisture] floor



Figure 25. An adult female of a commonly encountered reddish-brown spider thought to belong to the family Nesticidae, in Valentine Cave, Lava Beds National Monument, California. Photo by Jean Krejca.



Figure 26. A large basket-web spider in Maze Cave, Lava Beds National Monument, California. Photo by Jean Krejca.



Figure 27. A large basket-web in Maze Cave, Lava Beds National Monument, California. Note spider near top of image in center. Photo by Jean Krejca.



Figure 28. A spider, perhaps *Cybaeus* sp. (Cybaeidae) commonly encountered under stones in dry to normal areas of caves, especially in the entrance and twilight zones. Maze Cave, Lava Beds National Monument, California. Photo by Jean Krejca.



Figure 29. Typical web configuration of the spider species picture in Figure 28 (perhaps *Cybaeus* sp.), in Rollercoaster Cave, Lava Beds National Monument, California. Note abundant moth wings which, in this case may belong to prey of the spider, but which are often attributed to roosting bats. Photo by Jean Krejca.



Figure 30. An unidentified minute green-abdomened spider encountered in several of the caves, here in Bulevard Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

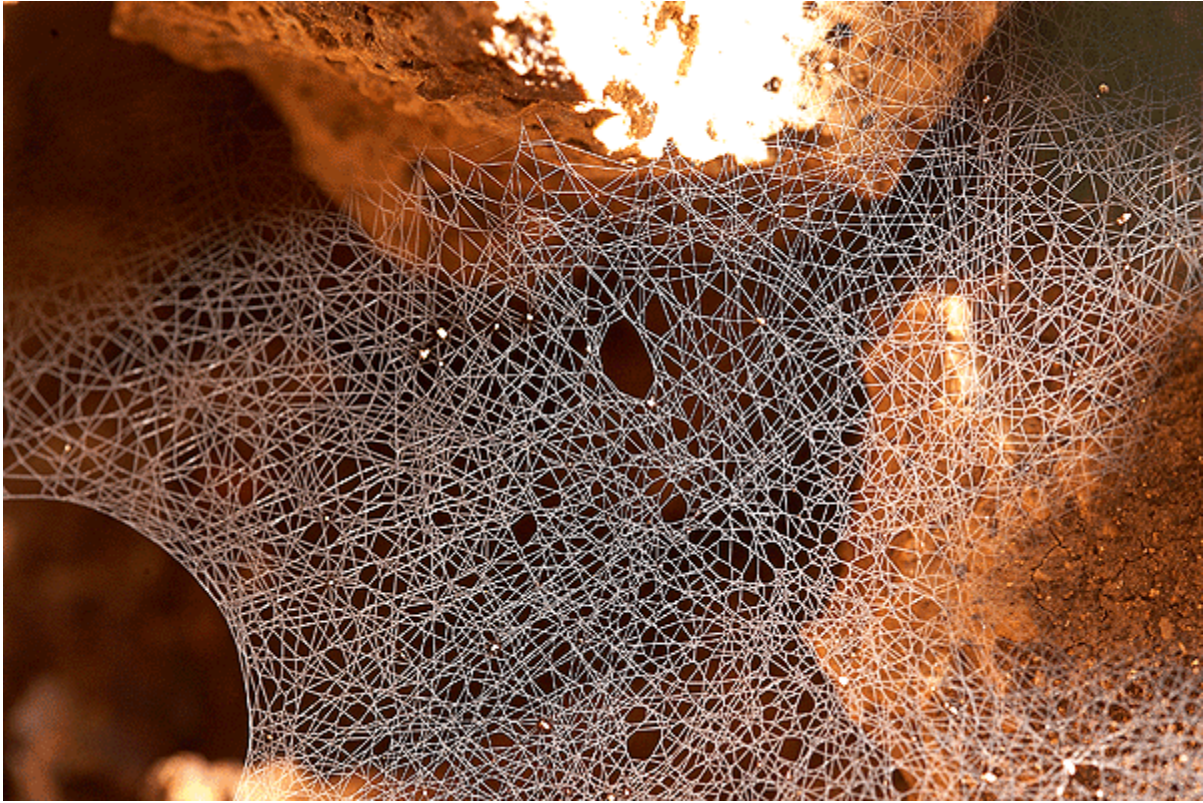


Figure 31. A sheet web thought to belong to a spider in the family Linyphiidae. Maze Cave, Lava Beds National Monument, California. Photo by Jean Krejca.



Figure 32. A pseudoscorpion from a cave at Lava Beds National Monument, California. This individual is either a troglophile or an accidental – note the relatively thick and short chelae relative to the specimen in Figure 33. Inset with finger provides scale. Photos by Jean Krejca.



Figure 33. A troglotic pseudoscorpion from a Lyon's Road Cave at Lava Beds National Monument, California. Note the relatively slender, elongate chelae relative to the specimen in Figure 32, and the long sensory setae. Photo by Jean Krejca & Steve Taylor.



Figure 34. A symphylan on moss in twilight zone of Four Star Cave, Lava Beds National Monument, California. Part of a finger tip provides scale. Photo by Jean Krejca.

in Four Star Cave in the twilight zone (<1 lux) in relatively high humidity (87.1%) and typical to slightly warm cave temperatures (air, 11.8 °C; soil, 10.6 °C). Because of its pale yellowish coloration, we suspect this millipede (Figure 35) could possibly be a troglobite, and thus of particular interest. Spirobolid millipedes, obvious accidentals or entrance zone troglaphiles, were recorded as sight records in Caldwell Ice Cave, Fossil Cave, Four Star Cave, Lyon's Road Cave, and Pearl Cave. All but one of the spirobolids were dead on normal moisture floors. It is probable that most of these specimens, as they were sight records, were misidentifications of the Paeromopodid millipede (Chordeumatida) we report below.



Figure 35. An unusual looking polydesmid millipede on moss in twilight zone of Four Star Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

By far the most interesting family of millipedes at Lava Beds National Monument is the Chordeumatida, represented by three taxa. We hand collected one specimen of the beautiful troglaphilic or accidental millipede *Californiulus* sp. (Paeromopodidae) (Figure 36) from Caldwell Ice Cave. This species, or a closely related one, is also found in caves of the Yosemite/Sequoia NP area (JKK pers. comm.). It may be that the dead millipedes we attributed to Spirobolida (above) actually belong to this taxon. Three specimens perhaps belonging to the family Conotylidae were collected from Caldwell Ice Cave and Lazaroff's Hole. These specimens are probably accidentals, but occurred in relatively dark conditions in the twilight zone (0 and <1 lux) under moderately high humidities (76.1 & 83.9%) and normal to warm temperatures (air, 9.1 & 13.3 °C; soil, 7.8 & 11.8 °C).



Figure 36. *Californiulus* sp. (Chordeumatida: Paeromopodidae) in Caldwell Ice Cave, Lava Beds National Monument, California. Photo by Jean Krejca and Steve Taylor.

The most commonly encountered millipede in our study, and most visible to cave visitors at Lava Beds National Monuement, is *Plumatyla humerosa* (Chordeumatida: Conotylidae) (Figure 37A, and cover photograph). It was recorded from Big Painted, Bulevard, Caldwell Ice, Catacombs, Coral Reef, Cox Ice, Craig, Crazy, Crystal, Deep Cavern, Fossil, Four Star, Lazaroff's Hole, Lyon's Road, Maze, Merrill Ice, Nirvana, NSS #8851, Pearl, Post Office, Rollercoaster, Spider, The Lonely Palace, Upper Heppe, Upper Thicket, and Valentine caves. Most records are based on hand collections or sight records (Figure 37B). This species was encountered frequently in most caves with a significant dark zone and high humidity. It was found almost exclusively where temperatures were in the range of those we found to be typical of deep-cave environments relatively unaffected by multi-entrance airflow issues (Figure 38, and see Figure 8B for comparison). Note that a number of records were from quite cold conditions (Figure 38). While light and relative humidity were somewhat more variable for this species (Figure 39), fully 90% of the records are from setting with less than 10 lux of available light, and 88.8% of the relative humidity readings at sites where this species was recorded were above 85 % relative humidity. Most (60%) of the individuals were found in conditions we characterized as 'normal' cave moisture, while 9.3% were found in dry conditions and 30.7% in wet conditions. Most specimens were found under rocks or on breakdown, or occasionally on

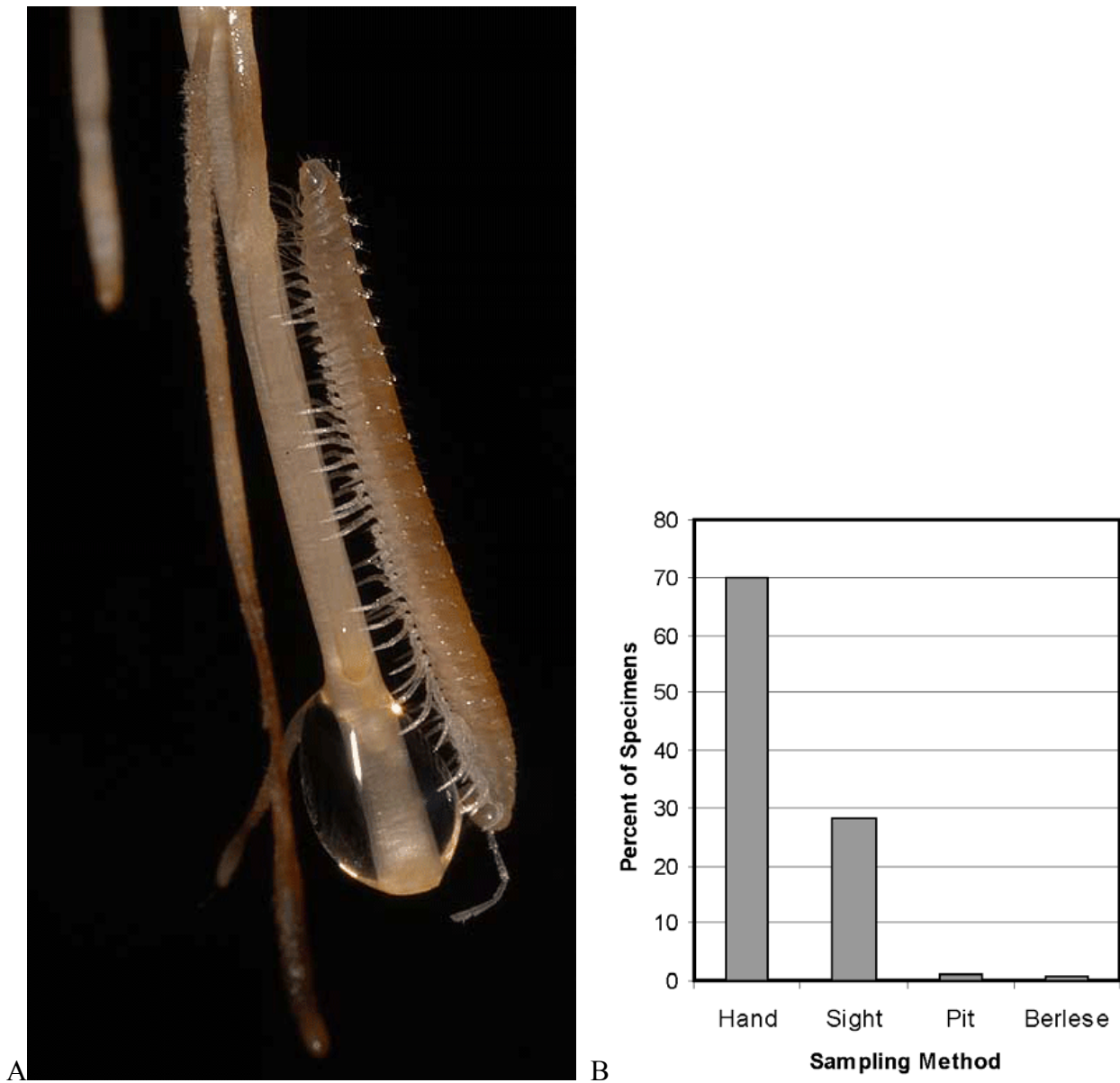


Figure 37. *Plumatyla humerosa* (Chordeumatida: Conotylidae), a common inhabitant of caves at Lava Beds National Monument. A. *P. humerosa* on a root extending down into Catacombs Cave. Photo by Jean Krejca. B. Sampling methods by which *P. humerosa* was recorded (n=170 specimens).

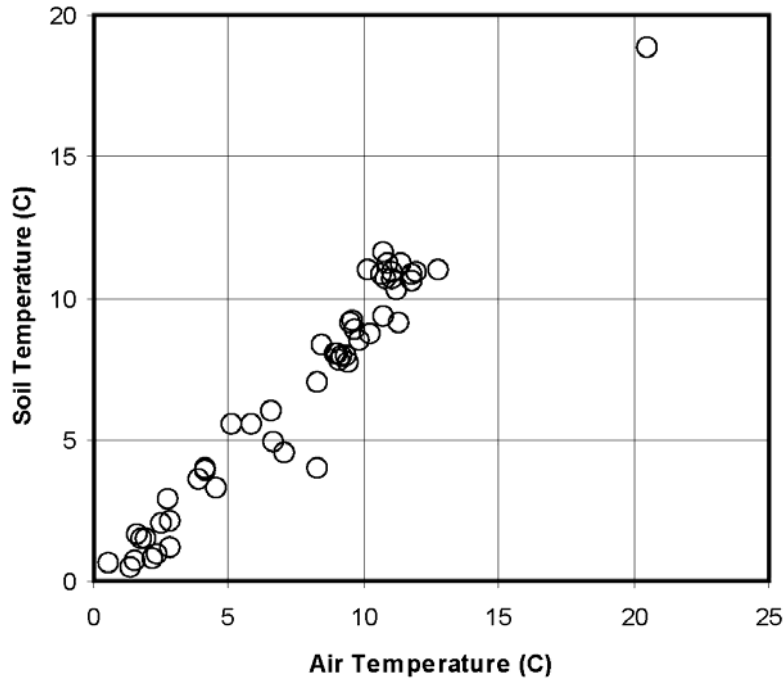


Figure 38. Temperature conditions under which *Plumatyla humerosa* was recorded (n=81 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.

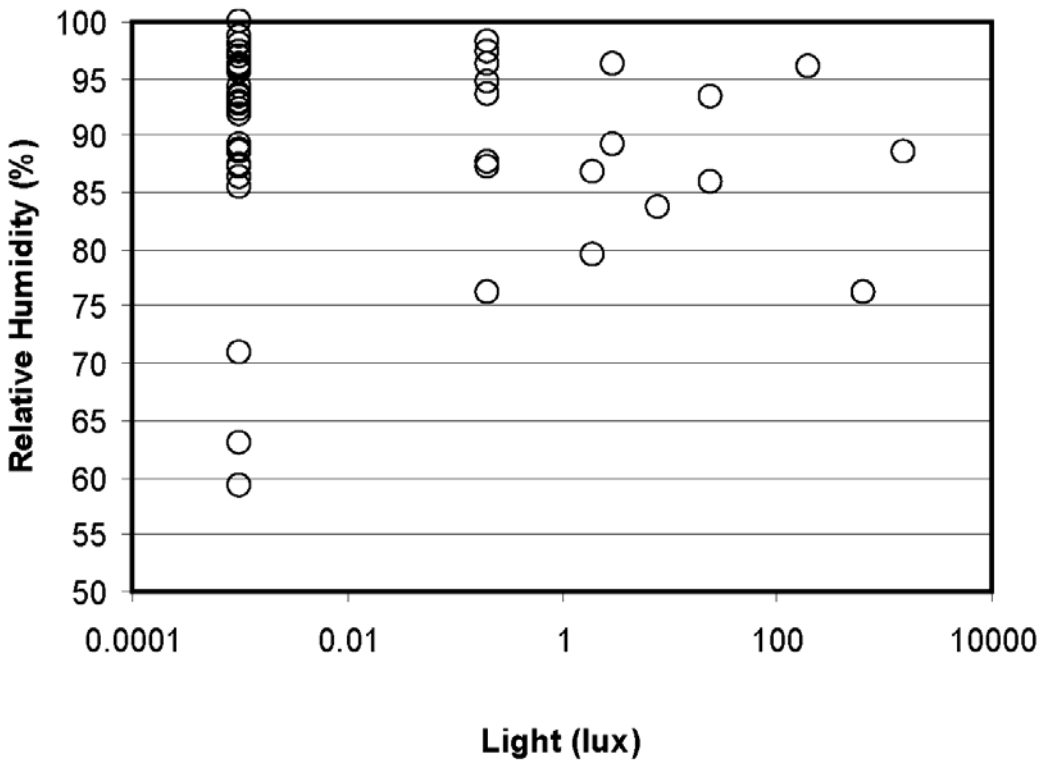


Figure 39. Light and humidity conditions under which *Plumatyla humerosa* was recorded (n=81 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.

bedrock (Figure 40), sometimes in association with guano deposits. Only 4.2% of the *P. humerosa* individuals encountered were found on ceilings, 4.2% on walls, and the rest (91.6%) on the floor. These last statistics may seem counterintuitive to persons familiar with caves at Lava Beds National Monument, because the animals on the walls and ceilings are much more obvious to the casual visitor. Thus, while this species appears to be widespread in caves at Lava Beds National Monument, it is clearly dependent on the maintenance of suitable environmental conditions for its continued prosperity. Because this species is white, often occurs on dark bedrock, and is common, it likely attracts the attention of numerous cave visitors, and park personnel in interpretive positions should become familiar with this species. Further, given the importance of this troglobite in caves at Lava Beds National Monument, it might be prudent to learn more about this animal, by conducting further studies to elucidate aspects of its biology.

