CAVE BIOLOGY IN THE US AND CANADA

By John Roth, October, 2000

The classification, history and survival strategies of cave animals helps explain the genetic uniqueness and vulnerability of many cave species to anthropogenic impacts.

Troglobites, also called eutroglobionts and obligate cavernicoles, are those species confined to caves or similar habitats such as mines and sometimes groundwater. Exceptions are those cases where individuals of such species are washed out of or occasionally wander out of a cave but do not reproduce outside. These are the surface "accidentals." In contrast, troglophiles can complete their life cycles within caves but often are found outside caves. Trogloxenes must complete at least part of their life cycle outside of caves.

Phreatobites are confined underground to permanently or seasonally water saturated areas, the phreatic zone. Many phreatobites, especially the smaller species, inhabit small spaces not considered to be caves. However, most known phreatobites in the U.S. live within basaltic or carbonate rocks with conduit flow and so may be considered either troglophiles or troglobites.

The term troglomorph has been used to describe the more highly modified troglobites (Christiansen 1962), such as terrestrial species that have adopted an "aquatic-type" regulatory system or certain springtails and cixiid planthoppers that have evolved larger or more pointed claws for moving on cave wet surfaces. Some cave springtails also have larger "springs" for escaping predators. Such forms, along with changes in size and elongated appendages and bodies, is often used to distinguish troglobites from their closest soil or interstitial relatives. Cave-adapted crayfish appear to have smaller mouthparts for chewing silt-detritus on cave floors, as opposed to their surface cousins who chew on larger size materials (Caine 1975). However, "regressive evolution," as in reduction in eyes, pigmentation, wings, spines, or cuticle coverings more often distinguishes troglobites from surface relatives rather than from soil animals.

Alternatively, only those showing such changes are said to be true troglobites while those species recently isolated in caves but not having yet evolved cave-adapted forms are said to be "troglobites in training." Such may be the case where surface ancestors have died out and the relict species is now confined to caves. If surface ancestors are present and the associated cave-restricted species does not show any troglomorphic changes, then a species may be considered a troglophile (Zacharda, pers. comm., 1997).

However, if the only troglobites are those with the troglomorphism most commonly used to distinguish them from soil animals, the elongation of bodies and appendanges to more efficiently search for food, than that would exclude certain parasites and commensals as well as some snails and beetles that have specialized on food-rich cricket and bat guano areas yet are confined to caves or similar habitats.

The varying use of morphology and habitat for defining troglobites, along with incomplete distribution records and some disagreement on what are morphologic cave adaptations, makes for some uncertainty. Therefore, described species of troglobites and phreatobites in the US ranges from to (Peck, 1997; Hobbs & Culver, 1997 (excludes Hawaii)). Most undescribed species that have been recorded are considered troglobites, about 420. My own compilation estimates there are from 1167 to 1390 troglobites and phreatobites, including presumed new species recorded but as yet undescribed. The number of troglophile species is similar and ranges from 1127 to 1377, of which about 60 are known only from caves. Culver & Holsinger (1992) estimated that the total number of species in the six troglobitic "hot spots" of US to be about 6,000. If Hawaii is included as another hot spot, then perhaps 5,800 species (76%) of troglobites in the US have not even been identified as separate species.

The importance of these classifications for cave conservation lies partlly in the relative proportion of troglophiles to troglobites. If most animals often found in caves are recently derived from or are soil/interstitial species, and hence are more likely troglophilic or even trogloxenic, than they on the average are going to be more widely distributed habitat-wise and geographically and hence less vulnerable to human-caused impacts than those more restricted species long dependent on caves. For example, the more troglophilic species of fish, salamanders, and springtails are more widespread then their troglobitic cousins (Christiansen & Culver 1987; Mitchell & Smith 1972; Cooper & Kuehne 1974).

Along with narrow endemism, the high diversity of cave species in the U.S. means that more species are vulnerable to human species. Even with better inventories of tropical caves, temperate caves still appear to have at least as many troglobitic species as tropical caves, especially among land-based troglobites. Stream dwelling invertebrates (Allan & Flecker 1993), ichneumonids (Janzen 1981) and spiders (Platnick 1991) follow similar patterns.

There are likely several reasons for this equality in caves species. Higher amounts of organic input in tropical caves doesn't set the stage for the evolution of food-poor adapted species found in temperate caves (Mitchell, 1969). Larger numbers of individuals in certain tropical caves may reduce genetic drift and speciation. Greater climatic changes in the temperate zones, may have increased isolation of cave populations and enhanced speciation. Tropical patterns of equable climate, low population densities, relatively large land masses (in 3D!) and small body size (Blackburn & Gaston 1996) parallels similar trends in large caves; the complex interplay of these factors may overshadow the possible anti-diversity effect of low energy input in most caves. How energy input is divided up into population densities and body size may be as important as the total input. Extinction rates in temperate caves south of Pleistocene ice sheets may be low because of equable microclimate, predictable inputs of organics and large karstic areas. Higher extinction rates on the surface would explain why there are so many cavernicolous species with no apparent surface ancestors.

The narrow endemism of most troglobites largely results from their being neoendemics, paleoendemics or relicts with high rates of extirpation and limited dispersal. Much narrow endemism at the species level may be due to rapid speciation of neoendemics as a result of genetic drift in small, isolated populations. The lack of genetic diversity within some caves suggests that there was a colonization by a single or few individuals (the founder effect) followed by divergence from other cave colonies through genetic drift. In contrast, there seems to be even less genetic drift in at least some trogloxenes, perhaps due to gene flow with surface individuals (Cockley, Gooch & Weston, 1977).

Since genetic changes are not swamped and diluted by breeding within large populations, rapid speciation can occur, as evidenced by very large numbers of species within certain genera of cave beetles, springtails, amphipods, isopods, millipedes, spiders and crayfish who live in geologically recent caves. Many examples occur in Hawaii where interstitial fauna from lava flows in the last several thousand years have invaded and speciated in caves with enough moisture and food. Some *Pseudanophthalmus* beetles known from single Appalachian caves probably derived directly from soil organisms in relatively recent times (Holsinger & Culver 1987).

High diversity and perhaps rapid changes in genetics appears to be the case among certain crickets (Caccone & Sbordoni 1987) and amphipods (Kane & Culver 1991). There also is great genetic diversity between some sibling milliped and *Ptomaphagus* beetle species from different caves (Laing, Carmody & Peck 1976 and 1976a). Recent molecular work with certain spiders, beetles and phreatobites indicates that many morphologically distinct species are actually complexes with many genetically species (Hedin 1997).

High genetic diversity also extends to some epigean forms, at least among *Nesticus* spiders. In both cases, limited dispersal, small populations and narrow physiological tolerances result in high genetic variation between populations (Hedin 1997).

Narrow endemism at higher taxon levels may be due to the continued evolution of troglobites being so fast as to differentiate them from ancestral forms at increasingly higher taxon levels even in geologically recent caves. Narrow endemism may also be due to high rates of extirpations and the constriction of the ranges of certain fish, amphipods, millipedes and whipscorpions. Range fragmentation due to extirpations may also help explain the many disjunct ranges of cave springtails, spiders and mites. It may also explain why medium size caves such as Oregon and Malheur Caves often have a higher ratio of troglobites to troglophiles than larger caves such as Mammoth and Carlsbad Caverns. Speciation and extirpation both may be higher in medium size caves but if extirpation selects against troglophiles and trogloxenes less adapted to caves than most troglobites, then medium size caves would end up with a higher troglobite to non-troglobite ratio than larger or smaller caves. Higher biodiversity speciation potential in the smallest caves would be offset by even higher extirpation rates and the likelihood many of the smallest caves with surface entrances would be too dry or food rich for the habitat of most troglobites.

Changes in climate since the late Pleistocene has created many relicts among cave species. There is much indirect support for surface movement of pre-adapted Appalachian species during cool, wet times of the Pleistocene and subsequent isolation and speciation of these species in caves during warmer and drier periods. Appalachian cave species derived from surface cousins probably include certain pseudoscorpions (Chamberlin & Malcolm 1960), terrestrial isopods (Holsinger & Culver 1987), and rhagidiid mites (Zacharada 1985). Cave or soon-to-be cave species also used the cooler, wetter climates to cross non-cave areas to colonize new caves and are now isolated from one another, as in the case of

Pseudanopthalmus carabid beetles (Krekeler 1973) in the East and *Eidmanella* spiders in Texas (Gertsch 1984).

Drier climates in the southwest and warmer climates in the southern Appalachians created drought barriers to genetic interchange. When springs failed through a lowering of the water table, troglobitic populations apparently developed among salamanders in Texas (Sweet 1982) and amphipods in the Appalachians (Holsinger & Culver 1987). However, speciation increases from climate change on most aquatic cave species seem lower than that for terrestrials, presumably because more are interstitial and are less likely to be isolated by climatic events and/or because of the effects of other isolation effects, such as stream capture. Similar differences have been found in tropical caves (Trajano 1995).

Some species are now isolated within caves that match former climatic conditions. A snail from Bixby Ice Cave in Iowa surived where a blast of cold air coming from the cave mimicked a Pleistocene climate. Before 1982, this was the only current site for this snail; it was only know otherwise from Pleistocene fossils. Glaciation and the present interglacial removed surface populations and left individuals in protective cave environments to evolve in isolation (Mitchell, 1969).

Other glacial/climatic relicts appear to include certain Idaho Catopecerinae beetles (Westcott, 1968), grylloblattids, and rhagid mites in Alberta and Iowa (Zacharda & Pugsley (1988). As Post-Pleistocene climate become drier, swampy ancestors of the cavefish become more restricted to the refugia of swamplike springs, and ultimately speciated due to the increased isolation of karstic systems (Willis & Brown 1985). The epigean ancestors of certain troglobitic springtails may only recently have became extinct (Christiansen & Culver 1968 and 1969).

Some relicts may also be paleoendemics. The temperature and relative humidity of warm Upper Shoshone Cave in the Mojave Desert of California resembles that of caves in Mexico. Upper Shoshone Cave has a species of whipscorpion related to those in Mexico (Briggs & Hom (1972). The whipscorpions may have moved overland during Pre-Pleistocene times when the climates were more temperate and before the rising California montains created rain shadows.