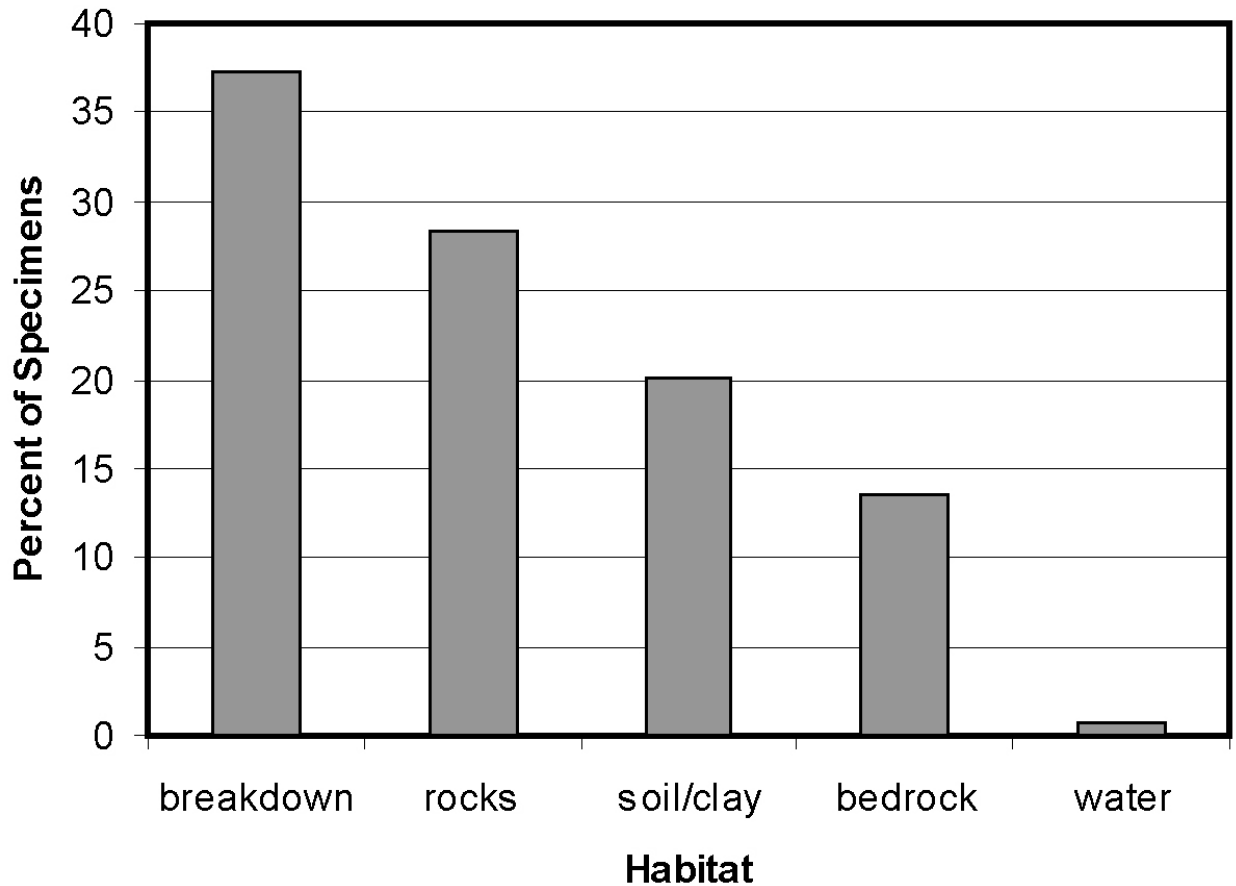


Figure 40. Substrate upon which *Plumatyla humerosa* was recorded (n=130 specimens) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005.

Phylum Arthropoda: Class Chilopoda: centipedes

Centipedes were fairly commonly encountered, especially in the twilight zone. A single specimen of the Order Geophilomorpha was seen in the dark zone (0 lux) of Rollercoaster Cave under conditions of high humidity (95.8%) and normal deep-cave temperatures (air, 6.6 °C; soil, 6.0 °C) in a crack on a normal [moisture] bedrock ceiling. This species is probably an edaphobite. The remaining material belongs to the order Lithobiomorpha (Figure 41A). Unidentified lithobiomorphs were hand collected in Big Painted, Buelevard, Caldwell Ice, Coral Reef, Fossil, Pearl, and Rollercoaster caves. Eight of these occurred deep into the twilight zone (<1 to 659 lux; 76.1-97.3% relative humidity; air, 5.1-13.1 °C; soil, 5.5-11.6 °C), one in the dark zone (0 lux, 97.4% relative humidity, air, 9.0 °C; soil, 8.0 °C), most often under rocks or on soil on normal [moisture] floors. Five additional specimens of Lithobiomorpha were identified to family (Lithobiidae), and were found primarily under rocks, on normal [moisture] floors in the twilight or dark zone (0-3 lux; 63.0-96.3 % relative humidity; air, 9.1-20.6 °C; soil, 7.8-18.8 °C). Lithobiidae were recorded from Caldwell Ice, Coral Reef, Fossil, Lazaroff's Hole, and NSS #8851 caves. The lithobiomorph centipedes are important predators, and are probably troglophiles, though it is possible that smaller pale individuals (Figure 41B), if adult, are more cave adapted.

Phylum Arthropoda: Class Insecta

Insects of 14 orders and numerous families (many still being identified) were recorded from caves at Lava Beds National Monument. They vary from being unimportant accidentals (such as mayflies) to strict troglobites with central roles in the cave community (*Haplocampa* sp. [Diplura]). Further research would doubtless yield additional taxa, as is evidenced by the fact that Crawford's 1989 sampling in November and December yielded an order of important cavernicoles (Grylloblattodea) not recorded during our study.

Order Microcoryphia: bristletails

A single bristletail, an accidental, was collected from the top of a rock on a dry floor in the entrance of NSS #8851 Cave.

Order Thysanura: silverfish

A single silverfish, an accidental, was collected from just inside the dripline of Caldwell Ice Cave (914 lux; 55.4 % relative humidity; air, 10.1 °C; soil, 9.5 °C) under a stone in gravel and *Neotoma* sp. guano on a normal [moisture] floor.

Order Ephemeroptera: mayflies

Two adult mayflies, both in the family Baetidae, were collected from Upper Heppe and Fossil caves. One from a breakdown block near a pool of water, and the other on rocks with moss and ferns. Both collections were from cave entrances (24-1650 lux) and are accidentals, perhaps blown in from Tule Lake, just to the north of the lava fields. The specimen from Fossil Cave belongs to the genus *Callibaetis* (det. R. E. DeWalt, INHS).



A



B

Figure 41. Centipedes (Chilopoda: Lithobiomorpha) from caves at Lava Beds National Monument, California. A. A large lithobiomorph from one of the caves. B. A small, pale lithobiomorph from Boulevard Cave. Photos by Jean Krejca and Steve Taylor.

Order Diplura: diplurans

Although diplurans are clearly hexapods, some consider them - along with the orders Collembola and Protura - to be more primitive (less derived) than the remainder of the Insecta. We found one species of Diplura, an undescribed species of *Haplocampa* (Campodeidae), which was previously reported by Ferguson (1992) from Lava Beds National Monument, based on Crawford's 1989 collections. The species is also listed from seven caves at Lava Beds National Monument by Crawford (in litt., 1998).

Haplocampa sp. (Figure 42) was present in 39 samples representing some 80 specimens, recorded by hand collections (77.6%), sight records (21.2%) and pitfall trap (1.2 %). It was recorded from Bulevard, Coda, Coral Reef, Cox Ice, Craig, Crazy, Crystal, Deep Cavern, Lazaroff's Hole, Lyon's Road, Maze, Merrill Ice, Nirvana, Pearl, Rollercoaster, Upper Heppe and Valentine caves. This species was found exclusively at temperatures typical of deep-cave situations (Figure 43) and almost always in conditions of humidity and light also typical of deep-cave settings lacking the effects of multiple entrances discussed earlier (e.g., drying of the air) (Figure 44). *Haplocampa* sp. was rarely (3.2% of specimens) found on dry substrates, and was about equally frequent on normal (47.6%) and wet (49.2%) substrates, with substrate most typically being composed of breakdown or rocks (Figure 45). Specimens were almost always found on the floor of caves (93.7 % of individuals), but also occasionally on the walls (3.8%) or ceiling (2.5%) of caves, where they are more readily apparent to casual cave visitors (see similar discussion under *Plumatyla humerosa* (Chordeumatida: Conotylidae), above). Like *P. humerosa*, *Haplocampa* sp. is an important and often visible troglobite that interpretive staff should be aware of and upon which further research is warranted.



Figure 42. *Haplocampa* sp. (Diplura: Campodeidae) in Nirvana Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

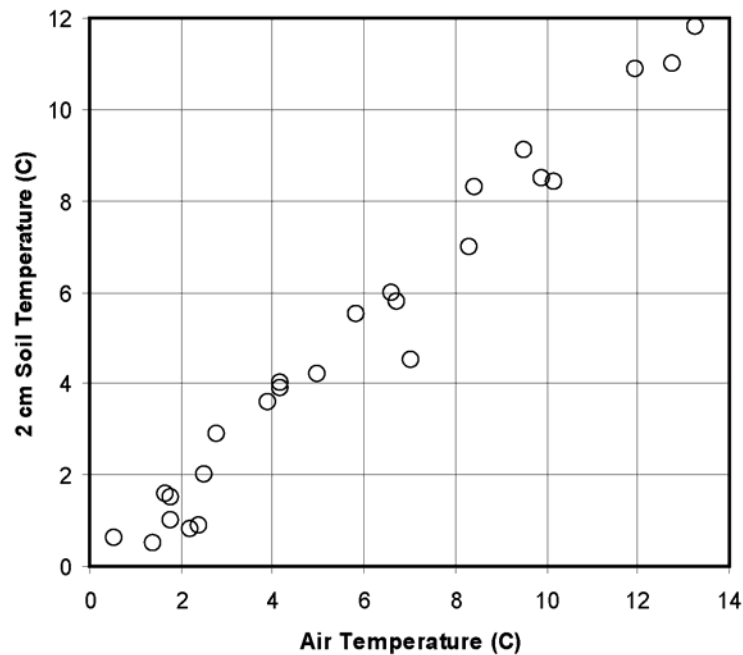


Figure 43. Air and 2 cm soil temperature at sites where *Haplocampa* sp. (Diplura: Campodeidae) was recorded during our survey of caves at Lava Beds National Monument, California, 2 June – 4 August, 2005.

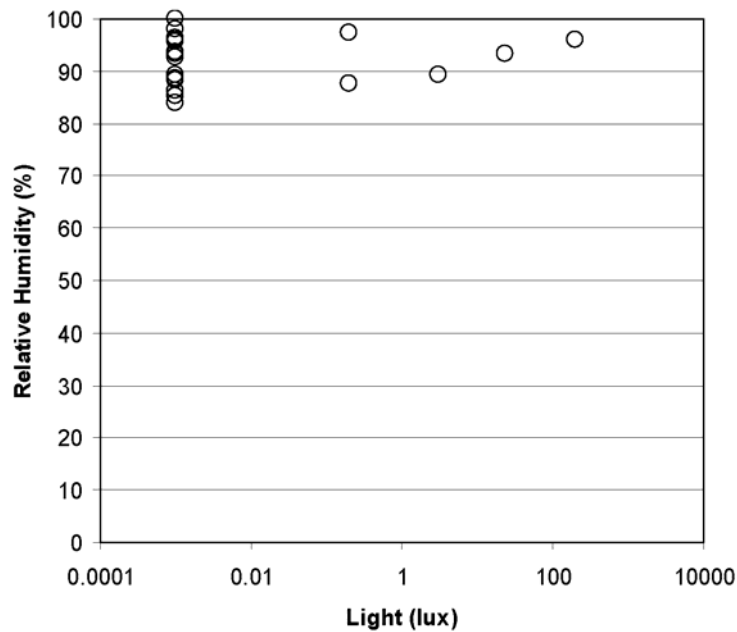


Figure 44. Light and humidity conditions under which *Haplocampa* sp. (Diplura: Campodeidae) was recorded (n=33 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.

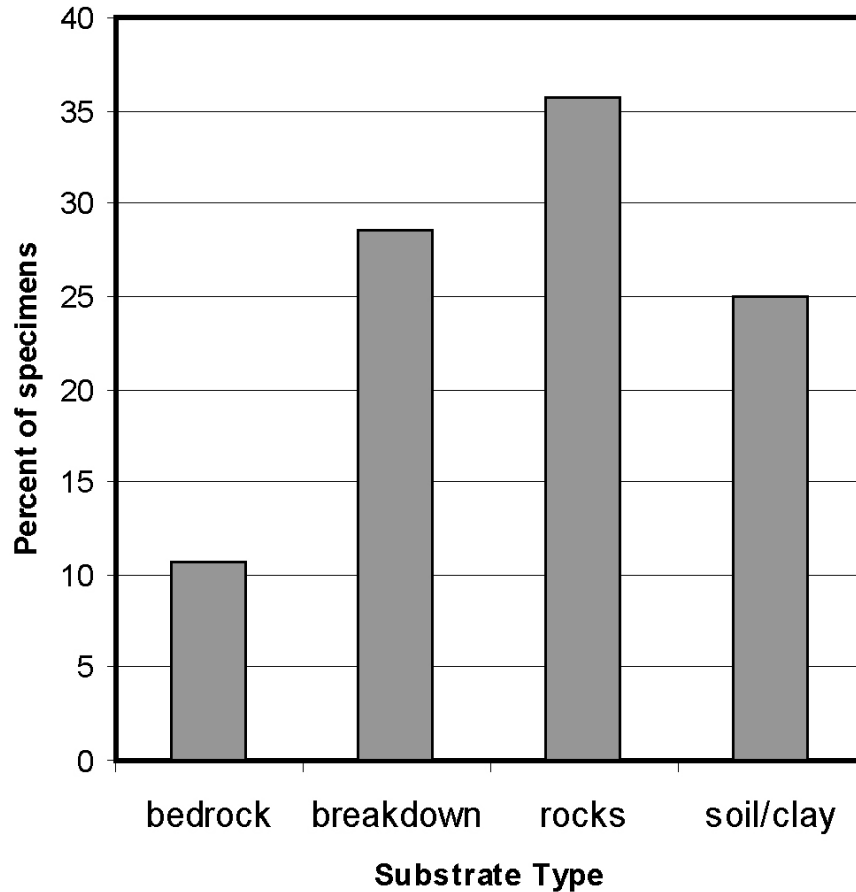


Figure 45. Substrate upon which *Haplocampa* sp. (Diplura: Campodeidae) was recorded (n=56 specimens) at caves in Lava Beds National Monument, California, during field work conducted between 2 June and 4 August, 2005.

Order Collembola: springtails

Springtails were one of the most abundant groups (n=291 specimens), occurring in 94 collections from 18 caves. Of the 94 collections, 82 (87%) were made when SJT and/or JKK were present (2-27 June, 2005), suggesting this group of very tiny organisms was largely overlooked by Pleszewski and Dunn during later collections, and we expect that springtails are present in good numbers in all caves at Lava Beds National Monument. While nearly 70 specimens (generally minute species and immatures) remain unidentified, we have placed the remaining material in the families Arrhopalitidae (globular springtails, formerly assigned to Sminthuridae [e.g., see Crawford {1998, in litt.}]) (6 specimens), Entomobryiidae (15 specimens), Hypogastruridae (23 specimens), and Onychiuridae (10 specimens), and Tomoceridae (167 specimens). A single sight record attributed to Poduridae (1 specimen) is perhaps better assigned to Onychiuridae or Hypogastruridae.