The blind catfishes of southwest Texas may have originated in the Pliocene or Miocene. The rise of the Mississipian Plateau in Pliocene to early Pleistocene times likely increased stream gradients and eliminated surface crayfish in sluggish streams, leaving their descendants in caves (Holsinger & Culver 1985). As most atyid shrimp live to the south, most U.S. cave shrimp are likely relicts of a widespread group of shrimp that inhabited the southeast during a milder climate several million years ago (Holsinger 1988).

Freshwater isopods, hadziid and sebidid amphipods, crayfish, and palaemonid shrimp may have arisen from marine ancestors during regressions of inland seas, as during the end of the Cretaceous in the Atlantic Coastal plain, northern Florida, and in Texas. The brachiobdellid worms on crayfish may had developed after this invasion as, unlike some crayfish, they show no tolerance of saltwater (Holt 1969). After adapting to freshwater, many groups speciated due to increased geologic barriers as water levels continued to fall. Amphipod invaders more closely related to presumed near surface ancestors, with wider geographic distributions and with vestigial eyes, may be more recent invaders than their more troglobitic cousins (Holsinger & Culver 1985).

The primitive traits, lack of surface cousins, and/or wide distribution in Africa, Europe and the Americas suggests that the millipede genus *Litocampa*, crangonyctid amphipods, asellid and cirolanid isopods, and perhaps certain anophthalmid beetles may predate the breakup of the supercontinent of Pangea over 200 million years ago (Barr & Holsinger 1985; Ferguson, 1981, 1981a; Holsinger & Culver 1985; Valentine 1952)). Original breakup of micro-continents or island arcs at this time may have isolated populations of harvestmen prior to the joining of those landmasses to California. Harvestmen from the Sierras may have colonized coastal fragments after they arrived and joined North America (Ubick & Briggs 1989). The rafting together of different paleoendemic groups during the assembling of the Sierra Nevada and Klamath Mountains may be one reason for a high biodiversity among some taxa and low biodiversity in others.

Limited dispersal likely is partly due to "regressive evolution." Adaptations to the cave environment, coupled with climatic change, can greatly reduce the ability of certain species to move from one cave to another. This includes wing reduction and lowered resistance to dessication due to limb elongation and loss of cuticle or scale coverings. Species with low vagility often have restricted geographic distributions and high endemic rates, as is the case for cave pseudoscorpions, some carabid beetles and certain spiders. Recolonization of glaciated areas in the U.S. and Canada and the Pleistocene oceanic part of Florida has been very slow for most troglobitic taxon. Genetic differences and vacant niches in the geologically fragmented Appalachian Valley suggest migration and gene flow between caves or drainage basins is low (Culver 1976). The small size of certain species may increase endemism (Barr & Holsinger 1985) although some spiders may overcome this through ballooning while some mites, copepods, ostracods and springtails probably dispersed widely through phoresis, transport on much larger animals.

Limited dispersal may also be due to low genetic variability within each cave. Species with small populations and highly adapted to the cave environment, such as some troglobitic crayfish, tend to low genetic variability within a cave (Koppleman & Figg 1995). Hedin (1997) also found little genetic differences between different habitats within a cave among *Nesticus* spiders. A stable and relatively predictable environment such as a cave tends to have narrow-niche specialists with low genetic variability. This reduces their ability to adapt to other caves with somewhat different habitats.

The effects of limited genetics and dispersal morphologies reinforce each other. Most of the terrestrial and the larger aquatic species (such as crayfish and fish) cannot easily move from one cave drainage system to another and thus cannot exchange genes that might increase genetic variability. Interstitial or surface movement by other troglobites may also be limited as their genetic interchange appears lower than that of many troglophiles and trogloxenes (Kane & Brunner 1986; Caccone 1985).

However, some terrestrial generalists or small aquatic troglobities with high mobility and genetic variability appear to be able to maintain gene flow between caves in continuous karst areas, as in the case of a carabid beetle, *Neaphanops tellkampfii* (Turanchik & Kane 1981). Some amphipods, isopods and flatworms colonize cave pools via drips and seeps from small tubes and crevices and so often are not restricted to single caves or cave systems (Dickson 1977; Holsinger 1978; Holsinger & Culver 1985). The larger species of *Stygobromus* amphipods appear to be the most generalist (selecting both streams and pools) and mobile and consequently have the more widespread ranges (Holsinger 1978).

Narrow endemism for troglobites is high regardless of the cause. The total known number of species of troglobites, troglophiles and phreatobites known from fewer than five caves in the US and Canada is about 489. This number continues to increase by about _10 per year as more new species are described than there are species found to have more extensive ranges. It is the more restricted troglobites that are most likely to be found even or especially in the best studied karstic areas in the U.S., such as Virginia (Hubbard & Smith 1997).

Since caves and mines often occur together, most species probably are found in more than locality. An undescribed species of dipluran (*Haplocampa*), for instance, is known only from Sunnyside Mine in northern California and undoubtedly must occur in nearby carbonate caves, as was found to be the case with a millipede whose type locality also was Sunnyside Mine.

The vulnerability of troglobites to human impacts comes from their survival strategies as well as their high endemism, rapid extinction and low dispersal. If K-selection is a lifestyle characterized by the need to economize energy (Chapman 1993), then it is ideally suited for life in food-poor caves. Troglobites often are K-selected, characterized by delayed and aperiodic reproduction, greater longevity, and low populations. There are fewer eggs per clutch and egg size increased, as among some troglobitic salamanders, beetles, cave crickets, and spiders (Howarth 1991; Peck 1986). In Shelta Cave in Alabama, only three egg-bearing females of a troglobitic crayfish was seen out of 400 crayfish over a six year period (Cooper 1975). The aperiodic and slow reproduction may make it less likely that there will be population crashes and extirpation in food-poor caves.

K-selection has been augmented by neoteny in certain cave salamanders and talitrid amphipods (Bousfield & Howarth 1976). Delayed sexual maturity can stabilize populations and extend the longevity of a species, useful traits if there is not enough food for normal growth patterns and if an opportunistic animal needs to live a long time in order to reproduce when food supplies are most favorable. The troglobitic crayfish *Orconectes australis a.* lives a minimum of 40 years (Cooper 1975). A phreatobic amphipod (*Crangonyx antennatus*) lived at least six years (Holsinger & Culver, 1987). Increased troglomorphism and longevity among the amblyopsid fish appear to be related to increased K-selection (Palunas 1989).

Since juveniles are often less specialized than the corresponding adults, neoteny may enable some species to adapt to a new environment such as a cave. In some cases neoteny may be favored because immature stages are more preadaptive to cave life, as in the case of planthopper nymphs in Hawaii (Howarth 1993). In blind catfish, neoteny may increase olfactory and touch senses (larger heads), energy economy (low growth rate, small size, fatty deposits) and adaptations to high water pressures similar to those of deep sea fishes (small body size, fat deposits, regression of swimbladder, reduction of muscles and weakly ossified skeleton) (Langecker & Longley (1993). Nerve cells in amblyopsid cavefish are arranged to be more sensitive to touch and vibrations and may be a result of neoteny (Poulson 1963, 1964). The absence of fin splitting in cavefish also appears to be neotenic (Cooper & Kuehne 1974).

Various stresses such as starvation may decrease hormonal levels, leading to delayed maturity in certain individuals. If this is selected for in the cave habitat, then these individuals may be those most likely to reproduce and pass on a genetic propensity to stress-induced neoteny. Stress may also disrupt cellular enzyme reactions, leading to an increased mutation rate that could yield traits selected for in cave habitats. Cave species often have more karyotypic and shape differences than their surface cousins although this may be more due to genetic drift less constrained by natural selection (esp. competition) than to increased mutation rates.

K-selection, neoteny and lower metabolism may be in response to a variety of stresses, not just those of low food or oxygen (Hupop 1985; Howarth 1993). Flooding may be one stress; terrestrial isopods have developed wax coatings, densely crowded hairs or various overlapping plates that help trap air and prevent the isopods from being drowned. Lowered oxygen demand through lower metabolism may aid in this adaptation. Terrestrial species in many humid caves must be able to get rid of excess water or risk "water poisoning" through dilution of their bodily fluids. Drought may be another stress. Dessication from incoming cold air occurs in winter in temperate caves and nightly in tropical ones.

The threat of human-caused habitat change to most cave animals is greatly magnified by their restricted geographic ranges and habitats, low reproduction and colonization rates and high extirpation rates. The most troglobitic of U.S. cavefish, *Speoplatyrhinus poulsoni*, for instance, has fewer than 250 individuals and all are located in one site (Proudlove, 1997).

The pseudoscorpion *Kleptochthonis packardi* has not been seen for over a hundred years and so is presumed gone forever. A species is generally considered extinct when it has not been seen for at least fifty years. As most U.S. cave species have only been described in the last 50 years, no other troglobite in the U.S. is known to have become extinct. To this can be added the difficulty and rarity of resampling of most cave species. However, the number of possible extinct species is at least thirteen, including the beetles *Batrisodes profundus* (Alabama) and *Pseudanopthalmus krameri, P. krekeleri, P. tullahoma* and an undescribed species (Ohio, Hobbs 1996; WV list), a snail (*Helicodiscus punctatellus*), a flatworm (*Sphalloplana virginiana*), two amphipods and one isopod at a Univ. of Indiana campus (Lewis 1996), and a crab and barnacle in Texas (Russell, 1974). In most of these cases either the only known sites were destroyed or efforts at relocating the species failed. If all these species have become extinct, this would be about a one percent extinction rate, about the same as the rate of presumed or possibly extinct species in the U.S of the taxon recently reviewed by the Natural Heritage programs and The Nature Conservancy (Stein & Stephanie, 1997). Except for West Virigina, those states with the highest extinction rates for all reviewed species also roughly parallel those states with the highest number of possible G1 cave species.

The actual extinction rate of cave species is likely to be higher and closer to the extinction rates of freshwater species in the US, not surprising given the sensitivity of both habitats to disturbance. The percentage of U.S. aquatic species classified as vulnerable, imperiled or extinct ranges from 35-37% for amphibians and fishes to 65% for crayfish and 67% for unionid mussels (Richter et al. 1996:1082). If all cave species in the U.S. with less than six known sites were designated as G1 species, then ___% of the troglobites and ____% of the troglophiles would be critically imperiled.

6.5% of the reviewed taxon were G1 species (Stein & Stephanie, 1997), much lower than

Extirpations of species with less than six known sites include *Pseudanopthalmus troglodytes* (Kentucky), the pseudoscorpions *Trichoniscus nearcticus* and *Kleptochthonis packardi* the snail *Antrorbis breweri*, and the shrimp *Palaemonias alabamae*. Contamination from pesticides, fertilizers, herbicides, sewage, and feedlots may have eliminated the Illinois Cave Amphipod from half of its historic sites, prompting its recent listing as federally endangered.

The most important threats to cave habitat are changes in water and nutrients, and, to a lesser extent, to toxic chemicals, oxygen loss and more direct human impacts such as mining, collecting and caving. The most important factors implicated in historic declines in U.S. aquatics are similar and include habitat destruction and changes in waterflow, sediment and nutrient loads (Richter et al. 1996). Of the factors in aquatic declines, only changes in channel shape (except siltation effects on bed structure) have not been suggested as a cause for the decline of cave species.

Species with less than six known sites are designated G1 if they are critically imperiled. In the US this could include about 1400 caves, of which % are privately owned and ______________ are managed by various government agencies. At present the cave with the most endemic species is Oregon Caves (10 species), followed by Mammoth (8 species) in Kentucky and Malheur Cave (7) in Oregon.

Too little water mostly comes from enlargement of natural entrances and the opening of artifical ones. This results in chimney and reverse chimney effects as dry summer air enters upper elevation passages and cold winter air enters lower passages. As cold winter air enters caves it warms up and the relative humidity drops. Biological surveys in Oregon Caves indicates that the location of most cave populations are affected more by this seasonal change in airflow than by any other factor. The resulting dessication from modification of cave entrances has affected animals in at least five Park Service, two Forest Service and twelve private showcaves.

Fire suppression on the surface has increased shrub density and evapotranspiration and apparently has reduced waterflow in Wind Cave in South Dakota and Oregon Caves. Regional changes in albedo and subsequent changes in atmospheric convection may increase precipitation in urbanizing areas and decrease it in deforested areas. Decreased waterflow into a cave may also reduce the amount of incoming organics.

Pumping of regional aquifers threatens phreatobites in the Edwards Plateau of Texas, desert pupfish and snails in Nevada, and amphipod species in Oregon near Roseberg and in Polk County. The building of a levee around Estelline Salt Hole in Texas may have caused the extinction of at least some of its endemic fauna, a cave barnacle not yet described and the only known troglobitic crab in the contingous U.S. (Russell, 1974). The drying up of springs on a university campus in Indiana may have resulted in the loss of two isopod and one amphipod species.

Too much water has largely come from flooding by dams. Nickjack Cave in Tennessee, a cave with eight type localities, was mostly flooded. It is the only site of *Gammarus pupurascens*, a phreatobite that may have survived the flooding. The Normandy Cave in Tennessee flooded at least two caves of a G1 terrestrial *Pseudanoapthalmus* beetle species. The species may still exist in a nearby cave that was not flooded. The Melones Dam in California flooded some caves with narrow endemics. Several species of troglobitic isopods and harvestmen were successfully transplanted to a nearby mine before type localites were flooded. Meramac Dam flooded biologically signicant caves in Missouri.

Flooding can result in too much food, too little and/or changes in food seasonality. Dams on the Green River near Mammoth Cave, for example, have lowered the seasonal variation in subsurface water levels, resulting in less food access for both terrestrial and aquatic organisms that, respectively, rely on the stranding or inundation of food sources at different times of the year (Lisowski & Poulson, 1981; Poulson 1992). Increased waterflow can also wash away guano or stop the growth of actinomycetes "cave slime" upon which a harvestmen (*Speleomaster lexi*) and some rare flies appear to depend on.

Too little water can also result from dams and deforestation. Dams can prevent the periodic breaching of adjacent drainage basins and thus prevent the periodic migration of aquatic troglobities and their exchange of genetic material. Dams often increase channel erosion downstream and siltation upstream. Deforestation tends to increase flooding during periods of heavy precipitation but will lower waterflow during drought and the succession of densely stocked secondary forests.

Too much or too little water from dams, deforestation, pumping or concentration of waterflow by buildings and asphalt can result in siltation that can clog gills and filter feeders, change river channel shapes, destroy breeding habitats and increase organic or heavy metal input. Siltation can decrease prey items through increased mortality or drift due to sedimentation or subtrate instability. Siltation was cited as the leading cause of water quality impairment across the U.S. in 1992 (EPA, 1994).

Although agriculture is the main contributor, other siltation sources include mining, deforestation and development. A major powerline route has been proposed that would go directly over Slussers Chapel Cave where lives *Stygobromus fergusoni*, a possible G1 species tracked by Virginia as a Special Concern species. This would likely increase siltation due to the many dirt roads used to access the powerlines (Kastning 1996).

Too much food largely results from groundwater pollution and cave commercialization. The increase of one resource (ie. food) often decreases biodiversity. A example on the surface would be where nitrates or phosphates have so enriched a lake that only a few species of bluegreen algae flourish. Their toxins and consumption of oxygen drastically lowers the biodiversity of lake fauna. The effects of increased organics in caves is usually less dramatic. However, the introduction of raw sewage and dairy wastes so impacted Horse Cave in Kentucky that large parts of the cave lost their troglobites and troglophiles and became dominated by tubificid worms. Runoff of hog and poultry feces into karst groundwaters pose serious threats to troglobites in parts of Virginia, West Virginia and Arkansas. Leaking septic fields from residential development pose an even more widespread threat in most of the eastern U.S.

Most western caves have been less impacted due to differential erosion; most Eastern karst is located in low elevation, relatively flat areas while more erosion resistant limestones in the drier West are more likely found in mountainous areas unsuitable for present-day urbanization.

Cave communities tend to be food-regulated rather than predator-regulated and so can be more affected by increased organics.
Even slight increases in organics from pollution can cause the paradox of enrichment in which less cave-adapted species move into a cave to better utilize a rich energy source. There they outcompete native species. Trogloxenes tend to be more common than troglobites near high-energy food sources (Poulson & Kane 1981). There is suspicion in some Arkansas caves that increased troglophilic crayfish near cave entrances with more food from human impacts may be predating on troglophilic species**.

In showcaves, most human-caused organics occurs near trails. This largely results from cotton lint, shedding of human skin flakes, and the growth of alien algae near electric lights. Disturbance of clay soils can also increase the availability of food at least on a microbial level. A more cave-adapted cricket in Carlsbad Caverns is preyed upon by a more aggressive cricket that is more common in the food-rich trail areas. Low biodiversity near food-rich trails have also been found in Oregon and Mammoth Caves and Jewel and Wind Caves in South Dakota.

Although there are cave species adapted to low oxygen/high carbon dioxide and cave waters usually are well oxygenated, the introduction of additional organics can affect cave communities, especially those in areas with already low oxygen, as in some marine or organically-rich caves, and among species that are oxygen sensitive, such as certain ostracods. Oxygen loss can come from siltation and logging slash as well as from human sewage or food tossed into showcave pools. Increased organics can increase bacterial concentrations so much that they interfere with the movement of oxygen through interstitial medium. Slight additions of dextrose sugar to karst aquifer sediments caused anaerobic conditions that decimated isopod populations (Edler & Dodds 1992). Recolonization may be slow because of limited dispersal and the loss of specific genetic adaptations to a particular cave.

Too little food largely results from closure or restrictions of cave entrances which in turn is correlated to increasing urbanization and litigation concerns. The snail *Antrorbis breweri* may have become extirpated from its type locality as the only large entrance to Manitou Cave in Alabama was closed by a metal door.

The initial deforestation of much of the East in the 1800s likely first increased organic influx into caves. The second deforestation occurring from ongoing urbanization in much of Maryland, Florida and northern

Alabama may be decreasing organic inputs overall yet drastically concentrating it in some areas. Leakage of septic systems, sewage lagoons and trash-filled sinkholes is most likely in the conduit flow systems typical of most karst and lava tube areas. Once contaminated, there is little filtration or bioremediation in such fastflow systems.

The effects of sealed caves and paved over ground surfaces are likely to be similar to certain natural effects. Where rocks or thick soils prevent organics from reaching caves, troglobitic crayfish are absent in Florida (Franz & Lee 1982). And where thick soils have plugged entry of organics in lava tubes in Hawaii, cave biodiversity is sparse.

Some aquatic amphipods in British Columbia, the upper Mississipi drainage, and Massachusetts appear to have survived for thousands of years in deep aquifers under glacial ice (Peck & Christiansen 1990; Smith 1985). At present there are similar amphipods under Antarctic ice. Perhaps *Stygobromus cooperi* survived the temporary sealing of its only known site, Silers Cave in Virginia. The cave is now gated and access is restricted to protect this rare amphipod.

Cement, asphalt, and siltation are likely to cause similar effects. Paving projects may even completely destroy caves, as in the case of McElwee Cave in Viginia. Showalters Cave, the only known site of the flatworm *Sphalloplana virginiana*, was filled in with rocks and dirt. The only known site of a new species of *Pseudanophthalmus*, Indian Cave in Virginia has been bulldozed shut. The stream entrance in Cassell Cave, the site of a G1 amphipod, has been almost silted shut.

Cave entrances are a major source of food input into caves as a result of falling organics, flood debris, and aerosol deposition. Some flies and millipedes appear dependent on moonmilk, a fine-grained calcite often associated with filamentous bacteria and large entrances. Aerosol deposition and concentration of dissolved organics by evaporation may favor the occurrence of moonmilk near entrances. Entrance closures destroys this ecosystem.

The migration of bats, woodrats and crickets through entrances provides additional food. Fly, snail, mite and beetle cavernicoles dependent on bat, woodrat or cricket guano are particularly at risk because they appear to be more narrowly endemic than most troglobites, perhaps because they are less likely to be able to move from cave to cave through food-poor interstitial cracks.