Globular springtails (Arrhopalitidae) were recorded from Caldwell Ice, Catacomb, Coral Reef and Valentine caves. Unfortunately, 4 of the 6 specimens are only represented by sight

records, the remaining two by hand collections. Arrhopalitids were found under normal deep-cave conditions (0 to <1 lux; 76.1-98.2% relative humidity; air, 9.1-11.1 °C; soil, 7.8-10.9 °C) on the cave floor, usually in wet conditions, such as on the surface of small drip pools. Several species in the United States belonging to the genus *Arrhopalites* are troglobites (Zeppelini and Christiansen 2003), and we hope to have our material examined by the expert on this group in the fall of 2006.

Entomobryiid springtails were recorded from Caldwell Ice, Catacombs, Coral Reef, Craig, Fossil, Lyon's Road, Maze, and Rollercoaster caves, and were found in all cave zones (0 to 1537 lux; 55.4-96.2% relative humidity; air, 4.2-11.3 °C; soil, 4.0-11.6 °C). These springtails were usually found on the floor, sometimes in association with soil or organic material. While some may be troglaphiles, others are likely accidentals.

Hypogastrurid springtails were recorded from Caldwell Ice, Fossil, and Rollercoaster caves, generally under deep-cave conditions (0 to <1 lux; 93.9-97.3% relative humidity; air, 8.3-10.8 °C; soil, 7.0-11.1 °C) on the cave floor.

Onychurid springtails, possibly a troglobitic species, were collected in the twilight or dark zones of caves (0 to 25 lux; 88.2-85.9% relative humidity; air, 10.2-10.3 °C; soil, 8.4-8.7 °C) from Coral Reef, Four Star, and Pearl caves. They were taken from the cave floor both by hand collection and Berlese extraction of litter.

Tomocerid springtails (Figure 46) were frequently collected, and probably belong to the commonly cavernicolous genus *Tomocerus*. Crawford (in litt., 1998) reports *Tomocerus curtus* and *Tomocerus californicus* in his samples from 1989 collections at Lava Beds National Monument, and our material is thus likely attributable to those two species. We found these springtails in Bulevard, Catacombs, Coral Reef, Craig, Fossil, Four Star, Maze, Nirvana, NSS #8851, Pearl, Rollercoaster, Spider, Upper Heppe, Upper Thicket, and Valentine caves. Most of the 166 specimens (73.5%) were hand-collected, most others (25.9%) were sight records. These springtails were found almost exclusively in the dark or twilight zones (Figure 47), with 91.8% of the light meter readings at collection sites being less than 10 lux, and 91.7% of the relative humidity values being greater than 85% relative humidity. Tomocerids were found at a variety of temperatures (Figure 48), but 87.8% of the air temperature readings were between 8.4 and 11.9 °C, and 89.8% of the 2 cm soil temperature readings were between 7.9 and 11.2 °C, suggesting that while these animals appear cave adapted – perhaps even functioning as troglobites – they are less capable of dealing with the near-freezing temperatures at which other troglobites, notably *Plumatyla humerosa* (Figure 38) and *Haplocampa* sp. (Figure 43), are commonly found. Tomocerids were usually found on the floor (88.6% of specimens), occasionally on cave walls (10.8%) and usually were associated with substrate moisture levels characterized as “normal” (70.3%) or “wet” (27.3%). Specimens were most commonly found on bedrock or substrates, but also on other surfaces (Figure 49), and these springtails were quite commonly associated with guano (14 specimens), mosses or ferns in the twilight zone (13 specimens) or litter and *Neotoma* sp. middens (6 specimens). Overall, tomocerid springtails are both common and important members of the cave community at Lava Beds National Monument which can easily be overlooked, and are seemingly of little importance in comparison to the “charismatic megafauna” taxa (*Plumatyla humerosa* and *Haplocampa* sp.). But these animals are important in that they are the prey for the invertebrate predators found in the cave – without these springtails feeding on the



A



B

Figure 46. A springtail of the family Tomoceridae (probably *Tomocerus* sp.), a common inhabitant of caves at Lava Beds National Monument. A. Fingertip provides scale. B. Close—up of an individual in Valentine Cave. Photos by Jean Krejca.

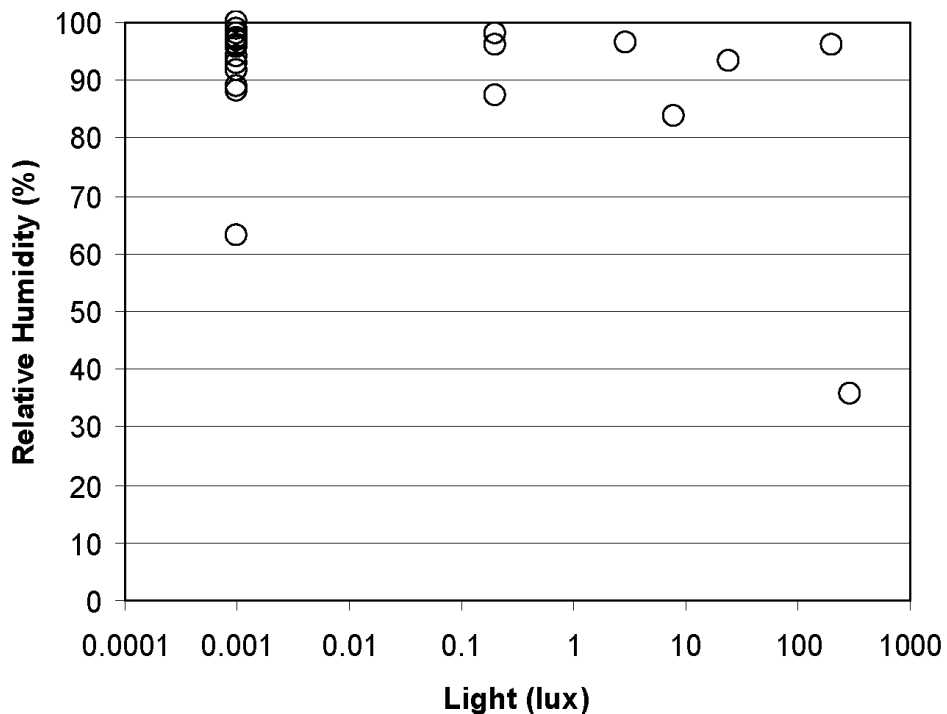


Figure 47. Light and humidity conditions under which Tomoceridae were recorded (n=48 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.

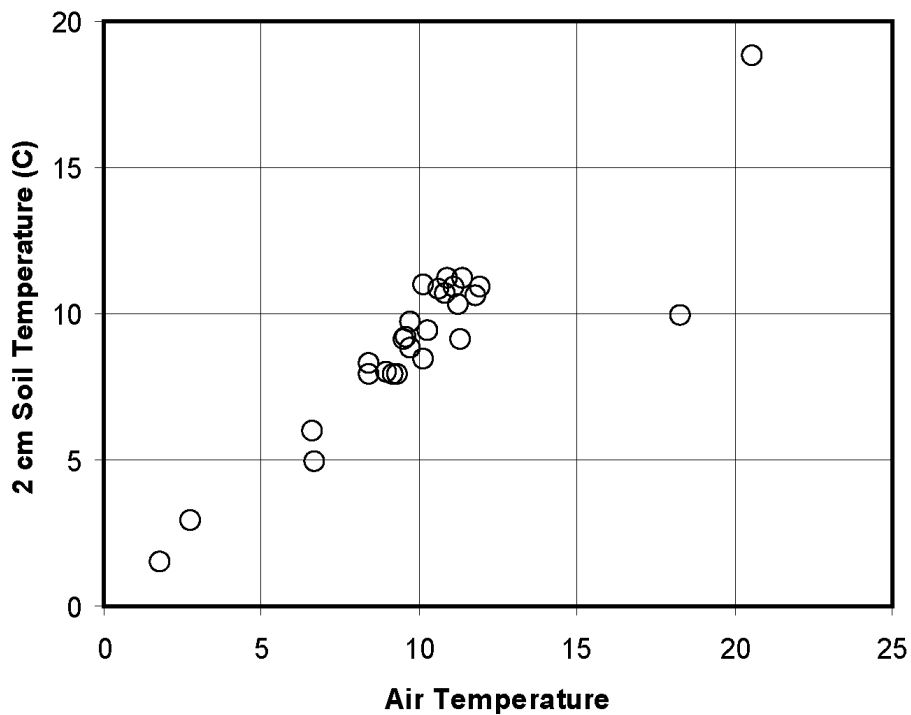


Figure 48. Air and 2 cm soil temperature at sites where Tomoceridae were recorded (n=49 samples) during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.

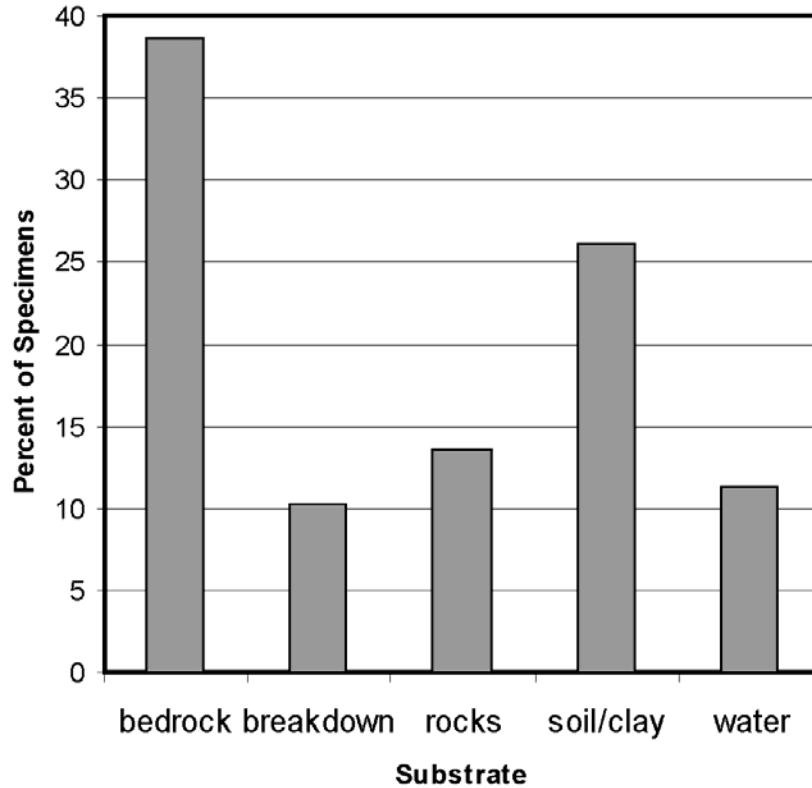


Figure 49. Substrate upon which Tomoceridae were recorded (n=88 specimens) at caves in Lava Beds National Monument, California, during field work conducted between 2 June and 4 August, 2005.

bacterial and fungi growing on feces and other organic debris, the food web of the cave would be incomplete.

Order Psocoptera: book and barklice

Six Psocoptera, perhaps troglophiles, were hand-collected from Craig, Maze, NSS #8851, Rollercoaster, and Valentine caves, where they were most commonly found in deep-cave conditions (0-<1 lux; 96.1-97.3% relative humidity; air, 4.2-9.5 °C; soil, 4.0-9.1 °C). They were found exclusively on the floor, usually (4 of 6 collections) in normal moisture conditions, under a variety of substrates, sometimes on the surface of small pools on bedrock.

Order Thysanoptera: thrips

A single thrip, an accidental, was extracted via Berlese funnel from *Neotoma* sp. midden material from the floor in the dark zone (0 lux; relative humidity 96.7 %; air, 8.4 °C; soil, 7.9 °C) in Rollercoaster Cave.

Order Orthoptera: Family Rhaphidophoridae: cave and camel crickets

Thirty-eight specimens of the cave (or camel) cricket *Ceuthophilus inyo* (Figure 50) were recorded from Bulevard, Coral Reef, Cox Ice, Lazroff's Hole, Lyon's Road, Maze, NSS #8851, Pearl, Spider, Township, and Valentine caves, as well as in the Research Center building in which we stayed during our field visit. This species is a facultative troglaxene, and probably leaves the cave to feed at night, returning to roost in the caves during the daytime, as has been noted for other cave-inhabiting *Ceuthophilus* species (e.g., Campbell 1976, Taylor et al. 2005). In the caves, most records were hand collections (60.5% of specimens) or sight records (36.8%), and while they were reported from a wide range of temperatures (Figure 51), they generally were most abundant at temperatures ranging from 8 to 13 °C, and rarely were encountered at lower temperatures. This species was most commonly encountered in the twilight zone and at humidities in excess of 85% (Figure 52), where it was found in similar numbers on dry (55.9 % of specimens) and normal [moisture] (44.1%) substrates, usually on the cave floor (78.8 % of specimens) or ceiling (21.2 %). *Ceuthophilus inyo* was most commonly found under or on rocks, on breakdown, or on bedrock (Figure 53). Although this species is obviously a common resident or visitor in other habitats (as evidenced by our finding it in a building), it clearly utilizes high-humidity, sheltered habitats in caves, which thus provide an important refuge for this species. Although it's guano is probably not the major energy input into the lava tubes – in contrast to central Texas *Ceuthophilus* species (Taylor et al. 2005) – these crickets do provide energy to the cave community, and may utilize lava tubes as both a daytime refuge and as breeding habitat. Like other important cavernicoles at Lava Beds National Monument, this species deserves further study.

To our surprise, we did not encounter *Pristoceuthophilus caelatus*, another raphidophorid (Orthoptera), previously reported by Crawford (in litt., 1998) as occurring in half of the ten caves he inventoried in November and December of 1989 in Lava Beds National Monument, including several caves that we also sampled intensively. As this species is relatively large and apparent compared to many of the springtails, mites, etc. that we recorded, and because we both have experience finding *Pristoceuthophilus* in caves elsewhere in California, we suspect its apparent absence may reflect a seasonal difference in faunal composition. This same theory may also apply to the grylloblattid *Grylloblatta gurneyi*, (Order Grylloblattodea): Crawford reported this species from seven of the ten caves he sampled, and we have observed grylloblattids in lava tube caves elsewhere in the western United States (e.g., Oregon, Washington).

Order Homoptera: Family Cicadellidae: leafhoppers

A leafhopper, an accidental, was collected from a Berlese litter sample collected from a dry floor with bedrock and rocs in the twilight zone (25 lux; 85.9% relative humidity; air, 10.3 °C; soil 8.7, °C) in Pearl Cave.

Order Lepidoptera: butterflies, moths, and skippers

Lepidoptera were reported from Bulevard, Caldwell Ice, Catacombs, Craig, Spider, and Township caves. Most, but not all, are likely accidentals which have wandered into the entrance or twilight zone of the lava tubes. One such lepidopteran was identified as belonging to the



Figure 50. *Ceuthophilus inyo* (Orthoptera: Rhaphidophoridae) in Maze Cave, , Lava Beds National Monument, California. Photo by Jean Krejca.

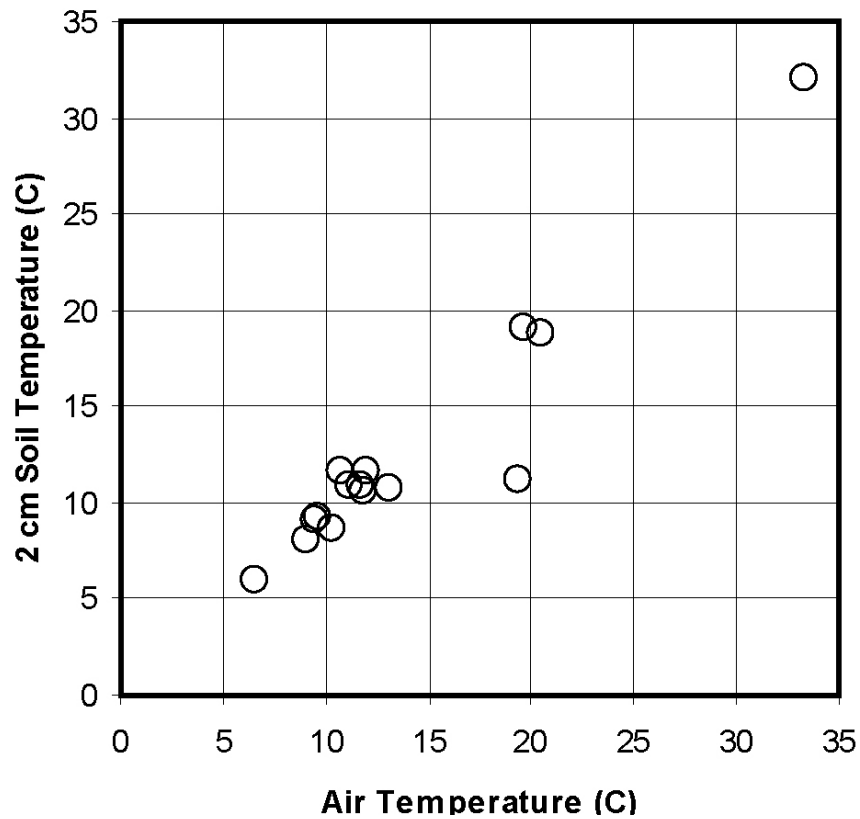


Figure 51. Air and 2 cm soil temperature at sites where *Ceuthophilus inyo* (Orthoptera: Rhaphidophoridae) was recorded (n=21 samples) during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.