The decline of woodrats in Ohio and Indiana (Lewis, Pursell & Huffman 1996) has threatened those species largely dependent on woodrat guano in caves. Bats and crickets (at least the troglobitic *Caeconomibius* genus) often are colonial and even slight disurbances and reductions and numbers can cause complete abandonment of a roosting site. The loss of cricket guano in White's Cave near Mammoth Cave may have resulted in the extinction of *Helicodiscus punctatellus*, a troglobitic snail. At least twenty five caves in the U.S. have been gated and/or have seasonal closures in order to protect either nursery or roosting sites for rare bat species and those invertebrates dependent on bat guano. Some entrance in Mammmoth Cave National Park have been outfitted with small tubes to allow for cricket migrations (Poulson, Lavoie & Helf, 1997).

The introduction of alien species poses another threat, especially in Hawaii and Texas. Alien species include certain troglophilic springtails, isopods, mites and millipedes. In clothing lint deposits in Carlsbad Caverns, entire alien communities have developed, complete with spiders, mites and ants not previously known from the caverns.

At present the most obvious threat of aliens to cave endemics is not competition but predation. Although ants normally do not venture very far into large caves, fire ants have overrun some of the smaller yet biological signifcant caves in Texas. Extinction of prey and predator species is most likely when a predator has few species to choose from, as is the case for both troglobitic prey and predators. Reduced metabolism (most groups), reaction to alarm chemicals (fish), spines (crayfish: Hobbs 1972), cuticle thickness (most groups) and intraspecific aggression (fish & springtails (Christiansen 1992)) may put some cave species at greater risk from both competition and predation.

In some cases competition is less in caves compared to the surface, especially in food-poor caves. However, competition probably is the most important biotic interaction in caves (Holsinger & Culver 1987) and affects the biodiversity and distribution of springtails (Christiansen 1970; Irwin (1958), pselaphid beetles (Peck, 1975), carabid beetles (Barr 1967a; McKinney 1975) isopods (Bechler 1985; Culver & Ehlinger (1980), crayfish (Cooper 1975), and amphipods (Bechler 1985; Dickson 1976, 1977). Where the ranges of similar *Meta* spiders overlap either one or the other species is found in a particular cave (Chapman 1993).

It appears likely that, as with U.S. aquatic species (Richter et al 1996), the competitive threat of alien species is increasing relative to the historic reasons for the decline of native cave species. Since alien impacts tend to increase on smaller land areas, aliens may threaten hundreds of tiny "islands" in the U.S., each one being the home of a G1 caves species.

Aside from changes in water, food, and alien species, the next most critical impact is from non-organic pollution. This includes de-icing salts and heavy metals from highway runoff, and bleach used to treat well water and control showcave algae. Coins thrown into pools in showcaves can kill life through copper or nickel poisoning. A population of what may be a new taxon of cavefish in Sloan's Valley Cave is at risk from heavy metal runoff from a land fill site in Kentucky (Tercaps 1992). Ammonium salts has caused catastrophic deoxygenation at Meramac Spring in Missouri (Chapman 1993).

Some of the more cave-adapted species tend to be more sensitive to both bleach and heavy metals (Bosnak & Morgan, 1981). Initial low structural, genetic, and functional diversity of many groundwater communities may make them unstable under pollution stress.

Aside from its usually concomitant low reproduction rates, increased longevity also puts species at risk because of bioaccumulation. Some long-lived troglobitic crayfish contain more heavy metals than their surface cousins (Dickson et al 1979).

Even efforts at cave restoration may be harmful. Some troglobitic crayfish die from small amounts of sodium hypochlorite, the chemical most often used to kill alien algae around electric lights in show caves (Mathews, et al 1977). Removal of old wooden boards or other organics during cleanups might cause the collapse of troglobitic populations artificially concentrated in those areas.

Increased human traffic in a cave can also reduce its biodiversity, in one case first affecting the terrestrial cave fauna and then the aquatics (Tercaps 1992). Part of the impact is from increased siltation. Some impact may be disturbance of the limited cover of a rare isopod and other benthic species (Hobbs, 1996). Studies in Washington suggest that human activities in well-traveled caves can severely impact a *Haplocampa* dipluran (Crawford & Senger 1988).

Commercial collecting of cavefish has occurred in parts of Kentucky and Missouri (Canaday & Vitello, 1996; Culver 1986). Caves biota can even take several years to recover from sampling surveys (Peck).

Vandalized yet biologically significant caves include Dolloff (logging) and Empire Caves in California, Cudjoe's and Patton Cave in Virginia and Patton Cave in West Virginia. Gating caves does not always protect them; there have been repeated breakins in such biologically significant caves as Samwell Cave in California and Logan Cave in Arkansas. Destroyed gates include Canoe Cave in Virginia. Even with the installation of internal monitors in caves, there rarely is a rapid response to cave breakins and gates may remain broken for many months.

Staff at showcaves are more likely to repair broken gates quickly although showcaves have their own problems. For example, certain cave-adapted ostracods can be killed by 1/20 normal sunlight (Maguire 1960), the same intensity as occurs in incandescent lights in commercialized caves. The introduction of organics is also greater in showcaves than in wild caves. Researchers have been unable to locate several rare species in showcaves, including Indiana's Wyandotte Cave, the type locality of the pseudoscoropion *Kleptochthonius packardi*.

One of the lesser impacts is quarrying, which is also increased by urbanization and road building. Type localities for possible G1 species include Erhart's Cave in Virginia and Alabaster Cave in California. The only known site for the beetle *Pseudoanopthalmus krekeleri* was Rich Mountain Caves in West Virginia. All three caves have been destroyed by quarrying.

About twenty cases of catastrophic impacts have been recorded on particular caves or cave systems in the U.S. Few of these have impacted G1 caves so far. Of more serious concern to cave biology conservation has been the slower decline of several regional aquifers in volume and quality, especially the Edwards Aquifer and the _____ Aquifer in Florida, areas with many phreatobites. Declines have also occurred in aquifers little studied but potentially rich in phreatobites, such as the Oglala Aquifer in South Dakota.

Protection of cave species varies from state to state in terms of state laws, ownership and management of caves by conservation-oriented entities (____% of possible G1 caves), and tracking by Natural Heritage programs. of states with possible G1 caves have some laws protecting cave biota. Not surprisingly, the vertebrate "charismatic megafauna," such as it is for caves, has been the focus. The Nature Conservancy program, for example, affords some type of protection for bats in 45 caves, fish and salamanders in six caves and invertebrates in 14 caves (Hall 1996). A similar bias towards vertebrates exists among Alabama aquatic species federally listed as emperiled (Lydeard & Mayden 1996).

The number of possible G1 caves in the U.S. is about 884. About 316 of these mostly troglobitc species are known only from single caves. Since the ratio of known to unknown troglobite species in the US is ____, there may be as many as _____ G1 caves with little afforded protection such as ownership or mangement by conservation entities.

The percent of possible G1 cave species tracked by Natural Heritage programs ranges from _____ % to _____%, with an average of ____%. Reasons for the great range included staffing levels, prioritizing of the most likely endangered species, and the number of biospeleologist advocates in each of those states. Although more caves in the West are protected by public ownership and low urbanization rates, a higher percentage of species are not tracked because of fewer studies and recommendations for tracking. Staffing levels generally do not increase in those states with high biodiversity and so many more species are not tracked in the more southern states. In some states such as Florida, there is greater emphasis on aquatic species than on terrestrials because of the concern with declining water quality. Consequently aquatic species with less than six known sites are more likely to be designated G1 than are terrestrial species.

Partly as a result of the need to avoid labelling poorly known species as either troglobites or troglophiles, the term cavernicolous (=troglobiont) has become more popular and is used to refer to any animal living its entire life cycle in a cave. A synonym for cavernicole is caverniate (Chapman 1993). Cryptozoa ("hidden animals") has been used for species living in darkness beneath stones, logs, bark and similar area. Widening this term or using "cryptobiont" to refer to animals in soil, ground litter and caves has not been widely adopted (Chapman 1993).

Troglophiles (=facultative cavernicole) can complete their life cycles in caves but they can also be found outside of caves, usually in similar habitats such as those with high humidities. Some troglophilic species may look troglobitic or troglomorphic, as in the loss of pigmentation, but this may be related to similar habitats (as in soils) or to environmental changes, as in the lack of carotenoids in the diet of cave crayfish. Troglobitic crayfish, on the other hand, have lost or have never developed the ability to oxidize dietary carotenoids (Wolfe & Cornwell 1964).

Some troglophilic species can complete their life cycle in a cave although some individuals can live their entire life cycles outside of caves, especially on the surface or in surface litter. Evidence for a troglophilic species would include reproduction in caves, a cave population structure in which all age classes are fairly evenly represented, suitable food supplies, and evidence that there is no diurnal or seasonal migration out of the cave. Species that straddle the troglophile/trogloxene line might include animal groups in which some individuals may stay in the cave their entire life cycles while others regularly move outside to feed, as appears to be the case for certain crickets and perhaps some grylloblattids.

Some biospeleologists have subdivided troglophiles into those species confined to caves (but showing few if any troglobitic shapes) and those species also occurring in epigean habitats (Hamilton-Smith (1971). However this classification has not been widely used.

Edaphobites are the soil equivalent of troglobites. They usually are confined to deep soil habitats but occasionally occur in caves. They share some traits with troglobites, such as loss of pigments, wings, eyes and thick cuticles (surface coverings). Compared to both surface and cave relatives, various deep soil animals have shorter antennae and/or legs among beetles, isopods, and springtails (Eisenbeis & Wichard 1987), presumbably because it helps prevent entanglement, adhesion to water films and/or water loss. Edaphobites may also share traits with and grade into endogean species, those living in deep ground litter or soil (Holsinger & Culver, 1987:12-3). Soil animals have also been divided into euedaphons (natural pores), epedaphons (on surface or larger hollows in the litter) and hemiedaphon (diggers, burrowers).

The smallest species found in caves, such as bacteria, protozoa, copepods, and ostracods, often can find suitable habitat regardless of the size of the underground opening, especially if they are aquatic. Therefore, they are less likely to be specifically cave adapted. Cold-loving bacteria expected in caves are absent (Brock, Passman & Yoder (1973) and even chemotrophic bacteria appear related to those from similar habitats, such as deep sea vents. Most caves have enough microbial food so that those elongated bacteria adapted to extremely low food supplies are not dominant in cave ecosystems.

Although fungi and bacteria are not usually cave classified, other tiny species such as various crustaceans and arthropods are phreatobites if confined to the area of permanently or seasonally water saturated areas (=phreatic zone). They inhabit the hyporheic zone if found under a stream and are meiofauna if found in small pores (interstitial) below the soil zone. A common European term for phreatobite is stygobiont or stygofauna.

With increased sampling of phreatobites and meiofauna and hyporheic and interstitial habitats, etc. it is clear that species composition can be similar between caves and other underground habitats, especially for the smaller aquatic species. Many species do move into caves from their primary home in interstitial cracks. Some *Pseudanophthalmus* beetles known from single Appalachian caves probably derived directly from soil organisms in relatively recent times (Holsinger & Culver 1987). Fong and Culver (1994) found that one amphipod species in the headwaters of a cave stream may have invaded from the interstitial zone while another species may have moved upstream into the cave from a resurgence. Many examples occur in Hawaii where interstitial fauna from lava flows in the last several thousand years have invaded and speciated in caves with enough moisture and food.

However, cavers are not just sampling a portion of meiofauna. For example, there are distinct differences between interstitial and cave springtails and isopods (Henry & Magniez 1983). Carbonate caves form distinct assemblages of animals, as evidenced by increased dispersal between closely adjacent karst areas and the high biodiversity of troglobites in those areas with a high density of caves. Basins on opposite sides of drainage divides have more cave species in common if the divides are carbonate than if they are non-carbonate rock (Holsinger & Culver, 1987).

The deeper one goes in most caves, the less likelihood there is of interstitial or other connections with other areas. Consequently both aquatic and terrestrial species are likely to be less widely distributed and more troglobitic than those species more closely connected to less deep groundwaters and interstitial zones (Chapman 1993).

Any one species may be both a troglophile or a trogloxene depending of the nature of particular caves. In food-rich caves based on bat guano, the Ozark blind salamander *Typlotriton spelaeus* completes its life cycle inside a cave and is considered a troglophile. In food-poor caves, the larval salamanders must travel to the twilight zone or outside to find food (Mohr & Poulson 1966). Members of most taxonomic groups known from caves have been classified as trogloxenes in more northern caves and troglophiles in caves to the south in North America, presumably because there is enough food in southern caves to allow species to complete their life cycles there. Troglophilic populations of millipedes occur in the southern, lowland part of the range and epigean populations occur in the northern part (Shear 1971).

In so called "regressive evolution," some species have reduced:

or lost eyes: centipedes, fish, millipedes, reduvids (Gagne & Howarth 1974a) spiders (Gertsch 1973); water treaders (Gagne & Howarth 1975); thread-legged bugs ('Gagne & Howarth 1975); harvestmen (Goodnight & G. 1960);

pigmentation: crayfish (Hobbs III 1972); fish (Poulson (1963); planthoppers (Fennah 1973); reduvids (Gagne & Howarth 1974a); pseudoscorpions (Chamberlin & Malcolm 1960); thread-legged bugs (Gagne & Howarth 1975); water treaders (Gagne & Howaerth 1975); harvestmen (Goodnight & G. 1960);

reduced protection from light (Maguire 1960)

reduced or absent wings: beetles; planthoppers (Fennah 1973);

pineal glands: blind catfish and cavefish (Langecker & Longley 1993);

circadian rhythms;

"lungs" - spiders, (reduced metabolism, high humidity);

cuticle thickness (spiders,. harvestmen (Goodnight & G. 1960);

or lost scales - fish Christiansen 1992.

egg clutch number with egg size increased - salamanders (Peck 1986); beetles; cave crickets
intraspecific aggression (fish, springtails Christiansen 1992))

aggregation (some springtails and fish)

reaction to alarm substances in some fish

more and/or longer sensory setai ("hairs") anopththalmid beetles - (Valentine 1952); crayfish (Hobbs 1972); pseudoscorpions (Chamberlin & Malcolm 1960);. These may help in detecting water or air currents as well as prey.

Longer appendages and/or bodies - cave crickets; water treaders (Gagne & Howarth 1974); crayfish (spines and tubercules, Hobbs 1972); harvestmen

(Goodnight & G. 1960); chthoniid pseudoscorpions (Barr 1985); amphipods (Holsinger Encyl).

low oxygen tolerance - amphipods Hervant et al. 1995); crayfish (Dicks & Franz 1980); some have enlarged gill chambers. Some cavefish use less oxygen (Biwas 1991).

increased longevity: crayfish (Streever 1995)

lowered metabolism - crayfish (Burbank, Edwards & B. 1948; Hobbs III 1972); cavefish (Poulson 1963, 1964); spiders (Hadley, Ahearn & Howarth 1981); trogloxene crickets (Studier, Lavoie, Wares & Linn 1986); European isopods & amphipods; springtails (Thibaud 1994).

increased fat storage and tolerance of fasting in Mexican cavefish

Troglobites who cruise for food tend to be slender. This increases their ability to cover large areas in search of food while it reduces their energy needs for large bodies (Barr, 1985). Elongation of bodies and appendages is perhaps the most important example of evolutionary convergence among cave animals.
Both adaptation and genetic drift are involved, depending on the species. Such change saves energy.

Some specialized cavernicolous traits have evolved. Blind catfish in the high pressure artesian systems of southwest Texas exhibit deep sea type traits such as loss of their swim bladder. An endemic cricket on the Farallon Islands of California forms clusters that seem critical to their survival (Rentz, 1972).

Biodiversity: Biodiversity largely depends on habitat distribution and the rates of speciation, colonization, extirpation, and extinction. How the rates increase or decrease biodiversity often depend on scale. For example, extirpation will at least temporarily decrease biodiversity locally but it may enhance regional diversity because it allows competitors to coexist on a regional basis.

Probably because of extremes such as flooding, dryness and food scarcity, and the difficulty of colonization, many caves have low biodiversity. But some caves are fairly diverse, especially those that are large, have organic inputs like flood debris and guano and/or are connected to other karst areas. They are most likely to have surfaces of great diversity, high moisture, and high organic content, all areas that can have high biodiversity (Poulson & Culver 1969).

Changes in gravel size, for example, can favor one species of isopod over another due in part to changes in competitive interactions (Culver & Ehlinger (1980). The amphipod *Lirceus usdagalun* favors currents with velocity/depth ratios greater than .67 (Estes (1978). A small amphipod species favors habitat under small rocks and gravels while two species of the larger isopods live under larger rocks and gravels (Holsinger & Culver, 1987). Beetles who feed between gravels are small while species who pursue larger prey on the cave floor are larger (Barr 1985). Flatworm seem to prefer quiet waters where they can glide along on the underside of the water's surface tension. Larval salamanders may find it easier to search for prey in quiet water (Holsinger & Culver, 1987). Mites in Iowa appear limited to areas of small soil particles perhaps because that is critical for food sources (Irwin (1959)

With limited food supplies and suitable habitat, species packing can be very limited. Three species crustacean communities in West Virginia and in the Powell Valley of Virginia were resistant to invasion while two-species communities were not (Holsinter and Culver 1987)

Large, fairly continuous karst areas tend to have high biodiversity, perhaps because of greater habitat diversity and greater ease in migration and lower extinction areas compared to smaller or more fragmented karst areas (Culver, Holsinger, & Roger 1973). Population densities are higher, being attributed to alternative sources of prey (Barr & Holsinger 1985). This and greater migration probably reduces the chances of both extinction and long-term extirpation. The less highly diverse caves areas are associated with more drastic populations fluctuations that likely would increase extirpation (Barr cave ecology). The development of cave-adapted traits often depends on both isolation of subsuface and surface populations and the presence of a large subsurface habitat (Culver 1995).

Areas with more caves per square mile have higher biodiversity, presumably in part because this indicates greater karst development, suitable habitat, and migrations rates that would offset extinction rates. A single cave with greater habitat diversity may have greater persistance of a particular habitat because of the greater likelihood that, even with a change in the cave, such as flooding, there would be a greater likelihood that somewhere in the cave that habitat could still be found. There would also be greater opportunity for surface species to contribute both food and genetics to the underground.

Smaller karst areas, however, sometimes have a higher endemic rate, perhaps because increased isolation increases genetic drift and subsequent speciation. Genetic differences and vacant niches in the geologically fragmented Appalachian Valley suggest migration and gene flow between caves or drainage basins is low (Culver 1976). Yet increased speciation may have resulted in this area having more species per unit area of exposed karst than does the more continuous Missisipian Plateau of Kentucky and Tennessee. Genetic differentiation is higher in the Appalachian Valley among cave crickets compared to the Plateau (Caccone & Sbordoni 1987). Widespread springtail species appear to invade large areas and then become speciated through gene flow barriers with later dispersal from newly adapted cave forms (Christiansen & Culver 1987) Except in guano, chemolithotropic and perhaps tropical caves, though, populations are small enough even in large karst areas that genetic drift appears to be high.

Although better inventories of tropical caves have narrowed the gap, temperate caves still appear to have at least as many troglobitic species as tropical caves, especially among land-based troglobites. This may be because higher amounts of organic input in tropical caves doesn't set the stage for the evolution of food-poor adapted species found in temperate caves (Mitchell, 1969). Larger numbers of individuals in certain tropical caves may reduce genetic drift and speciation. Greater climatic changes in the temperate zones, such as glaciation, may have increased isolation of cave populations and enhanced speciation.

The study of the effects on cave species of tropical forest contriction during the Pleistocene has just begun. Epigean species are thought to be able to expand their ranges during humid interglacial and then be confined to caves and subsequent speciation during the drier glacial periods. Some areas that have undergone recent and great climatic fluctuations in Brazil have more troglobites compared to troglophiles compared to forest refugia areas. The pattern with aquatic species seem less clear, presumably because more are interstitial and are less likely to be isolated by climatic events and/or because of the effects of other isolation effects, such as stream capture (Trajano 1995).