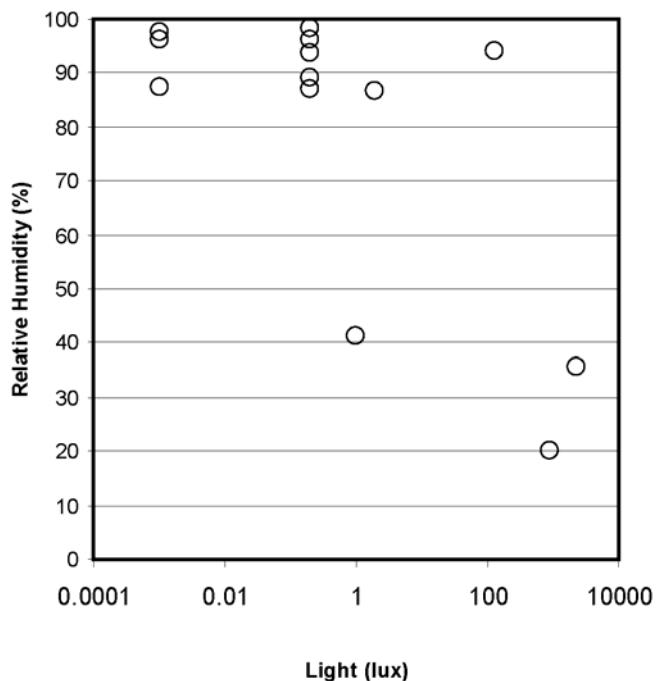


Figure 52. Light and humidity conditions under which *Ceuthophilus inyo* (Orthoptera: Rhaphidophoridae) was recorded (n=21 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.

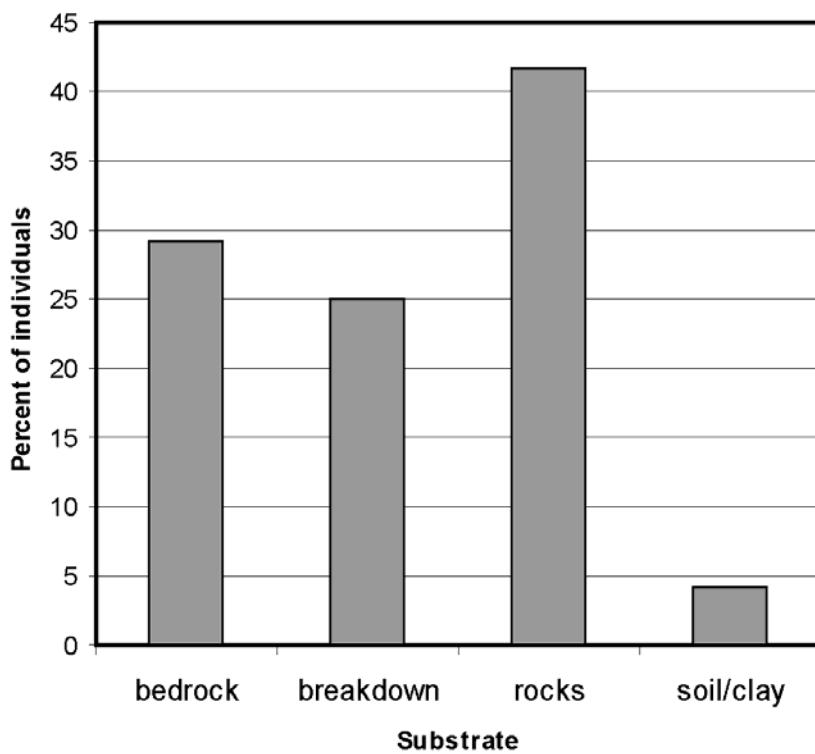


Figure 53. Substrate upon which *Ceuthophilus inyo* (Orthoptera: Rhaphidophoridae) was recorded (n=24 specimens) at caves in Lava Beds National Monument, California, during field work conducted between 2 June and 4 August, 2005.



Figure 54. A moth, perhaps a Plume Moth (Pterophoridae), in the entrance of Catacombs Cave, Lava Beds National Monument, California. Accidentals, such as this moth, commonly wander into caves. Photo by Jean Krejca.

family HesperIIDae, another is probably Pterophoridae (Figure 54). But several small moths are normally associated with guano, and some of our material may represent such guanophiles. Some lepidoptera were noted only on the basis of wings found on the cave floor – a record the feeding activity of bats (which commonly leave moth wings below their roost sites) or spiders (e.g., Figure 29). Lepidoptera were recorded as sight records (5), hand collections (3) and from Berlese extraction of leaf litter (1) from all cave zones (0-1970 lux; 32.5-88.9% RH; air, 2.9-18.9 °C; soil 2.1-19.8 °C), and from cave floors, walls and ceilings.

Order Coleoptera: beetles

Larvae and adults of several beetles, many likely accidentals, remain to be identified, but we recorded four families of beetles from caves at Lava Beds National Monument. Unidentified beetles were reported from Caldwell Ice, Maze, Pearl, Rollercoaster, and Valentine caves, and were recorded via hand collections (4 specimens), berlese extraction of litter (23 specimens), and sight records (2 specimens). Most of this material was larval (70%), the rest adults. These animals were found at normal deep-cave temperatures (air, 8.3-11.2 °C; soil 7.0-10.9 °C), in the dark or twilight zones (0-25 lux) at high humidities (85.8-98.2 %), mostly (96.4% of specimens) on the floor and mostly (89.3% of specimens) under normal moisture conditions. The majority (24 specimens) of these beetles were associated with *Neotoma* middens or guano on bedrock or soil/clay floors.

Order Coleoptera: Family Tenebrionidae: darkling beetles

A single adult darkling beetle was hand-collected from the floor of the twilight zone in Lazaroff's Hole, and is an accidental.

Order Coleoptera: Family Scarabaeidae: scarab beetles

A single adult scarab beetle was hand-collected from the floor of the twilight zone in Spider Cave, and is an accidental.

Order Coleoptera: Family Chrysomelidae: leaf beetles

An adult leaf beetle was hand-collected from the floor of the entrance in Cox Ice Cave, and is an accidental.

Order Coleoptera: Family Staphylinidae: rove beetles

Adult rove beetles (Figure 55), perhaps troglophiles, were found in Catacombs, Coda, Coral Reef, Maze, and Rollercoaster caves, mostly (6 specimens) as hand collections from normal [moisture] cave floors, often in association with *Neotoma* middens, vegetation (moss, ferns), or guano. Except for one individual found in a cave entrance (6400 lux; 45.9 % RH; air, 14.3 °C; soil 10.5 °C), these beetles were found in typical dark zone conditions (0-<1 lux; 85.1-97.3 % RH; air, 5.0-10.8 °C; soil 4.2-11.6 °C).



Figure 55. A rove beetle (Staphylinidae), in Rollercoaster Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

Order Hymenoptera: Family Formicidae: ants

Foraging worker ants, all the same species (perhaps *Camponotus* sp.) and certainly accidental, were occasionally encountered in the entrance, twilight, and dark zones of caves (Coda, Coral Reef, Fossil, Maze, NSS #8851, and Spider caves), and probably occasionally wander in to all caves at Lava Beds National Monument. Except in two cases in the entrances of caves, all ants were found singly. They were recorded in a wide range of environmental conditions (0-6400 lux; 45.9-96.9 % RH; air, 9.6-20.6 °C; soil 9.2-18.8 °C) on normal to dry cave floors on bedrock, rocks, or breakdown, sometimes in association with leaf litter or moss.

Order Hymenoptera: Family Apidae: bees

A single sight record of a bee which flew into the entrance of Four Star Cave, represents an accidental occurrence (though bees do sometimes locate their hives in cave entrances).

Order Siphonaptera: fleas

Four fleas were hand-collected from the floor of Coda Cave in the dark zone (0 lux) under normal to cold deep cave conditions (85.1 % RH; air, 5.0 °C; soil 4.2 °C). These are ectoparasites of mammals, but because they are likely parasites of *Neotoma* sp., they may be regular residents of Lava Beds National Monument caves.

Order Diptera: flies

Among the most abundant, in terms of numbers of specimens (n=340), orders encountered in this study is the Diptera. Many of the flies remain to be identified, and among the unidentified material are numerous examples of two important families, the troglomorphic Sphaeroceridae (Figures 56, 57) and the troglomorphic Heleomyzidae (Figure 57) and. In addition



Figure 56. A small dung-fly (Sphaeroceridae), in Rollercoaster Cave, Lava Beds National Monument, California. Note fungal hyphae on right side of image, indicative of decomposing organic matter. Photo by Jean Krejca.

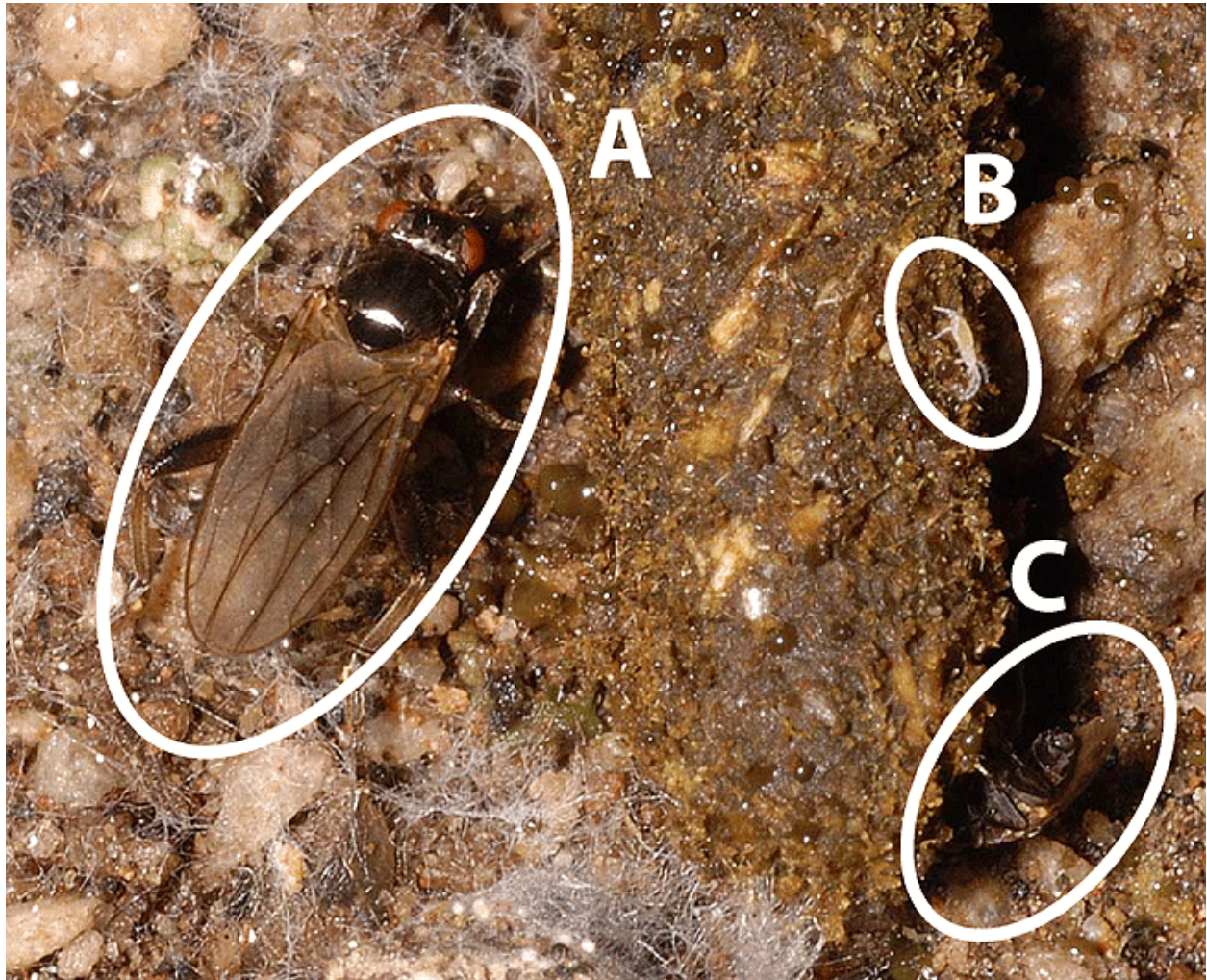


Figure 57. Flies and mite in association with decomposing *Neotoma* guano pellet, in Rollercoaster Cave, Lava Beds National Monument, California. Note abundant fungal hyphae. A. *Aecothea specus* (Aldrich) (Heleomyzidae), a common troglodene. B. A rhagidiid mite. C. A small dung-fly (Sphaeroceridae). Photo by Jean Krejca.

to these two families, much of the remaining material is comprised of accidentals, which are dominated by the cyclorhaphous Brachycera.

Order Diptera: Family Tipulidae: crane flies

Crane flies were hand collected from Craig, Deep Cavern, Spider, Township, and Upper Heppe caves in the entrance or twilight zones (0-47 lux; 45-93.3 % relative humidity; air, 1.8-18.9 °C; soil, 1.5-19.8 °C) on the ceiling or floor on breakdown, rocks, or bedrock, and under dry conditions. These flies are considered accidentals, though they are common in cave entrances which they probably utilize as shelter.

Order Diptera: Family Mycetophilidae: fungus gnats

Fungus gnats were found, primarily on cave floors, in Boulevard, Deep Cavern, Fossil, Lyon's Road, Merrill Ice, Upper Heppe, and Upper Thicket caves. Most specimens were hand collected (n=15), but also were recorded from pitfall traps (3) and as sight records (2). They probably represent troglaphiles or troglaxenes. In addition to adults (n=16), we recorded one larva and 3 pupae (Figure 58). Mycetophilids were usually found under environmental conditions typical of deep-cave dark zones with no influence of multi-entrance airflow (Figures 59, 60).

Order Diptera: Family Psychodidae: moth flies

An adult moth fly, an accidental, was hand collected at Caldwell Ice Cave from the floor under typical twilight zone conditions (<1 lux; 76.1 % relative humidity; air, 9.1 °C; soil, 7.8 °C).

Order Diptera: Family Chironomidae: midges

Midges were collected only from floor-collected Berlese samples from *Neotoma* middens or guano in Pearl, Rollercoaster, and Upper Heppe caves, under dry to normal conditions in the twilight or dark zones (0-844 lux; 77.9-96.7 % relative humidity; air, 6.9-10.3 °C; soil, 7.9-8.7 °C). Although it is tempting to dismiss these records as accidentals, there seems to be a pattern of their occurrence in midden material.

Order Diptera: Family Sciaridae: black fungus gnats

Adult sciarids (Figure 61), probably troglaphiles, were recorded from Big Painted, Coral Reef, Lyon's Road, Merrill Ice and Upper Heppe caves, where most (5 individuals) were hand collected from the floor under a variety of environmental conditions (0-844 lux; 76.1-88.2 % relative humidity; air, 5.1-10.2 °C; soil, 4.0-8.4 °C).

Order Diptera: Family Culicidae: mosquitoes

Adult mosquitoes, considered facultative troglaxenes or accidentals, were hand collected from Boulevard, Nirvana, and Spider caves, where they were mostly recorded from the walls or ceilings of the twilight or entrance zones (0-94,400 lux; 40.4-97.4 % relative humidity; air, 9.0-19.7 °C; soil, 8.0-19.1 °C).



Figure 58. A fungus gnat (*Mycetophilidae*) pupa suspended from the ceiling deep within Lyon's Road Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

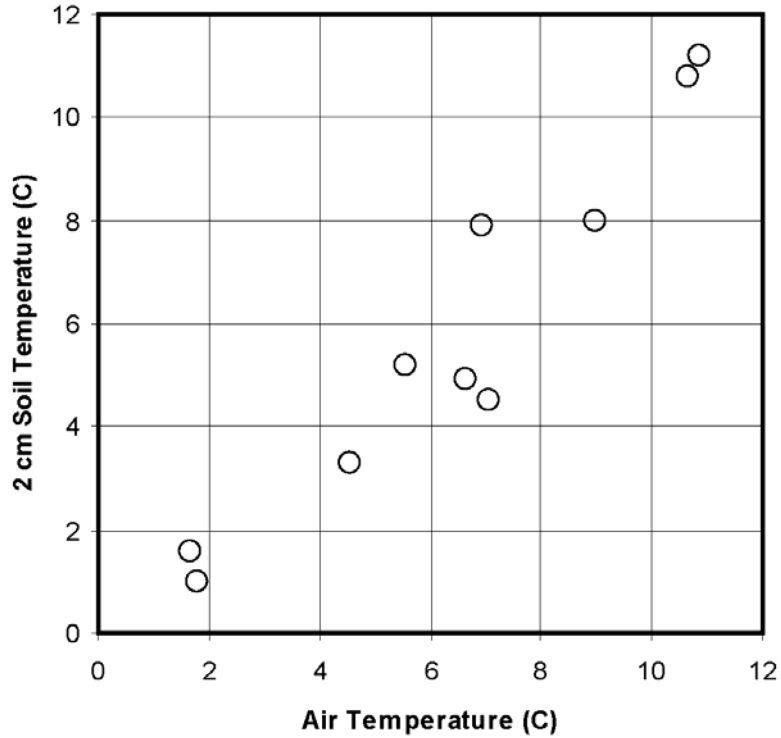


Figure 59. Air and 2 cm soil temperature at sites where Mycetophilidae were recorded (n=11 samples) during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.

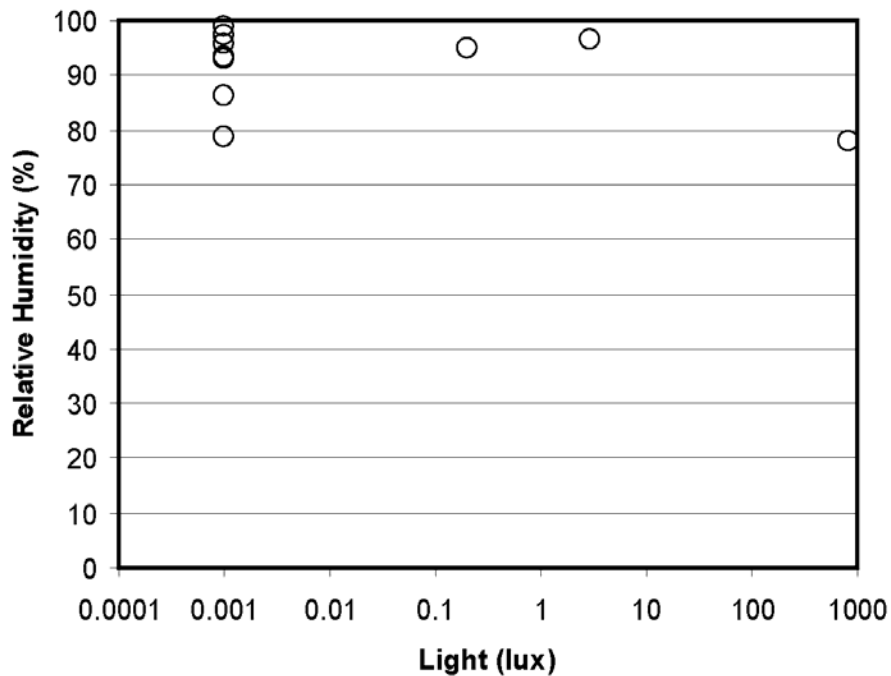


Figure 60. Light and humidity conditions under which Mycetophilidae were recorded (n=11 samples) at caves in Lava Beds National Monument, California, 2 June through 4 August 2005. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.



Figure 61. A black fungus gnat (Sciaridae) in Maze Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

Order Diptera: Family Bombyliidae: bee flies

A sight record of an adult bombyliid fly in the entrance of Catacombs Cave flying near dry bedrock wall/ceiling represents an accidental occurrence (1970 lux; 32.5 % relative humidity; air, 17.2 °C; soil, 11.2 °C).

Order Diptera: Family Scatopsidae: minute black scavenger flies

A sight record of an adult scatopsid fly in the entrance of Spider Cave represents an accidental occurrence (no environmental data).

Order Diptera: Family Syrphidae: flower flies

A sight record of an adult flower fly in the entrance of Catacombs Cave flying near dry bedrock wall/ceiling represents an accidental occurrence (1970 lux; 32.5 % relative humidity; air, 17.2 °C; soil, 11.2 °C).

Phylum Chordata: Subphylum Vertebrata

Although we made no special effort to record vertebrates from the caves, they clearly are an important source of nutrient input into caves of Lava Beds National Monument, and because they influence the structure of invertebrate communities, we discuss the most frequently encountered taxa below.

Class Aves: Order Passeriformes: Family Hirundinidae: swallows

We observed swallows flying in the entrance of Boulevard cave, and in one instance a swallow flew from one entrance to another. Swallows may use walls and ceilings of the entrance and twilight zones for nesting sites.

Class Aves: Order Strigiformes: owls

We observed abundant evidence of owl (probably great-horned owl, *Bubo virginianus* [Strigidae]) usage of the large entrances of Caldwell Ice Cave, including a nest (Figure 62), and found regurgitated owl pellets at several locations in this cave in the entrance and twilight zones.

Class Mammalia: mammals

On a number of occasions we encountered unidentified mammal bones in caves, including many rodent bones and some carnivore bones.

Order Rodentia: Family Cricetidae: *Neotoma* sp.: woodrat

By far the most important mammals, in terms of energy contributed to the cave community, are the woodrats (*Neotoma cinerea* [bushy-tailed woodrat] and *Neotoma fuscipes* [dusky-footed woodrat]). Though we never saw these animals, and heard them only once, evidence of their presence was common in most of the caves we visited. Latrine areas with woodrat guano accumulations provided excellent substrate for microbial and fungal (Figure 63) growth, and were perfect habitats in which to search for various flies, springtails, mites, spiders, and other cavernicoles (Figure 57). These rats also bring in vegetative material from outside the cave to form their 'middens' and to line their nests (Figure 64), and this plant material provides additional nutrients for cave-inhabiting invertebrates. In addition, these animals sometimes die in the caves, as evidenced by the accumulations of rodent bones sometimes encountered, and their bodies provide a rich source of nutrients for opportunistic inhabitants of the caves. Management of caves at Lava Beds National Monument should, therefore, include management practices that maintain natural population levels of these rodents in the caves.

Order Rodentia: Family Erethizontidae: *Erethizon dorsatum*: porcupine

Porcupine quills in Coral Reef Cave suggest this species may be a facultative troglodite in caves at Lava Beds National Monument.



Figure 62. JoAnn Jacoby traverses a ledge above a large open pit and below an owl nest (probably great-horned owl, *Bubo virginianus* [Strigidae]) in Caldwell Ice Cave, Lava Beds National Monument, California. Photo by Jean Krejca.



Figure 63. Fungal growth on a single pellet of *Neotoma* sp. guano in Maze Cave, Lava Beds National Monument, California. Photo by Jean Krejca.



Figure 64. Woodrat (*Neotoma* sp.) nest in Catacombs Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

Order Lagomorpha: Family Ochotonidae: *Ochotona princeps*: pika

Fecal pellets of pikas were encountered in Boulevard and Upper Heppe caves in twilight (198-317 lux) and these animals probably utilize cave entrances to some extent.

Order Chiroptera: Family Vespertilionidae: bats

Bats are important members of the cave community, though in most caves at Lava Beds National Monument their importance is minimal in comparison to the woodrats, *Neotoma* spp. Where they do occur in large numbers, however, their guano provides a rich energy base for other cavernicoles. Lava Beds National Monument has 14 bats species recorded from it, and houses the northern-most population of the Mexican free-tailed bat, *Tadarida brasiliensis mexicana*, as well as the largest hibernaculum of *Corynorhinus townsendii townsendii* (Townsend's big-eared bat). We generally avoided visiting known bat caves during our field sampling, and thus only encountered small numbers of bats – this also means that our study almost certainly under-represents the diversity of guanophilic invertebrates that are associated with large accumulations of bat guano. Evidence of bats came most commonly in the form of skeletal remains (Figure 65, 66) and guano. Such evidence was encountered in Boulevard, Caldwell Ice, Four Star, Lyon's Road, and Nirvana caves under a variety of environmental conditions (Figures 67, 68). Skeletons such as the one in figure 65 are quite fragile and easily overlooked. They provide a record of past bat use of the caves, and as such are a valuable resource for future research efforts. Cave resource managers should be concerned about the potential for trampling of bat skeletons in caves of Lava Beds National Monument.



Figure 65. Bat skeleton in Valentine Cave, Lava Beds National Monument, California. Photo by Jean Krejca.



Figure 66. Bat skull from Lyon's Road Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

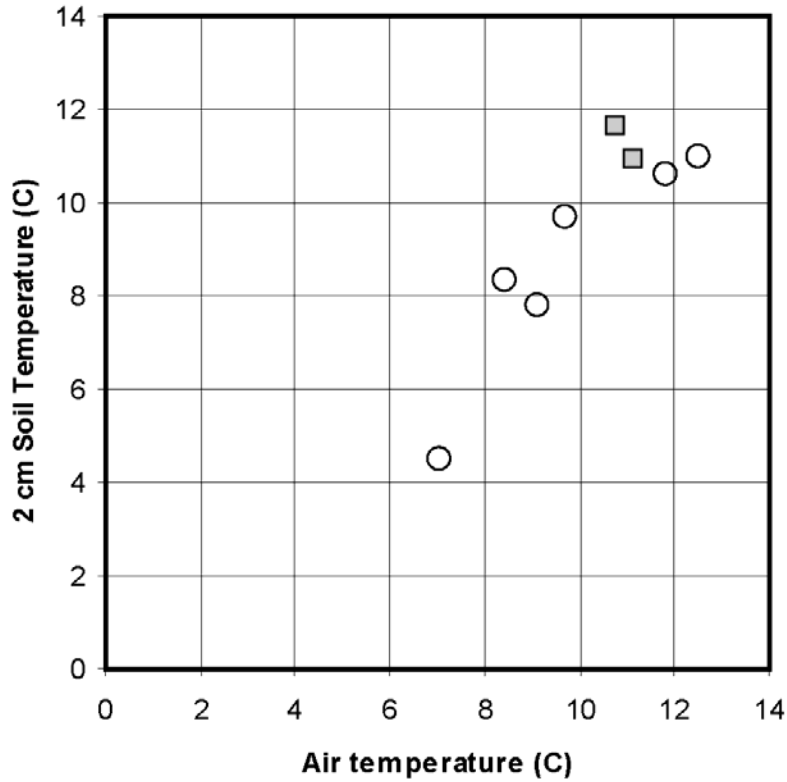


Figure 67. Air and 2 cm soil temperature at sites where evidence of bats (open circles) and living *Corynorhinus townsendii* were encountered during our survey of caves at Lava Beds National Moneument, California, 2 June through 4 August, 2005.

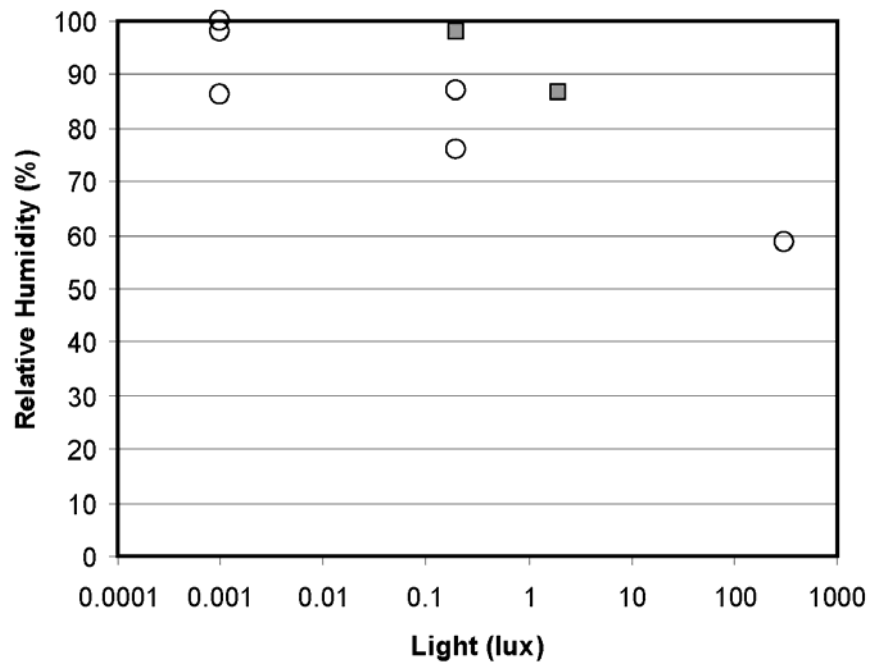


Figure 68. Light and humidity conditions under which evidence of bats (open circles) and living *Corynorhinus townsendii* were encountered at caves in Lava Beds National Monument, California, 2 June through 4 August 2005. Meter readings of “<1 lux” were coded as 0.2 lux, values of 0 lux have been changed to 0.001 lux to allow them to be plotted on the log₁₀ scale.

Order Chiroptera: Family Vespertilionidae: *Corynorhinus townsendii* (Townsend's Big Eared Bat)

The only living bat species we encountered was *Corynorhinus townsendii* (Townsend's Big Eared Bat), which was observed in Coral Reef, Rollercoaster and Valentine caves. This species was found under temperature conditions at the upper end of the range at which skeletal and guano evidence were observed (Figure 67), and always at high humidities (Figure 68) in the twilight zone. These bats are a valuable resource, and cave resource managers should consider the possibility that caves, or portions of caves, where the species is frequently encountered should have some restrictions to access.

Plants

Cave entrances and the twilight zone have a moderating effect on environmental parameters and thus in harsh climates, especially in the arid western United States, they can provide refuge for plant taxa not commonly encountered in harsher surface environs. Such taxa include mosses (Figure 69) and ferns (Figure 70). While we did not make any particular effort to inventory the flora found in the entrance and twilight zones of the caves we visited, we did photograph one fern though to be *Aspidotis californica* (Figure 70), a rather unusual species for the area. Another cave, Fern Cave, is named for the lush growth of ferns found in the entrance area.



Figure 69. Jean Krejca (left) collecting in the moss-covered entrance of Four Star Cave, while JoAnn Jacoby (right) takes notes. Caves provide a refugium of low light levels and consistently higher humidity for sensitive plant taxa. Photo by Steve Taylor.



Figure 70. The fern *Aspidotis californica* in a cave entrance at Lava Beds National Monument. Photo by Steve Taylor.

Comparison of the Fauna of Inventoried Caves

The caves at Lava Beds National Monument do not exist in isolation from one another. Groups of caves often correspond with segments of the same lava tube (Figure 71), which may continue for a considerable distance across the landscape. In addition, groups of caves are separated by distinct lava flows (Figure 72) that have occurred over time, and represent potential barriers (or perhaps corridors?) for cave invertebrates. In addition, the caves are influenced by the varied vegetative zones (Lahr 1960, Erhard 1979) and at different elevations. All these factors have potential explanatory value when we try to look for patterns in the distribution of the fauna at Lava Beds National Monument.

For purposes of searching for possible patterns among caves, and to facilitate management of individual caves, we tallied taxon presence absence (1/0) at the caves based on the level of identification we have thus far achieved Table 3. Some unidentified material was excluded from this analysis, notably unidentified springtails, flies, and spiders, along with *Neotoma* sp. (because we failed to consistently record its occurrence in caves, and feel that

woodrats are much more widespread in the caves than our data indicate). Addition of these taxa could alter the outcome of our analysis.