In food-poor caves you can't have both large populations sizes and high biodiversity. K-selection and rarity itself may be favored because there is less likely to be populations increases that outstrip resources that lead to crashes and extinction (Holsinger & Culver 1987). However, there is less support among biologists for such group selection than there is for selection at lower taxonomic levels.

Biodiversity effects population structure and numbers in other ways. Changes in predator populations are less dramatic where there are more choices in prey species. Larger species are also more likely to find suitable niches in biodiverse caves (Barr & Holsinger 1985).

Griffith & Poulson (1993) demonstrated competition between individuals of the same beetle species especially when beetle density was high and when a beetle had almost uncovered a cricket egg. High energy food sources that are patchy in distribution are more likely to be competed for than low energy food sources. Interference competition develops when its benefits outweigh its costs: digging for an egg may take hours while chase, fights and thefts may take only seconds.

Larger, more evenly distributed food supplies can allow for greater migration, establishment, and lessened competition (Holsinger & Culver 1885). An more active and aggressive amphipod when at high densities eliminated an isopod species from preferred habitat (Bechler 1985). In food rich areas, the more aggressive *Typhlichthys* fish may fray the fins of the more troglobitic *Amblyopsis* fish and drive it out of the area. The generalized feeding of the cave salamander *Eurycea lucifuga* may exclude other salamanders from some cave habitats (Peck & Richardson 1976).

Competition in some cases may decline with increasing time species spend in caves (Culver 1976). This suggests that competition can lead to niche separation through speciation. In one study, competition decreased as the size difference between two isopod species increased (Culver & Ehlinger (1980). The competitively more successfull *Typhlichthys* cavefish may have split *Amblyopsis* cavefish into two isolated areas where they subsequently speciated (Woods & Inger (1957).

Specialized feeding tends to reduce competition. Grazers, such as springtails, feed on microfungi while burrowers such as fly larvae and earthworms feed on bacteria.

Competition may also lead to niche separation through metamorphosis. Larval Ozark cave salamanders live in the twilight zone of caves and have functional eyes. They then move to the dark zones, undergo metamorphosis and a fold of skin grows over their eyes.

Evolutionary changes in cave animals result from selection and genetic drift due to the loss of evolutionary constraints. Poulson argues that regression (loss of eyes, etc.) has largely resulted from genetic drift while cave-adaptated traits (longer appendages, etc.) result from selection for those traits (Poulson 1985). Some reduced traits may be augmented by both neutral mutations and natural selection while added traits may be slower because only natural selection operates (Culver 1995). Also, since reduced traits may also be due largely to suppression of function by controller genes, this persumably can happen faster in evolutionary terms than can the addition of new genetic material.

Apparent holdovers show that few if any species are perfectly adapted to their environment; they all have an evolutionary history in which certain forms and behaviors were favored over others but not equally. Even disadvantageous traits could be carried over if the their genetic coding was close to the genes of a highly selected trait. Cave salamander larvae still lunge unsucessfully at their prey in total darkness (Culver (1973).

As opposed to the relicts, "preadaptations" may help surface or interstitial species move into caves as an "adaptive shift." Such traits may include form and behavior suitable for the high carbon dioxide and low food of certain nocturnal, wet and soil habitats.

Some of the earliest arthropod colonizers of the land were relatively unspecialized and themselves pre-adapted to life in the soil. This may be why there are so many "primitive" troglobites, such as springtails, millipedes, diplurans, grylloblatids, thermosbaenacid crustaceans, and crickets. Some of these rather unspecialized animals apparently made the change from sea to cave directly or through a freshwater phase, such as remipedia, atyidid shrimp, polychaete annelids, desmoscolecid nematodes, amphipods, planarians, and cirolanid isopods.

Trechine beetles in the eastern U.S. may have first become adapted to soil habitats and later to cave ones (Barr & Holsinger 1985). Nocturnal carabid beetles, with their chemical/tactile hunting and narrower and less binocular field of vision (Bauer & Kredler (1992) may have been more selected as cave ancestors than their more visually oriented daytime counterparts. The surface pseudoscorpions from the families with the most cave-adapted species tend to have reduced eyes and sluggisly wait for their prey in damp humus or duff instead of actively pursuing it (Chamberlin & Malcolm 1960). Soil animals that became cave animals probably also include certain catopid beetles, linyphiid spiders and mites (Barr cave ecology)

Aquatic pre-adaptations have also been common. Cavefish presumably arose from ancestors similar to present-day *Chologaster* of the same family. These fish can live in surface streams but they feed at night, avoid light, orient their bodies in the direction of streamflow, and suck in great amounts of water when they open up their mouths. Similarly, blind catfish in Texas arose from nocturnal catfish with well-developed touch and taste senses. All of these traits would help their progeny adapt to food-poor environments in caves (Rosen 1962). Marine sebid amphipods are weakly pigmented, mostly eyeless species living on the ocean bottom. (Holsinger 1986).

Many species are scavengers and opportunistic, eating whatever is available. There appears to be increased geophagy, the eating of sediments among some troglobites (Thibaud 1994). Cave species are more likely to be generalists when their food is seasonal. For example, the beetle *Neaphaenops tellkampfi* preys on cave cricket eggs and nymphs, food that is highly seasonal. During the off season it feeds on springtails (Kane & Ryan 1983). The lack of competition in some caves has allowed for such niche expansion. Variation in genetic makeup may be limited because the coarse-grained seasonal entry of organics (guano and leaf litter) allows only a few flexible alleles to persist. This genetic restriction allows the species to be generalists that can benefit from all the various seasonal cycles of organic input (Koppleman & Figg 1995).

Food and moisture largely determines the makeup of cave communities and the physical makeup of individuals. Food scarcity is one of the main forces in evolution in cavefish (Poulson 1963). Where rocks or thick soils prevent organics from reaching caves, troglobitic crayfish are absent in Florida (Franz & Lee 1982). Where thick soils have plugged entry of organics in lava tubes in Hawaii, cave biodiversity is sparse. Organic content is important for some springtails but only when combined with suitable wetness and soil particle size (Christianse, Wilson & Tecklin 1961). The density of some cave invertebrates correlates with the abundance of microfungi but not with bacteria (Dickson & Kirk 1976). Digestive enzymes in cave crickets are produced by microbes, mostly Gram + and a yeast (Lavoie & Kennedy 1989)

The highest biodiversity and populations in food poor caves and interstitial zones often occur where food is most common, the edge effect. This can be where the dark zone and the detritus infall from entrances meet (Peck 1976) or at a fluctuating groundwater table. The tradeoff for living deeper in the cave, at least for salamanders, may be greater safety from predators (Peck & Richardson 1976).

Food scarcity may actually allow certain animals to survive because it may protect them from competition. These animals are adapted to a cave environment in which there is little food. Consequently. abundant food brought by human visitors to the cave may bring in surface animals better adapted to using this introduced food. They in turn may outcompete the cave adapted life.

Sources: Most food comes in from the outside through water and, to a lesser extent through the feces and leaf litter brought in by trogloxenes and the bodies of accidentals. Flood debris is a major food source and ultimately supports large populations of crayfish and cave fish.

The major food source within caves are microfungi and bacteria.
Isopods probably feed on bacteria but even if they don't, the burrowing or browsing may keep channels for water flow open and disperse bacteria, thus reducing bacterial activity (Edler & Dodds 1992).

Bacteria in turn affect cave materials. Actinomycetes often give cave mud its distinctive smell known as "caver's perfume." Moonmilk is a white, fine grained material that can absorb a great deal of water. It has a mysterious ability to heal infections in European livestock. This sounds like a quaint superstition but in moonmilk is often found actinomycetes. These bacteria are the main producers of antibiotics.

Springtails have waxy, water repellent bodies that enable them to graze on the fungi in pools. Flatworms patrol the underside of the water's surface and grab unsuspecting springtails. They are the sharks of the cave world. Mites prey on springtail young on the water's surface.

Dripping water supplies food for cave slime bacteria and fungi. Such slime seems especially abundant in flowstone areas. Airborne particulates and evaporation may enhance organics near cave entrances and may help explain the abundance of filamentous bacteria that forms moonmilk in those areas. Moonmilk tends to be absent or solidified closest to the outside, suggesting that temperature or relative humidities changes may be too extreme for optimum bacterial growth in those areas.

The accumulation of storage products and the high proportion of inactive cells in bacterial communities in low organic groundwaters suggest these are adaptations to low food supplies. Some bacteria have elongated shapes or extend their shapes to capture more food. Bacteria can shrink to very small sizes in the absence of food and helps them move through interstial medium till they can find more food. Many cave bacteria can break down the more resistant types of food, those most likely to survive entry into caves. These included fulvic and humic acids and lignins. However the number and proportion of extremely oligotrophic (low food adapted) bacteria in karst waters appears low, perhaps because karst conduit flow can transfer organics more quickly than can more diffuse groundwater flow.

Large amounts of bacteria can occur in sufur, as appears to be the case in Lost River Cave in Kentucky and in the halocline/thermocline of Crystal Beach Spring in Florida.
Mussels in the latter case may depend on the bacteria for food (Garman 1997), similar to mollusc dependence on bacteria near submarie volcanic vents.

Various species compete for the energy in feces. If the pellets are too small, fungi may consume them first.

Lesser food sources include cricket eggs predated upon by beetles. Snails are among the few animals that can secrete enzymes that can break down insect skeletons. They feed on bat guano rich in these skeletons. Like snails, flatworms lay down sticky trails of slime but they use these trails to trap prey.

Where crickets deep in the cave get their food is still somewhat puzzling. Cricket and fruit remains occur in cricket stomachs but this can only account for part of the food supply. Bacteria such as actinomycetes may consume organic material in rainwater entering the cave. Bacteria on sand grains may in turn become food for the crickets. Sand grains have been found in the stomachs of these crickets although the grains could have been eaten accidentally. A substance in cave cricket guts that resembles applesauce has not been identified (Northrup, 1988).