Examination of Table 3 reveals that there is considerable differences among caves in numbers of taxa recorded (Figure 73), with an average of 7.13 taxa per cave. Based on the earlier detection of methodological discrepancies between the first part of the field work (2 June – 17 June when SJT, JKK, and JJ were present) versus the latter portion ending 4 August, we evaluated differences between these two periods and found that there were significantly more taxa recorded per cave (two tailed t-test, unequal variance: $t=5.252$, $df=26$, $p<0.0001$) in the first part of the study (mean=10.125 taxa per cave) than in the latter part of the study (mean=3.714 taxa per cave). This finding limits considerably our ability to interpret the distributional data in light of the factors discussed earlier in this section, but because the caves sampled during the two periods are well intermingled and because restricting the analysis to the first part of the field work would result in too few caves to draw meaningful conclusions, we decided to move forward with the analysis in spite of the shortcomings of the data.

We first grouped caves by the five regions indicated in Figure 72 (i.e., A-E), and these are listed in Table 4. There are large differences between the zones in mean number of taxa (4.5-12 taxa per cave), but these differences can largely be explained by the uneven sampling discussed in the preceding paragraph (Figure 74).



Figure 71. View of typical terrain at Lava Beds National Monument. Note collapsed lava tube segments in foreground. Photo by Jean Krejca.

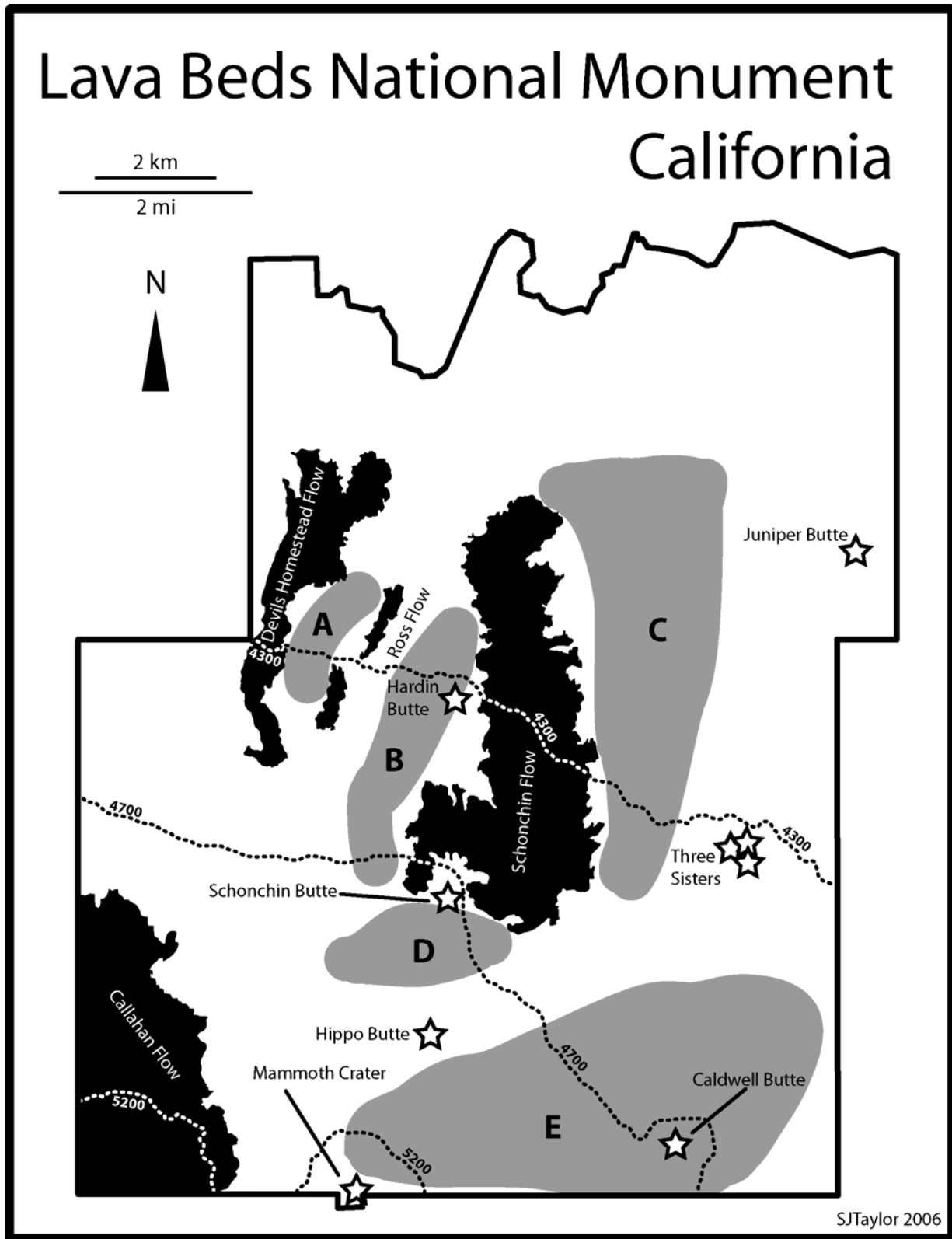


Figure 72. Map of Lava Beds National Park showing major flows (black), areas in which caves were sampled (gray), major buttes (stars), and elevation contours (dotted lines).

Table 3. Taxon presence absence at caves inventoried between 2 June and 4 August 2005 at Lava Beds National Monument.

Taxon	Sentinel Cave	Willy's Pipe Dream Cave	The Lonely Palace	Crazy Cave	Crystal Cave	Post Office Cave	Big Painted Cave	Upper Thicket Cave	Cox Ice Cave	Merrill Ice Cave	Deep Cavern Cave	Township Cave	Nirvana Cave	Coda Cave	Craig Cave	Lazaroff's Hole	NSS #8851	Four Star Cave	Catacombs Cave	Spider Cave	Valentine Cave	Fossil Cave	Lyon's Road Cave	Maze Cave	Pearl Cave	Upper Heppe Cave	Bulevard Cave	Coral Reef Cave	Rollercoaster Cave	Caldwell Ice Cave	total		
Neotoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	
Pseudoscorpiones (TB)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	
Symphyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Californiulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Julida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Polydesmida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Geophilomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Microcoryphia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Thysanura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Baetidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	
Callibaetis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Thysanoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Cicadellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	
Tenebrionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scarabiidae?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Chrysomelidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Apidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Siphonaptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Psychodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Bombyliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scatopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Syrphidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hirundinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Strigiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Erethizon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	

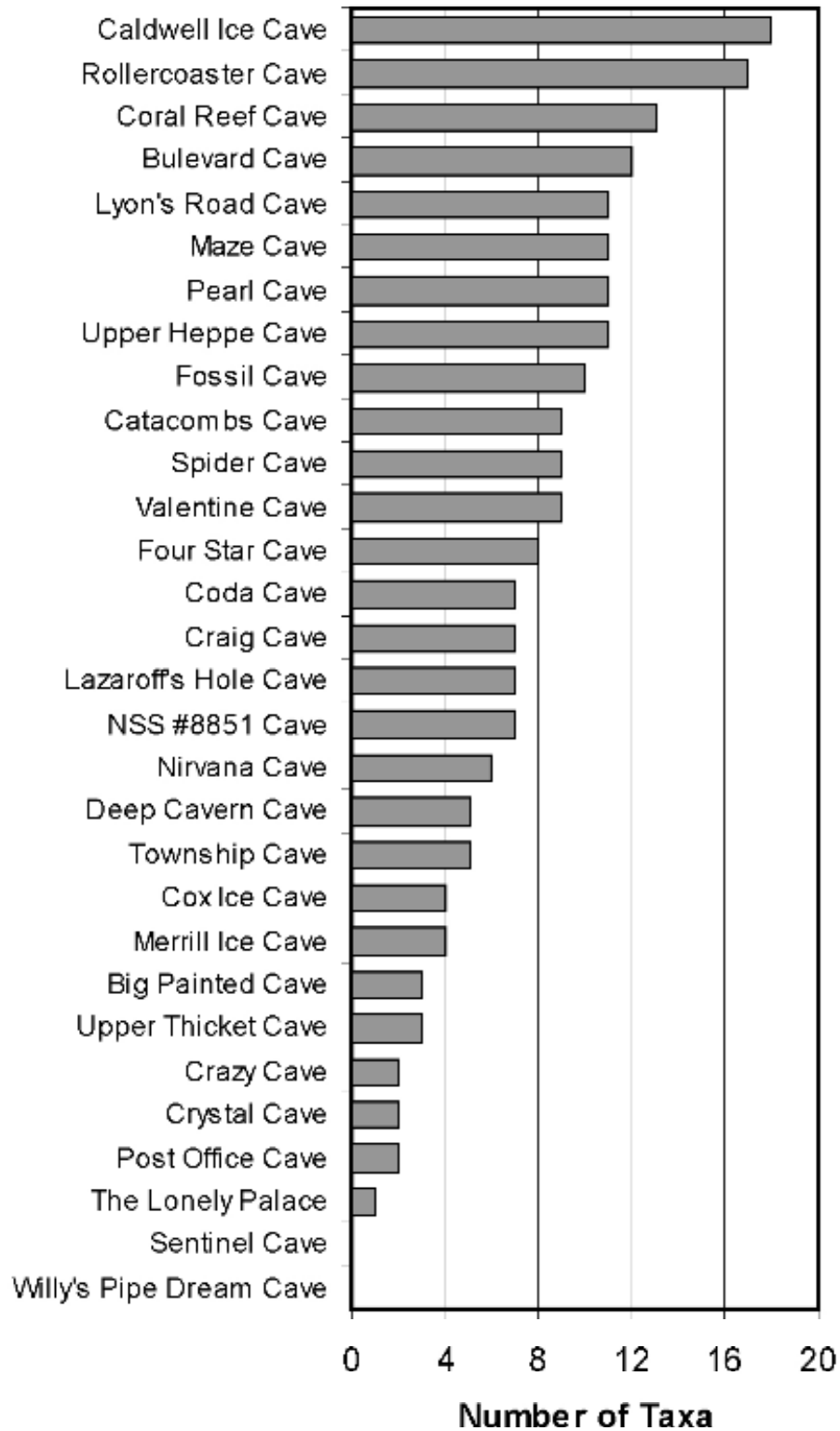


Figure 73. Number of taxa recorded per cave in our 2 June – 4 August 2005 bioinventory at Lava Beds National Monument.

Table 4. Cave groups based on regions delineated in Figure 72. Coda Cave is not included because we lacked location data for this site.

- | | |
|-------------------------|--------------------|
| Group A: | Group D |
| Four Star Cave | Big Painted Cave |
| Pearl Cave | Merrill Ice Cave |
| Rollercoaster Cave | Lazaroff's Hole |
| Group B: | Group E |
| Crazy Cave | Crystal Cave |
| Township Cave | Post Office Cave |
| Nirvana Cave | Upper Thicket Cave |
| NSS #8851 Cave | Cox Ice Cave |
| Bulevard Cave | Craig Cave |
| Group C | Catacombs Cave |
| Sentinel Cave | Spider Cave |
| Willy's Pipe Dream Cave | Valentine Cave |
| The Lonely Palace | Maze Cave |
| Deep Cavern Cave | Upper Heppe Cav3 |
| Fossil Cave | Coral Reef Cave |
| Lyon's Road Cave | Caldwell Ice Cave |

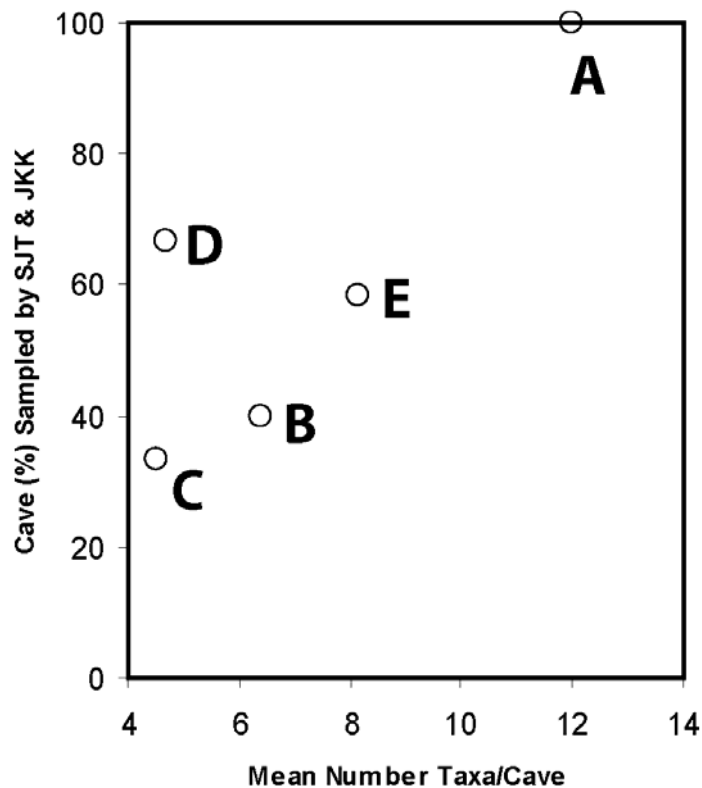


Figure 74. Mean number of taxa per cave by zones indicated alphabetically in Figure 72, versus percent of caves in that zone that were sampled by SJT and/or JKK during the 2 June – 4 August 2005 bioinventory of caves at Lava Beds National Monument, California.

Another approach to examining the data in Table 3 is to look at elevation or vegetation zones. We used the vegetative zones delineated by Lahr (1960) to examine the possibility that vegetation zone could explain variation in taxon richness. But Lahr's (1960) four vegetation zone zones are divided on the basis of elevation (indicated on Figure 72), so we could not separate elevation versus vegetation effects, and had to assume that an trend detectable by this method resulted from some combination of factors related to these two variables. We found that as we moved up in elevation through Lahr's (1960) vegetative zones that there was a sequential increase in taxon richness: annual brome grass area (<4300 feet, 3.5 taxa per cave), sage/perennial bunch grass/juniper area (4300-4700 feet, 7.7 taxa per cave), mountain mahogany/ bitterbrush area (4700-5200 feet, 8.7 taxa per cave), and yellow pine/bitterbrush/ mountain mahogany area (>5200 feet, 11 taxa per cave). Unfortunately, when we plotted these data against the percentage of caves sampled by SJT and/or JKK (Figure 75), we found an apparent strong effect of field crew on taxon richness by vegetative zone/altitude, and thus we cannot draw any conclusions from these data. In fact, when we exclude the data collected by RP & SD, the average taxon richness cave (of the 16 remaining sites) for the four vegetative/elevation zones is 10, 9.6, 11.0, & 11 , respectively, suggesting that there is not effect of vegetation or elevation at the scale of this study. It would be interesting to conduct such an analysis on a larger scale across lava fields of the western United States.

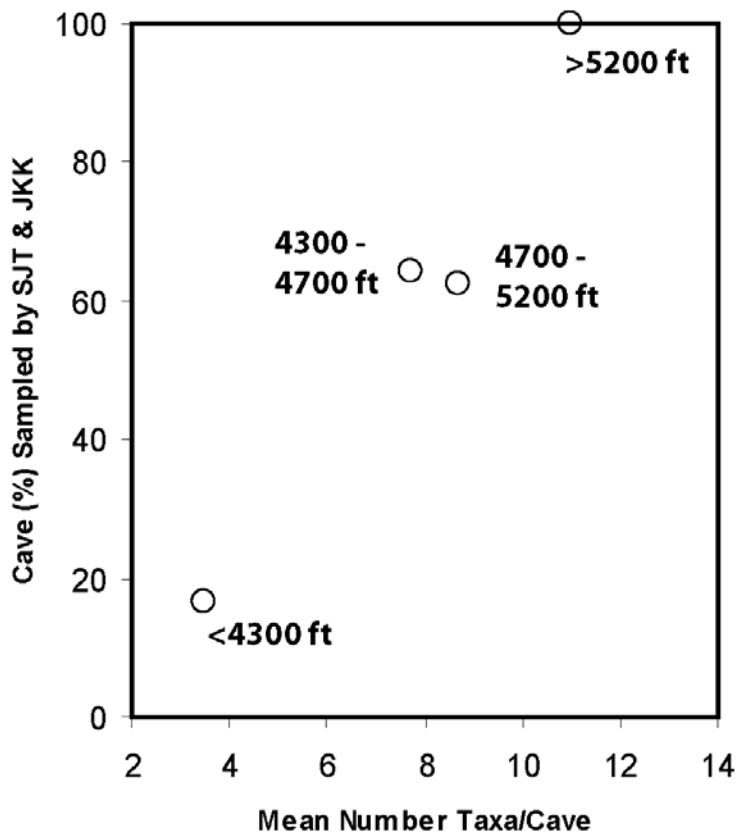


Figure 75. Mean number of taxa per cave by elevation zones (corresponding to vegetation areas delineated by Lahr [1960]), versus percent of caves in that zone that were sampled by SJT and/or JKK during the 2 June – 4 August 2005 bioinventory of caves at Lava Beds National Monument, California.

Finally, we focus on the taxa we consider to be the most important in the caves at Lava Beds National Monument – do these taxa show any distributional patterns? From Table 5, we can see that some of these taxa, such as the troglobitic pseudoscorpion and troglobitic trichoniscid isopod were each found in only one of the regions indicated on Figure 72, and also only in one vegetative/elevation zone. For the trichoniscid, the fact that they were found in three caves yet only one zone is suggestive of the possibility that they may be restricted in distribution at Lava Beds National Monument. Further field work in the National Monument and in surrounding lava fields would be necessary to determine if this species is as highly restricted in distribution as it appears. Other taxa, such as the troglobitic dipluran (*Haplocampa* sp.), the common troglobitic millipede (*Plumatyla humerosa*), the tomocerid springtails, and the cave cricket (*Ceuthophilus inyo*) seem to occur in caves across all regions of Lava Beds National Monument.

Cave communities at Lava Beds National Monument

From the information we have amassed and examined above, we can sketch a general picture of cave communities at Lava Beds National Monument. Most of the passage the casual visitor encounters while exploring the lava tubes appears to be a harsh environment of bare, unforgiving bedrock, with little evidence of life (Figure 76). But when we get down on our hands and knees and take a closer look, there is much to see. The fauna varies considerably as one moves from the entrance, influenced by fluctuating light, humidity, and temperature deeper into the cave where conditions of total darkness prevail and humidity is elevated to a relatively constant value above about 85 % (Figure 77). Temperature in the deep zone varies from near freezing to about 12 °C, depending upon the configuration of the cave. Some taxa occur throughout this temperature range, but others appear to be primarily restricted to the warmer end. In addition to the two troglobites *Plumatyla humerosa* and *Haplocampa* sp. (Diplura) that are frequently encountered by cave visitors, smaller organisms such as rhagidiid mites and tomocerid springtails comprise important components of the cave community. Woodrats and bats provide much of the energy input into these caves, and the *Neotoma* middens, along with feces of both taxa, are the most rich and visible energy sources in many of the caves. Tree roots sometimes penetrate through cracks in the cave ceilings and provide additional habitat, as well as a route for water to enter the caves (Figures 37, 78).

The only obvious threat to cave communities which we encountered during our bioinventory was visitation. Tourists visiting the caves undoubtedly trample cave invertebrates, and in heavily visited caves, the number of casualties may be quite high. Indeed, during our bioinventory we observed a centipede that was freshly crushed in a footprint that matched the boot of one of our party – it is all too easy to crush tiny invertebrates even when you care about them! Cave adapted animals generally have low metabolic rates, long lives, and low rates of reproduction (Culver 1982, Howarth 1983, Poulson and White 1969), and thus the high visitation caves have been, and probably will continue to be, seriously impacted by human activities. Fortunately, most visitation is restricted to relatively few caves, and resource managers must keep in mind the educational value of allowing access, while balancing this against sensitive resources. We have identified several taxa with more restricted distributions, and they generally occur at caves with lower levels of visitation. We recommend that cave resource managers restrict access to such caves, especially given that there is a large number of other caves available

Table 5. Numbers of caves by zone indicated in Figure 72 (A), and by elevation/vegetation zone (B), in which taxa of special interest were found during the 2 June – 4 August 2005 bioinventory of caves at Lava Beds National Monument, California. Coda Cave is not included in this summary because we lacked location data for this site.

A

Taxon	A	B	C	D	E	Total Number of Zones
PseudoscorpionesTB	0	0	1	0	0	1
Trichoniscidae	0	0	0	0	3	1
Corynorhinus	1	0	0	0	2	2
Arrhopalitidae	0	0	0	0	4	1
Rhagidiidae	2	3	1	0	4	3
Ceuthophilus	1	3	1	1	5	5
Tomoceridae	3	3	1	0	8	4
Haplocampa	2	3	2	2	7	5
Plumatyla	3	4	4	3	12	5

B

Taxon	<4300	4300- 4700	4700- 5200	>5200	Total Number of Zones
PseudoscorpionesTB	0	1	0	0	1
Trichoniscidae	0	0	3	0	1
Corynorhinus	0	2	1	0	2
Arrhopalitidae	0	1	3	0	2
Rhagidiidae	1	6	2	1	4
Ceuthophilus	1	7	3	0	3
Tomoceridae	1	9	4	1	4
Haplocampa	1	9	5	1	4
Plumatyla	3	14	8	1	4



Figure 76. Lava tubes can appear to be only barren bedrock devoid of life, as in this section of passage in Valentine Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

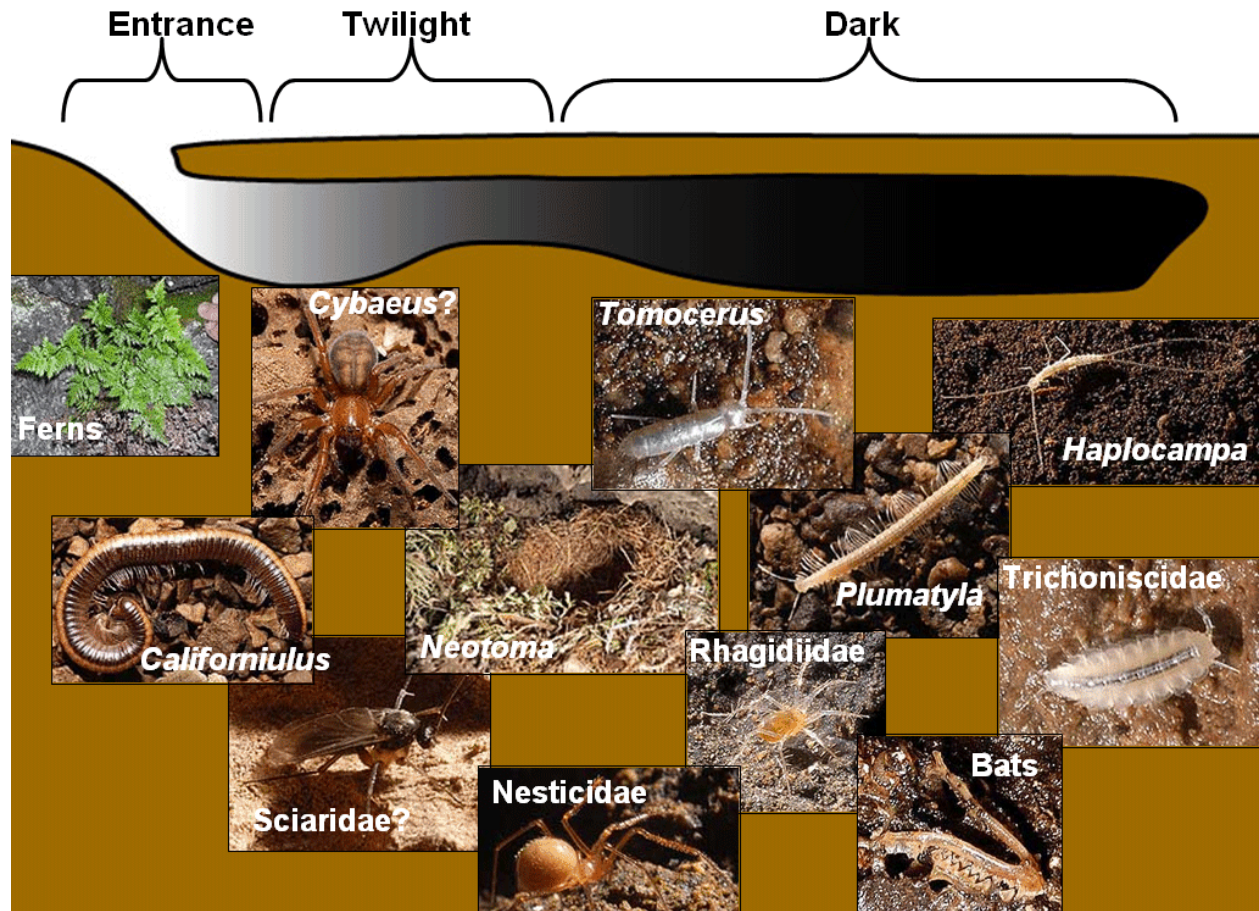


Figure 77. A diagrammatic representation of cave zones commonly found at Lava Beds National Monument, and some of the organisms which can be found in these areas.



Figure 78. A tree root in the ceiling of Catacombs Cave, Lava Beds National Monument, California. Photo by Jean Krjeca.

for visitors to enjoy. In addition, it is important to try to bridge the gap between scientific study and interpretation/education. We recommend that park personnel work to educate interpretive staff with regards to the diverse, fascinating, and perhaps totally unique fauna that inhabits the caves. We also recommend that interpretive displays be developed that provide detailed information about the cave fauna, including images that will allow visitors to understand what they see in the caves.

Training of NPS staff

During the course of our field work, we had the opportunity to work closely in the caves (Figure 79) with NPS Lava Beds National Monument staff (Robert Pleszewski, Sean Dunn, and Dave Larson), who were exposed to various collecting techniques and to methods for field identification of common taxa. We also discussed an assortment of potential management issues with Lava Beds National Monument's Chief of Resources, Dave Larson, and provided NPS staff with a presentation on our findings prior to the completion of our field work.

Future monitoring and research

Our study has highlighted several taxa as being quite important in the caves. Maintenance of natural vegetative communities around caves seems not to be a problem at present, but continuing to manage for natural communities is encouraged – bats, cave crickets, and woodrats all forage outside of the caves (bringing energy to the rest of the cave community) and require natural habitat to ensure their continued well being. The extent of the distribution of woodrats (*Neotoma* spp.) in the caves warrants more detailed study, as do the common troglobites *Haplocampa* sp. (Diplura) and *Plumatyla humerosa* – we know virtually nothing of their life history and needs. How can such valuable resources be managed if we don't know what they do? We hope to have names for the dipluran, trichoniscid, and the troglobitic pseudoscorpion – these taxa will probably turn out to be new species, and, at least until further studies are made in the region, may be considered endemic to the area. Further, the role of the smaller organisms and cycling of nutrients in the caves warrants further study. And finally, we noted that two taxa recovered by Crawford in his 1989 inventory were not present in our sampling – are there seasonal patterns to faunal diversity and abundance? Further study is needed to address these questions.

While we were pleased to have the additional material collected by RP and SD, which provided additional distributional records for some taxa, differences between their sampling and ours highlighted the value of having a professional conduct future monitoring at Lava Beds National Monument. It is, however, certainly possible to train appropriate personnel to carry out monitoring, and we suggest that if this is done the focus be on a few important taxa. Monitoring by non-biospeleologists might be most effective if inventories are conducted as timed area searches, with segments of passage delineated and then inventoried only for the presence of *Haplocampa* sp. and *Plumatyla humerosa* – these two taxa are large, hard to misidentify, and often easily seen. Because such inventories are likely to have a lot of noise in the data, it is necessary to conduct numerous inventories over a number of years before trends are detectable. The transect-based quadrat approach is not recommended for monitoring because few organisms were detected by this method. Monitoring should include collection of detailed information regarding temperature and humidity, but we caution that humidity measurement must only be carried out with appropriate equipment, designed to function well above 95% relative humidity

(i.e., not Onset HOBO ® or Kestrel ® meters). Monitoring locations for timed area searches, and locations where temperature, humidity, and light readings are recorded, should be noted on maps of the caves. We also recommend that NPS continue to work with the Cave Research Foundation to map the caves in the park. Older cave maps should eventually be replaced with new maps based on modern cave survey standards, with all cave maps eventually moving into a GIS database.



Figure 79. NPS staff (red helmets, Sean Dunn [left] and Robert Pleszewski [right]) listen to Steve Taylor [right] as JoAnn Jacoby prepares to take notes at the entrance to Valentine Cave, Lava Beds National Monument, California. Photo by Jean Krejca.

Acknowledgements

We are most fortunate to have had JoAnn Jacoby (University of Illinois, Champaign, IL) along as our faithful field assistant for this study. Her energetic and cheerful demeanor, clear and diligent note taking skills, and sharp eyes for detecting little critters greatly improved this project. In addition, JoAnn read and improved an earlier version of this document. We greatly appreciate the efforts of Robert Pleszewski and Sean Dunn (Lava Beds National Monument, Tule Lake, CA) in collecting data from numerous caves after our departure from the field site, allowing us to provide a broader picture of the fauna of Lava Beds National Monument. Both also joined us for field work on numerous occasions and we appreciate their help. Robert Pleszewski also spent many hours searching through files and helping us determine which caves to visit, providing maps and directions to caves, constructing Berlese funnels, and ensuring that many other details of our field work ran as smoothly as possible. Dave Larson (Chief of Resources at Lava Beds National Monument, Tule Lake, CA), was instrumental in following through on the lengthy process of securing funding for this study, arranging for our visit, securing appropriate permissions and permits, assisting with field work, and attending to numerous details needed to ensure the successful collaboration between bureaucracies (National Park Service, Illinois Natural History Survey, & University of Illinois). We are also grateful to the Cave Research Foundation and the Lava Beds Natural History Association for providing excellent research facilities in the form of the Lava Beds Research Center, which made preparations for daily field work, sample processing, and data entry much more efficient, and left us feeling fresh and rested each morning. We appreciate the efforts of Rob Meyers (Zara Environmental, Buda, TX), who made the initial sort of the field collected material into taxonomic groups and curated the material into well-labeled glass vials. We thank Dr. R. E. DeWalt (Illinois Natural History Survey, Champaign, IL) for identification of Ephemeroptera. We are grateful for the efforts of Kelly Fuhrmann (Zion National Park, Springdale, UT), who was instrumental in initiating this project when he worked at Lava Beds National Monument prior to moving on to another NPS facility – the study could not have been carried out without his early efforts towards organizing the project. Finally, we thank Rod Crawford (Burke Museum of Natural History and Culture, University of Washington, Seattle, WA), whose earlier work at Lava Beds National Monument laid the foundation for our study.

Literature Cited

- Barnard, J. L., 1977. The cavernicolous fauna of Hawaiian lava tubes, 9. Amphipoda, Crustacea from brackish lava ponds on Hawaii and Maui, USA. *Pacific Insects*, v. 17, pp. 267-300.
- Barnes, E. 2005. Relative humidity: An important environmental measurement. Agricultural Research Service, US Water Conservation Laboratory. Available online at: <http://www.uswcl.ars.ag.gov/events/exper/relhumeq.htm>
- Bellinger P. F., and Christiansen, K. A., 1974. The cavernicolous fauna of Hawaiiin USA lava tubes, Part 5: Collembola. *Pacific Insects*, v. 16, no. 1, pp. 31-40.
- Benedict, E. M., 1979. *Apochthonius forbesi*, new species from Oregon, USA (Pseudoscorpionida, Chthoniidae). *Journal of Arachnology*, v. 7, pp. 79-84.
- Bousfield, E. L., and Howarth, F. G., 1976. The cavernicolous fauna of Hawaiian lava tubes, Part 8: Terrestrial Amphipoda: Talitridae including a new genus and species with notes on its biology. *Pacific Insects*, v. 17, no. 1, pp. 144-154.
- Briggs, T. S., 1974. Troglotic harvestmen recently discovered in North American lava tubes: Travuniidae, Erebomastriidae, Triaenonychidae, Opiliones. *Journal of Arachnology*, v. 1, pp. 205-214.
- Brindle, A., 1980. The cavernicolous fauna of Hawaiiin lava tubes, 12. A new blind troglotic earwig (Dermaptera, Carcinophoridae), with a revision of the related surface living earwigs of the Hawaiian Islands. *Pacific Insects*, v. 21, no. 4. pp. 261-274.
- Campbell, G. D. 1976. Activity rhythm of the cave cricket, *Ceuthophilus conicaudus* Hubbell. *American Midland Naturalist*, v. 96, pp. 350-366.
- Crawford, Rod. 1998. Letter to Kelly Furhmann, Lava Beds National Monument. 9 March 1998. 1 p, with 2 pp attached taxon list.
- Culver, D. C. 1982. *Cave Life*. Harvard University Press, Cambridge, Massachusetts.
- Erhard, D. H. 1979. Plant communities and habitat types in the Lava Beds National Monument, California. MS Thesis (Rangland Resources), Oregon State University. 172 pp.
- Fennah, T. G., 1973. The cavernicolous fauna of Hawaiian lava tubes, Part 4: Two new blind *Oliarus* (Fulgoroidea, Cixiidae). *Pacific Insects*, v. 15, no. 1, pp. 181-184.
- Ferguson, L. M. 1992. Diplura of lava tube caves. Pages 281-284 *in*: Rea, G. T. (ed.). *Proceedings of the 6th International Symposium on Vulcanospeleology*. Hilo, Hawaii (1991).
- Gagné, W. C., and Howarth, F. G., 1975a. The cavernicolous fauna of Hawaiian lava tubes, 6. Mesoveliidae or water treaders (Heteroptera). *Pacific Insects*, v. 16, no. 4, pp. 399-413.