Spiders may trap flying insects near cave entrances. However, because food is so scarce, many spiders in cave actively pursue their prey instead of waiting patiently for them to land in their webs. This appear especially true in tropical caves, as opposed to temperate ones (Brignoli (1973)

Spiders especially prey upon cave flies, moths and other creatures of the bat guano piles. This community is different from that of other cave life as bat droppings provide a rich food supply. Since troglobites generally are adapted to food poor habitats, it is not surprising that guanobites usually are troglophiles or trogloxenes. Less energy rich concentrations of guano, as those of cave crickets are more likely to be used by troglobites. Stygobromus feeds on the feces of Gammarus minus, a form of commensalism. Similar to surface enviroments, there are seasonal influxes of food that cause changes in the number of crickets and other insects that are born each season. Since fresh guano is even more localized than caves are, members of the guano community must be able to locate new guano fairly easily. They can do this either by catching a ride on bats or flying to new food under their own power.

The Mexican free-tail bat has a complex way to navigate and find food. During an initial food search, it uses a single frequency signal spaced at fairly wide intervals. Although this signal saves on energy, it gives the bat very little information but may simply tell it whether an insect is somewhere ahead of it. If an insect is detected, the bat switches to a frequency modulation signal. Changes in frequency of this signal allows better reflection of the sound signal off the insect when the wavelength approaches the size of the insect. This reflection helps the bat locate the insect more accurately. The bat now increases the rate of signals in order to get more information and, based on the doppler effect, may determine in what direction and how fast the insect is flying. Final capture is based on where the bat thinks the insect will be at that precise moment. An even more complicated signaling system occurs when the bats leave a cave. Then they employ multiple harmonics, frequencies that are even fractions of the original frequency, vibrating their vocal chords in much the same way that a rope can be vibrated at different whole number intervals of the initial wavelength.

Food scarcity is the most important ecologic result of total darkness. Without green plants, there is little food available except what is brought in from the outside such as eggs, feces, dead bodies and plant detritus from flooding. Only certain bacteria are not ultimately dependent on solar energy. Instead, these bacteria use the energy from the breakdown of iron, manganese, sulphur minerals.

Trogloxenes, such as grylloblattids and crickets, live in caves because they eat outside at night. Cave salamanders (*Eurycea lucifuga*) feeding in the dark zone of a cave had almost three times as much food in their stomach than did those feeding near the cave entrance (Peck & Richardson (1976).

This explains why few large animals live their entire lives in caves. Most cave creatures who spend all their life inside the earth have much less to eat and so have to be smaller. In Florida the smaller cave crayfish live on the ceiling of submerged passaged while the larger crayfish live on the floor where presumably more food is available (Hobbs III 1972)

Lack of food largely determines how cave life looks and how it behaves. Because over-population would rapidly deplete scarce food supplies and because there is less energy available for reproduction, fewer eggs are laid and sexual maturity is delayed. Those eggs that are laid are larger-- to give newborn salamanders a head start against starvation. Only an occasional amphipod or crayfish female may eat enough to reproduce and so the percentage of females with eggs in caves usually is small. Or those populations with high reproductive rates have become extinct (Holsinger & Culver, 1987).

Pseudoscorpions and centipedes immobilize their prey by injecting poison from their claws.

Slower body processes, perhaps a result of higher amounts of carbon dioxide gas, allow cave dwellers to eat less, live longer and maintain a more stable population. Some cave adapted crickets expend the same amount of energy but use it more efficiently. For example a troglobitic rhadine cricket in Texas is much more active than its troglophilic cousin on the surface. Some cavefish swim more efficiently and more frequently than their surface cousins in search of food (Poulson 1963).

Food-rich guano often support the most diverse communities, as in areas of cricket guano in Appalachian caves. Food quality/richness generally decreases from raccoon to bat to woodrat to cricket feces but remains high compared to other food sources. Consequently, the more mobile and metabolically active troglophiles tend to predominate on recent feces. As food value decreases over time, the community shifts and become more troglobitic.

Some cave species are neotenic, such as certain salamanders, talitrid amphipods (Bousfield & Howarth 1976), and perhaps bats. Since juveniles are often less specialized than the corresponding adults, neoteny may enable some species to adapt to a new environment such as a cave. In some cases neoteny may be favored because immature stages are more preadaptive to cave life, as in the case of planthopper nymphs in Hawaii (Howarth 1993). In blind catfish,
the larger heads of neoteny may increase olfactory and touch senses, energy economy (low growth rate, small size, fatty deposits) and high water pressures similar to those of deep sea fishes (small body size, fat deposits, regression of swimbladder, reduction of muscles and weakly ossified skeleton) (Langecker & Longley (1993). Nerve cells in amblyopsid cavefish are arranged to be more sensitive to touch and vibrations and may be a result of neoteny (Poulson 1963, 1964). The absence of fin splitting in cavefish also appears to be neotenic (Cooper & Kuehne 1974)
Delayed sexual maturity can stabilize populations and extend the longevity of a species, useful traits if there is not enough food for normal growth patterns and if an opportunistic animal needs to live a long time in order to reproduce when food supplies are most favorable. Various stresses such as starvation may decrease hormonal levels, leading to delayed maturity in certain individuals. If this neoteny is selected for in the cave habitat, then these individuals may be those most likely to reproduce and pass on a genetic propensity to stress-induced neoteny. Stress may also disrupt cellular enzyme reactions, leading to an increased mutation rate that could yield traits selected for in cave habitats. Cave species often have more karyotypic and shape differences than their surface cousins although this may be more due to genetic drift less constrained by natural selection (esp. competition) than to increased mutation rates.

If there is more food in aquatic habitats then neoteny in salamanders may enable them to spend their time where the most food is. The arrested development in neoteny of size and appendage and body segments also may allow larval forms to better utilize the smaller amounts of food (compared to the surface) as well as small interstitial spaces (Coineau & Boutin 1992; Gould 1977). Eyes in adult salamanders degenerate (Beshares & Brandon (1975a), perhaps in order to conserve energy in the adult's food-poor habitat.

Neoteny can be rapidly acquired in evolution, as in the case of humans, because the genetic material for its expression is already there. In the same way, cave-adapted species can rapidly reaquire surface traits, such as large eyes, because the genes that allow for large eyes have only been suppressed, not eliminated. For example surface exposure of karst underground conduits (karst windows) has resulted in the reevolution of eyed forms from eyeless individuals within a span of only tens of thousands of years (Culver 1995).

Troglomorphisms are morphological modifications (specializations) that distinguish troglobites from their closest surface, interstitial or soil cousins. Cave-adapted crayfish appear to have smaller mouthparts for chewing silt-detritus on cave floors, as opposed to their surface cousins who chew on larger size materials (Caine (1975). Among cave adapted species, limbs may be longer (salamanders (Glergue-Gazeau (1975), teeth number decreased (salamanders (Glergue-Gazeau (1975). head broader and flatter snout salamanders (Glergue-Gazeau (1975),
pigmentation reduced (salamanders (Glergue-Gazeau (1975)

Much of this appears related to energy conservation.

Although abiotic changes are less in caves than on the outside, the loss of self-regulating traits among cave species, such as thick cuticle protection from dryness, may make cave species more sensitive to what cave climate fluctuation do occur. Population fluctuations in certain carabid cave beetles are similar to carabids on the surface although cave habitat diversity can dampen such fluctuations (Kane & Ryan 1983).

The increased longevity may be partly achieved by neoteny and a slowing down of metabolism although any genetic link between the two is unclear. Species with high metabolism don't live as long as species with low rates of metabolism. A general rule of thumb is that mammals live on the average about 100 million heartbeats, regardless of whether it may be a mouse or an elephant. The exceptions to this rule often are neotenic species, such as bats, cave salamanders and humans. Neotenic species live longer, perhaps in part because their metabolism is even lower than their non-neotenic cousins with similar heartbeat rates.

predation - In one case the predation of salamanders on an isopod increased the density of an amphipod because it reduced competition (Culver (1975). In interstitial medium, predators approach the size of their prey. Symphylans spin threads which probably hinder pursuing predators. Springtails turn somersaults in mid-air to escape their pursuers. Some species may invade caves because of the absence of predators. Others, like salamanders, may invade caves because there are untapped prey.

Senses: Cave animals must rely on senses other than sight. Bats use reflected sound waves. Pack rats sniff out urine trails. Chemical senses have developed on insect legs and antennas and on the hairs of centipedes. Some cave crickets have extra long antenna and probably are oriented to air currents when they exit a cave in search of food at night (Campbell 1976).. Bat flies apparently use heat and carbon dioxide to locate their bat hosts (Caire, Honruff & Sohrabi). The cave salamander *Eurycea lucifuga* may orient itself to magnetic fields (Phillips 1977).

Some of the most cave adapted fish have smaller optic lobes in their brains, plus enlargement of those brain areas that are concerned with touch and equilibrium. Some cave amphipods may now be devoting more parts of their brain to processing non-visual information (Culver 1995).

Several groups of cave animals appear to be more sensitive to vibrations, including planthoppers
(Howarth, Hoch & Asche (1990).

Lateral lines that record pressure changes appear to have become more important in the evolution of some cave fish. Salamander larvae detect prey through water movement (Culver, 1973, 1975, 1985). Orientation to and selection of the weakest water currents among European amphipods.

Communication between individuals requires non-visual senses in caves. Planthoppers from different lava flows in Hawaii use different vibrations to communicate (Howarth, Hoch, & Asche (1990). Presumably this has led to sexual isolation of populations and increased chances for further speciation. the increased antennal size in *Gammarus minus* amphipods may be for increased sensitity to sex pheromenes involved in finding a mate (Culver 1995).

Humidity: Without the constraints of low humidity, cave species can evolve elongated appendages for various functions.
Unlike most insects, millipeds cannot restrict evaporation through their body walls (Crawford, 1974). Springtails breathe through troughs on their skin but this makes them vulnerable to dessication. As a result, cave-adapted springtails have enlarged third antennal segment organs sensitive to changes in humidity (Chapman 1993). Troglobitic species tend to have lower cuticle thickness or density compared to surface relatives (spiders: Hadles, Ahearn & Howarth, 1987). This may be especially true of species who have evolved into small voids with high humidities. These species may only move into larger voids (caves) if there is high humidity and a food source (Howarth (1987).