- Gagné, W. C., and Howarth, F. G., 1975b. The cavernicolous fauna of Hawaiian lava tubes, 7. Emasiinae or thread-legged bugs (Heteroptera, Reduviidae). *Pacific Insects*, v. 16, no. 4, pp. 415-426.
- Genter, D. L., 1986. Wintering bats of the upper Snake River Plain, Idaho, USA. Occurrence in lava-tube caves. *Great Basin Naturalist*, v. 46, pp. 241-244.
- Gertsch, W. J., 1973. The cavernicolous fauna of Hawaiian lava tubes, 3. Aranea, spiders. *Pacific Insects*, v. 15, pp. 163-180.
- Gurney, A. B., and Rentz, D. C., 1978. The cavernicolous fauna of Hawaiian, USA, lava tubes, 10. Crickets (Orthoptera, Gryllidae). *Pacific Insects*, v. 18, pp. 85-103.
- Halliday, R. B. 2004. Confirmation of the presence of *Scutigera immaculata* (Newport) in Australia (Symphyla: ScutigereLLidae). *Australian Journal of Entomology*, v. 43, pp. 43-45.
- Hoch, H. 2002. Hidden from the light of day: planthoppers in subterranean habitats (Hemiptera: Auchenorrhyncha: Fulgoromorpha). *Denisia*, v. 4, pp. 139-146.
- Holsinger, J. R., 1974. Systematics of the subterranean amphipod genus *Stygobromus* (Gammaridae), Part I: Species of the western United States. *Smithsonian Contributions to Zoology*, v. 160, pp. 1-63.
- Howarth, F. G., 1981. Community structure and niche differentiation in Hawaiian lava tubes; *in* Mueller-Dombois, D., Bridges, K W., and Carson, H. L. (eds.), *Island ecosystems: Biological organization in selected Hawaiian communities*, US/IBP Synthesis Series 15. Hutchison Ross Publishing Company, Stroudsburg, Pennsylvania, pp. 318-336.
- Howarth, F. G., 1982. Bioclimatic and geologic factors governing the evolution and distribution of Hawaiian, USA, cave insects: *Entomologia Generalis*, v. 8, pp. 17-26.
- Howarth, F. G. 1983. Ecology of cave arthropods. *Annual Review of Entomology*, v. 28, pp. 365-389.
- Howarth, F. G., 1987a. The evolution of non-relictual tropical troglobites: *International Journal of Speleology*, v. 16, pp. 1-16.
- Howarth, F. G., 1987b. Evolutionary ecology of Aeolian and subterranean habitats in Hawaii. *Trends in Ecology & Evolution*, v. 2, no. 7, pp. 220-223.
- Howarth, F. G., 1991. Hawaiian cave faunas: Macroevolution on young islands; *in* Dudley, E. C. (ed.), *The unity of evolutionary biology. Fourth International Congress of Systematic and Evolutionary Biology*. College Park, Maryland, USA. June 30- July 7 1990, v. 1. Dioscorides Press, Portland, Oregon, pp. 285-295.
- Lahr, J. W. 1960. A preliminary survey of the plant and animal resources of Lava Beds National Monument. Report to the National Park Service, 51 pp.

- Liebherr, J. K., and Samuelson, G. A., 1992. The first endemic troglobitic carabid beetles in Hawaiian lava tubes (Coleoptera: Carabidae). *Pan-Pacific Entomologist*, v. 68, pp. 157-168.
- Muchmore, W. B., 1979. The cavernicolous fauna of Hawaiian lava tubes, Part 11. A troglobitic pseudoscorpion (Pseudoscorpionida, Chthoniidae). *Pacific Insects*, v. 20, no. 2-3, pp. 187-190.
- Northup, D. E., and Welbourn, W. C., 1997. Life in the twilight zone- Lava-tube ecology. New Mexico Bureau of Mines Mineral Resources, Bulletin 156, pp. 69-81.
- Peck, S. B., 1973. A review of the invertebrate fauna of volcanic caves in western North America. National Speleological Society. Bulletin, v. 35, no. 4, pp. 99-107.
- Peck, S. B., 1982. Invertebrate faunas and zoogeographic significance of lava tube caves of Arizona and New Mexico. *Great Basin Naturalist*, v. 42, no. 3, pp. 405-412.
- Poulson, T. L. and W. B. White. 1969. The cave environment. *Science*, v. 165, pp. 971-981.
- Rosenberg, N.J., B.L. Blad, and S.B. Verma. 1990. *Microclimate*. Second edition. John Wiley & Sons, New York.
- Rudolph, D. C., W. R. Elliott, J. R. Reddell, and T. S. Briggs. 1985. The cave fauna of California. Unpublished manuscript.
- Schultz, G. A., 1973. The cavernicolous fauna of Hawaiian lava tubes, Part 2. Two new genera and species of blind isopod crustaceans (Oniscoidea, Philosciidae). *Pacific Insects*, v. 15, no. 1, pp. 153-162.
- Taylor, S. J., J. K. Krejca, and M. L. Denight. 2005. Foraging range and habitat use of *Ceuthophilus secretus* (Orthoptera: Rhaphidophoridae), a key troglodite in central Texas cave communities. *American Midland Naturalist*, v. 154, pp. 97-114.
- Tetens, O. 1930. Über einige meteorologische Begriffe. *Journal of Geophysics/Zeitschrift für Geophysik*, v. 6, pp. 297-309.
- Wirth, W. W., and Howarth, F. G., 1982. The "*Forcipomyia ingrami*" complex in Hawaii (Diptera: Ceratopogonidae). *Proceedings of the Hawaiian Entomological Society*, v. 14, no. 1, pp. 127- 152.
- Zacharda, M., 1982. The cavernicolous fauna of Hawaiian lava tubes, 13. A new subgenus and two new species of Rhagidiidae (Acari, Eupodoidea). *Pacific Insects*, v. 24, no. 3-4, pp. 275-280.
- Zeppelini, D. and K. Christiansen. 2003. *Arrhopalites* (Collembola: Arrhopalitidae) in U.S. caves with the description of seven new species. *Journal of Cave and Karst Studies*, v. 65, no. 1, pp. 36-42.

Appendix A. Summary of data from Crawford (1998, in litt.) resulting from his 1989 bioinventory of ten caves at Lava Beds National Monument, California.

Taxon	Merrill Ice Cave	Skull Cave	Cox Cave	Anglew./L. Pinnacle Cave	Arch Cave	Mushpot Cave	Catcombs Cave	Valentine Cave	Spider Cave	Fern Cave	Total Number of Sites
COLLEMBOLA (Springtails)											
Poduridae (white)	0	0	0	0	0	1	1	0	0	0	2
Poduridae (gray)	0	0	0	0	0	0	0	0	1	0	1
Isotomidae (3 spp.)	0	0	0	0	0	0	0	0	1	1	2
Enomobryidae (pigmented)	0	0	0	0	0	1	1	1	1	1	5
Enomobryidae (depigmented)	0	0	0	0	0	1	1	1	0	0	3
Tomocerus curtus (Tomocerinae)	0	0	0	0	1	1	1	0	0	0	3
Tomocerus californicus	0	0	0	0	0	1	1	1	1	1	5
Sminthuridae (depigmented)	0	0	0	0	0	0	1	1	0	0	2
DIPLURA; Campodeidae											
Haplocampa sp.	1	0	1	1	0	1	1	1	0	1	7
GRYLLOBLATTODEA											
Grylloblatta gurneyi	1	1	1	1	1	1	1	0	0	0	7
ORTHOPTERA; Crickets											
Pristoceuthophilus caelatus	0	0	0	0	0	1	1	1	1	1	5
Ceuthophilus inyo	0	0	0	0	0	0	0	1	0	1	2
PSOCOPTERA (wingless psocid)	0	0	0	0	0	0	1	0	1	1	3
SIPHONAPTERA (Fleas)	1	0	1	0	1	0	1	1	1	1	7
THYSANOPTERA (Thrips)	0	0	0	0	0	1	0	0	0	0	1
LEPIDOPTERA											
Moth larvae, indet.	0	0	0	1	0	0	0	0	1	0	2
Adult micromoths	0	0	0	0	0	0	0	0	0	1	1
Triphosa haesitata	0	0	0	0	1	0	0	1	0	0	2
Limenitis lorquini (spider prey)	0	0	0	0	1	0	0	0	0	0	1
COLEOPTERA (Beetles)											
Rhadine sp. (Carabidae)	0	0	0	0	0	0	1	0	0	1	2
Catops basilaris (Leiodidae)	0	0	0	0	0	0	0	0	0	1	1
Cryptophagus sp. (Cryptophagidae)	0	0	0	1	0	0	1	0	0	0	2
Acrolacha sp. (Staphylinidae)	0	0	0	0	1	0	0	0	0	0	1
Quedius spelaeus (Staphylinidae)	0	0	1	0	0	1	1	1	0	0	4
Eleodes sp.? (Tenebrionidae)	0	0	0	0	0	0	0	0	0	1	1
Aphodius nr. nevadensis (Scarab.)	0	0	0	0	1	0	0	0	0	0	1
Onthophagus sp. (Scarabaeidae)	1	0	0	0	0	0	0	0	0	0	1

Appendix A. Continued.

Taxon	Merrill Ice Cave	Skull Cave	Cox Cave	Anglew./L. Pinnacle Cave	Arch Cave	Mushpot Cave	Catacombs Cave	Valentine Cave	Spider Cave	Fern Cave	Total Number of Sites
DIPTERA (Flies)											
Tipulidae (Larvae)	1	0	0	0	0	0	0	0	0	0	1
Tipula sp. (spider prey)	0	0	0	0	0	0	0	0	1	0	1
Trichocera sp. (Trichoceridae)	0	0	0	1	0	0	1	0	0	0	2
Sciarid gnat #1	0	0	0	0	1	0	0	0	0	1	2
Sciarid gnat #2	1	0	1	1	0	1	1	1	1	1	8
Mycetophilid gnat #1	0	0	0	1	1	0	0	0	0	0	2
Speolepta sp. (Mycetophilidae)	0	0	0	0	0	0	0	0	1	0	1
Chironomid gnat #1	0	0	0	0	0	0	0	0	1	0	1
Leptocera sp. (Sphaeroceridae)	0	0	0	0	1	1	0	0	0	0	2
??cothea specus (Heleomyzidae)	0	0	0	1	1	1	1	1	1	1	7
HYMENOPTERA											
Myrmecine ant	0	0	0	0	1	0	0	0	0	0	1
Formicine ant	0	0	0	0	0	0	0	0	0	1	1
ACARIDA (Mites)											
Gamasodes sp. mites (on flies)	0	0	0	1	1	1	1	1	0	1	6
Large gamasoid mite, Ologamasid	0	0	0	0	0	1	1	0	0	0	2
Other gamasoid mites	0	0	0	0	0	1	1	1	1	1	5
Mites from mouse,											
Haemogamasus	1	0	0	0	0	0	0	0	0	0	1
Rhagidiid mite #1	0	0	0	0	1	1	1	0	1	0	4
Rhagidiid mite #2	1	0	0	0	0	0	0	0	0	0	1
Oribatid mites (damaeid type)	0	0	0	0	0	1	1	0	0	1	3
Oribatid mites (other spp.)	0	0	0	0	1	0	1	0	1	1	4
Pygmephorid-type mite	0	0	0	0	0	0	1	0	0	0	1
Actenedid & unknown mites	0	0	0	0	0	0	0	1	0	1	2
Trombidoid mite larva	1	0	0	0	0	0	1	0	0	0	2
Acariform mite hypopl (on flies)	0	0	0	1	1	1	1	1	0	1	6
Acariform mite hypopl (others)	0	0	0	0	1	0	0	0	0	1	2
Glycyphagid-like mite	0	0	0	0	0	0	0	0	1	0	1
Minute pale mite	0	0	0	0	0	1	0	0	1	0	2

Appendix A. Continued.

Taxon	Merrill Ice Cave	Skull Cave	Cox Cave	Anglew./L. Pinnacle Cave	Arch Cave	Mushpot Cave	Catacombs Cave	Valentine Cave	Spider Cave	Fern Cave	Total Number of Sites
ARANEIDA (Spiders)											
Usofila sp.	0	0	0	0	0	0	0	1	0	0	1
Callobius sp. (mainly webs)	0	1	0	1	1	1	1	1	1	0	7
Tetragnatha sp.	0	0	0	0	0	1	0	0	0	0	1
Metellina sp.	0	0	0	0	0	0	1	0	0	0	1
Nesticus silvesterii	0	0	0	0	0	0	0	0	0	1	1
Agelenid spider web	0	0	0	0	0	1	0	0	0	0	1
Calymmaria shastae	0	1	0	0	0	0	1	1	0	0	3
Arcuphantes cavaticus	1	1	0	0	1	1	1	1	1	0	7
CHILOPODA (Centipedes)											
Ethopolys sp.	0	0	0	0	0	0	0	1	0	0	1
DIPLOPODA (Millipedes)											
Plumatyla humerosa	1	0	1	1	0	1	1	0	1	1	7
Caseyid millipeds (indet. juv.)	0	0	0	0	0	1	0	0	0	0	1
Juliform millipeds (remains)	0	0	0	1	0	0	0	0	0	1	2
VERTEBRATE SIGN											
Peromyscus sign, scats in traps	1	0	1	1	1	1	1	1	1	1	9
Neotoma sign, nests etc.	0	1	1	1	1	0	0	0	1	1	6
Rabbit sign, scats	0	0	0	0	0	1	0	0	0	0	1
Bat sign, moth wings	0	1	1	0	1	1	0	0	1	0	5
Bat sign, guano	0	0	1	0	0	1	0	0	0	0	2
Bats, Plecotus townsendii	0	0	0	1	0	0	0	0	0	0	1
Bird sign, nests/roosts	0	1	1	0	0	0	0	0	0	0	2

Appendix B. Calculation of relative humidity using wet bulb and dry bulb temperatures in combination with barometric pressure.

Relative humidity was calculated using the following steps and equations (Barnes, 2005).

Step 1. Station pressure (P) was converted from inches Hg to kiloPascals:

$$P_{kPa} = P_{inches} (101 \text{ kPa} / 29.9213 \text{ inches Hg})$$

Step 2. A conversion factor, A , was calculated using wet bulb temperature (T_{wb}) (Rosenberg et al., 1990):

$$A = 0.00066(1.0 + 0.00115T_{wb})$$

Step 3. Saturation vapor pressure at T_{wb} (es_{wb}) was calculated (Tetens, 1930):

$$es_{wb} = e^{\left(\frac{16.78T_{wb} - 116.9}{T_{wb} + 237.3} \right)}$$

Step 4. Vapor pressure (e_d) was calculated using previous equations and dry bulb temperature (T_{db}):

$$e_d = es_{wb} - AP(T_{db} - T_{wb})$$

Step 5. Saturated vapor pressure (es_{db}) was calculated:

$$es_{db} = e^{\left(\frac{16.78T_{db} - 119.9}{T_{db} + 237.3} \right)}$$

Step 6. Finally, relative humidity (RH) was calculated:

$$RH = 100 \left(\frac{e_d}{es_{db}} \right)$$

Appendix C. Continued.

Photo Log		Cave	Crew	Date	Page of
Image Number	Photographer	Subject	Location Station Dist Bearing		

Appendix C. Continued.

Meter Log	Cave	Crew	Date	Page of
--------------	------	------	------	---------

SURFACE			
Barometric Pressure units: <input type="text"/> time: <input type="text"/> am pm	Kestrel: Wind <input type="text"/> m/s <input type="text"/> ft/s Air Temp <input type="text"/> C <input type="text"/> F RH <input type="text"/> %	Cave Location UTM z <input type="text"/> NAD <input type="text"/> mE <input type="text"/> mN EPE +/- <input type="text"/> m / ft	Light Meter: <input type="text"/> Units: <input type="text"/>

Location	Wet B	Dry B	Soil	Air	Light	Other