Mating of *Ceuthophilus* may be helped by a chemical substance on the female antennae and by the setai on the cerci of the male touching the female abdomen. The males of *C. carlsbadensis* often touch the females with their antennae as a preliminary to copulation. After this exchange, males turn around and waggle their posteriors at the female. If she is receptive she will turn around. Presumably by feeling with his cerci, the male fuses to the female after turning his abdomen over 180 degrees. The matings observed last approximately 3-5 minutes. Transfer of sperm is by means of a spermatophore, a glutinous ball of sperm (Northrup, 1988).

Reproduction:

The difficulty in finding mates admist the darkness and low numbers of individuals in most caves has been solved in various ways. Many cave species are parthenogenetic, as among isopods, crickets, amphipods, rotifers, flatworms and thysanurans. Their rates appear to be higher than those of their surface cousins. In a damp cellar in Switzerland is the only male Pscoptera that has ever been found.

Some parthenogenesis may arise when only a single female colonizes a particular cave. This is supported by a higher degrees of parthenogenesis at the northern eged of cricket ranges. Some of these parthenogenetic colonies may become secondarily bisexual when males arrive (Lamb & Wiley 1989).

However, finding mates may not be the prime concern. Female to male ratios often are very high in what may be non-parthenogenic species ranging from three to one in an isopod (Estes 1979) to ten to one in an amphipod genus (Culver & holsinger 1969). Parthenogenisis or populations with high female to male ratios may be favored in food poor environments because then most or all males become superfulous and compete with females for food. In situations where populations densities (and presumably food supplies) are high, male frequency increases (Dickson & Holsinger 1981)

Timing of reproduction seems less cued to diurnal or annual solar events and more towards ecologic events which may be more or less annual in nature. Organic influx from flooding appears to time reproduction among (crayfish (Jegla (1970), cavefish (Poulson 1964; Poulson & Smith), snails, isopods, amphipods (Poulson in Chapman 1993) and cave crickets (Kane & Ryan 1983). The beetle *Pseudanophthalmus tenuis* reproduces after annual floods add organics to mud banks (Keith). Many guanobic breed after bats bring in fresh guano in late spring. Disturbance of wood can cause fungi in caves to fruit (Chapman 1993).

Species of springtails with widespread distribution may have originated by convergent evolution. Multiple invasions of caves may have resulted in speciation of "sibling species" that are so similar in form, behavior and habitat preference that they are often regarded as a single species.

Temperature: Some milliped species prefer cool temperatures (Crawford, 1974). Grylloblatids, and certain amphipods and isopods will die if the temperature of their surroundings approaches sixty degrees F.
Although troglobites appear to have reduced circadian rhythms, other cave animals such as trogloxenes rely on other cues. Crickets may use changes in air flow or even the diurnal effects of the moon (earth tides) to known when to forage outside at night (Simon (1973). Some bats use the change in air pressure during stormy weather to know when not to exit the cave in search of insects.

Caves are valuable to scientists because they harbor animal communities that are simpler to study than those on the surface. This is partly because there are often fewer types and numbers of animals in caves and so there are usually not as many types of possible interactions compared with animals communties on the surface. Competition between individuals of the same species is easier to study because that may be the only type of competition present. Fluctuations in current flow and temperature may reduce populations in some caves so much that competitive interactions are not important (Culver 1994).

Still, there also are fewer complicating changes in most cave's physical environment, such as weather, etc. Simplicity in the cave environment reduces the number of selection pressures acting upong cave species, perhaps resulting in more precise adaptation to the remaining pressures, thus making these pressure easier to identify and study. Population sizes are relatively stable compared with most surface populations. Unlike the surface, there are many caves with very similar conditions and so there are many replicates as well as caves where species composition differ due to differences in migration, evolutionary time, etc. Ongoing colonization rates can be found in newly created and datable lava tubes, as in Hawaii.

Caves can highlight evolutionary mechanisms and rates. Unlike most surface populations, geographical distribution, population sizes and the time of colonization can often be accurately determined (Belles 1992). Even limited sampling often is adequate to characterize the small populations of caves.

Some selection pressure appear carried out to an extreme in caves, such as K-selection, parthenogenesis, and neoteny, and thus are easier to delineate and acertain relationships between metabolism and longevity, reproduction, size, etc.

Cave communties are important as models for the establishment and management of nature preserves throughout the world. Like caves or islands, most nature preserves will likely be or already are surrounded by man-made environments unfavorable to most forms of life. It is vitally important to know how such relatively small communities can survive. Cave comunities can give us important clues as to how to administer and protect these preserves.

Other barriers are geologic, as with large rivers separating many terrestrial species and a few aquatic ones. Even small streams may be barriers if there aren't enough meanders to supply limestone bluffs and cracks for colonization. Meander rich streams may eventually evolve into ones with reduced meanders, thus cutting off gene flow and resulting in sister species (Barr & Holsinger 1985).

Without the buoyant effect of water, cave areas above the phreatic zone are more likely to collapse and become plugged with silt. Rivers pose few barriers to phreatobites and may even aid in their dispersal. Suitable areas for migration are therefore likely to be more discontinuous for land animals than for aquatic animals. This may partly explain why aquatic troglobites tend to have wider distributions than terrestial ones. However, large amounts of folding and faulting of rock layers in the Appalachian Valley has created non-cave barriers between cavernous rocks for both land and water animals. A decrease in water levels since the latest Pleistocene may have reduced the amount of interchange resulting from connections between drainage basins during periods of high water.

One of the reasons for a relative lack of troglobites in the West is that, like lava tubes and gypsum caves, many parts of the West are newly arrived and may not have had many troglobites to begin with or, with the change in climate from latitude changes, the original cave dwellers became extinct. So speciation in many cases is just getting started.

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The National Park Service hosts a diverse array of biologically signficant caves. Except for central Texas and northern Florida, all of the eight cave biodiversity "hot spots" in the U.S. are represented, including the Appalachians (New River NRA, Great Smoky Mt. NP, Russell Cave NM), Cumberland Plateau (Cudjo Cave in Cumberland Gap HP), Interior Low Plateau (Mammoth NP), Ozark Plateau (New River & Ozark River), Hawaii (HI Volcanoes NP) and the Sierra-Klamaths (Oregon Caves NM, Sequoia-Kings Canyon NP). Carlsbad and Guadalupe Mts. NM partakes of the terrestial diversity of central Texas but not its aquatic fauna in the Edwards Aquifer.

Non-karstic cave areas are represented as well, including the sea caves of Channel Islands in California and Acadia in Maine, caves caused by earth movements in Wapatki in Arizona and the boulder caves of Pinnacles in California.

At least five parks manage biologically significant mines as well as caves, including Death Valley and Bighorn Canyon. Organ Pipe monitors a maternity colony of *Leptonycteris curasoae*, a federally listed endangered species. The only known day roost in the park is a mine with around 15,000 individuals, making it the largest known roost of this species in the U.S.

The park cave with the highest biodiversity is likely to be Mammoth Cave. It has ____.

Many park caves have endemics only known from a particular cave or sinkholes, including Oregon Caves (10 species), Mammoth (8), Cudjo (2) and Montezuma Well (2). Russell, Jewel, Wind Cave all have one endemic apeice. Grand Canyon has three caves with a total of four endemics. Great Smokies NP has two caves with one endemic apeice. Carlsbad Cavern NP has four endemics in the cave itself and three other endemics in three other caves in the park.

Water and food input are the most important habitat requirement for cave species and are those factors most likely affected by human impacts. Too little water mostly comes from enlargement of natural entrances and the opening of artifical ones. This results in chimney and reverse chimney effects as dry summer air enters upper elevation passages and cold winter air enters lower passages. As cold winter air enters caves it warms up and the relative humidity drops. Biological surveys in Oregon Caves indicates that the location of most cave populations are affected more by this seasonal change in airflow than by any other factor. The resulting dessication from modification of cave entrances has affected animals in at least five Park Service caves.

In part because dessication and/or freezing greatly affects cave geology, restoration of airflow has been a top priority in most NPS caves, including Carlsbad, Oregon, Wind and Mammoth Caves.

Fire suppression on the surface has increased shrub density and evapotranspiration and apparently has reduced waterflow in Wind Cave in South Dakota and Oregon Caves. Regional changes in albedo and subsequent changes in atmospheric convection may increase precipitation in urbanizing areas and decrease it in deforested areas. Decreased waterflow into a cave may also reduce the amount of incoming organics.

Flooding can result in too much food, too little and/or changes in food seasonality. Dams on the Green River near Mammoth Cave, for example, have lowered the seasonality variation in subsurface water levels, resulting in less food access for both terrestrial and aquatic organisms that, respectively, rely on the stranding or inundation of food sources at different times of the year (Lisowski & Poulson, 1981; Poulson 1992). Increased waterflow can also wash away guano or stop the growth of actinomycetes "cave slime" upon which a harvestmen (*Speleomaster lexi*) and some rare flies appear to depend on.

Cave communities tend to be food-regulated rather than predator-regulated and so can be more affected by increased organics.
Even slight increases in organics from pollution can cause the paradox of enrichment in which less cave-adapted species move into a cave to better utilize a rich energy source. There they outcompete native species. Trogloxenes tend to be more common than troglobites near high-energy food sources (Poulson & Kane (1981). There is suspicion in some Arkansas caves that increased troglophilic crayfish near cave entrances with more food from human impacts may be predating on troglophilic species**.

In showcaves, most human-caused organics occurs near trails. This largely results from cotton lint, shedding of human skin flakes, and the growth of alien algae near electric lights. Disturbance of clay soils can also increase the availability of food at least on a microbial level. A more cave-adapted cricket in Carlsbad Caverns is preyed upon by a more aggressive cricket that is more common in the food-rich trail areas. Low biodiversity near food-rich trails have also been found in Oregon and Mammoth Caves and Jewel and Wind Caves in South Dakota.