Chapter 9
Management of Subterranean Fauna in Karst*

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Abstract Ensuring the appropriate quantity and quality of energy flow from the surface to the subterranean environment is a universal challenge of managing subterranean fauna in karst. This chapter covers four major issues central to an understanding of the energy connections between the surface and the subsurface ecosystems. The first issue is that there needs to be a greater focus on species that are not restricted to subterranean habitats because some of these species act as major vectors of energy into subsurface ecosystems. The second issue is that a greater understanding of the paths of allochthonous energy into the subterranean ecosystem is necessary to ensure the long-term health of the subterranean fauna. Percolating water delivered from the epikarst appears to be more important than organic matter transported by sinking streams in supporting the biofilm that serves as the base of the aquatic food web. Energy transported by active movement of organisms from the surface is essential in supporting the terrestrial food web and possibly some aquatic species as well. The importance of many potential sources of energy, such as the organic matter left on the riparian zones of subterranean streams, has not been studied. The third issue is that management practices need to focus on factors that threaten the energy flow from the surface to the subsurface because, unlike many other threats to subterranean ecosystems, disruptions of such paths of energy are usually not overt and easily recognizable. The fourth issue is that the metabolic adaptation of many subterranean species to the underground environment may increase their resilience to disruptions of energy flow from the surface. Thus, management practices that recognize threats to such energy paths may allow for a higher probability of successful interventions leading to restoration of the health of subterranean ecosystems.

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* "When we try to pick out anything by itself, we find it hitched to everything else in the universe" – John Muir

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9.1 Introduction

Globally, there is growing awareness of a need for protection of organisms dwelling in subterranean habitats in karst regions. Subterranean organisms appear to be especially at risk because most species exhibit a suite of characteristics that increase their vulnerability to anthropogenic disturbance. These characteristics include limited geographic range (Barr and Holsinger 1985; Christman et al. 2005), poor vagility (Verovnik et al. 2004; Hoslinger 2005) and low reproductive potential, long life span and small population size (Culver et al. 1995). These life history characteristics are excellent adaptations to the subterranean environment, but they also lead to a slow population growth rate, and, in concert with the high degree of endemism and low dispersal ability, greatly reduce the ability of these organisms to rapidly recover from a reduction in population size for any reason. The vulnerability of the subterranean fauna is underscored by the fact that, a decade ago, over 20 subterranean invertebrate species were listed as federally threatened or endangered and about 600 were listed as critically imperiled in the United States alone (Culver et al. 2000), and the numbers are likely much higher now.

The identification of subterranean species at risk and the development of effective strategies for their management face a set of unique challenges. First, most of the physical space in the subterranean environment is too small to be accessible to humans. Cave passages, wells and even submerged caverns represent only small windows into vast expanses of unreachable space. Basic information on the ecology and life history of most subterranean species are unknown because gaining entry to their habitats is often technically challenging and because their lengthy life span and low population density render ecological studies difficult. Aquatic subterranean species pose additional problems because of conflict between management practices and demand for ground water from expanding urban and agricultural development, and these problems are especially acute in karst regions.

A large number of human activities pose threats to the subterranean fauna (Culver and Pipan 2009; Romero 2009; Tercafs 2001). It is impossible to provide an indepth discussion on managing subterranean fauna in karst areas to deal with all threats in one chapter in a collected volume. Instead, this chapter stresses the importance of surface-subsurface connections and develops the central theme that ensuring the appropriate quantity and quality of energy flow from the surface to the subterranean environment is a universal challenge of managing subterranean fauna in karst. This is the general conclusion drawn by many researchers who have examined this issue (Elliott 2000; Hamilton-Smith and Eberhard 2000; Humphreys 2000; Tercafs 2001; Culver and Pipan 2009). Although this volume and chapter focus on karst, subterranean fauna also exist in nonkarst habitats, especially habitats associated with groundwater such as wetlands and the hyporheic zone (Hancock and Boulton 2008; Humphreys 2009; Hahn 2009). The importance of surface-subsurface connections in terms of energy flow discussed in this chapter should apply in general to these nonkarst habitats as well, although the specific details may be more complicated in nonkarst habitats (Gibert and Culver 2009).

   This chapter begins with the example of Robber Baron Cave and the management issues that arise, focusing on the path of energy from the surface to the underground. It then details the different ways that energy is transferred from the surface to the subterranean ecosystems, following the theme that a thorough understanding of the connections between the surface and the subterranean environments in terms of energy flow is the key to effective management and protection of the subterranean fauna. The chapter concludes with a discussion on management of the subterranean fauna in light of the different paths of energy flow from the surface to the underground.

9.2   The Case of Robber Baron Cave

Robber Baron Cave is located in the City of San Antonio in the State of Texas, USA (Veni 1988). It was a commercialized show cave, drawing 300,000 visitors from 1926 to 1933. The owner had even physically modified the cave by erecting false cave walls to hide some passages from tourists. Because of its urban location, the cave has experienced much vandalism and associated human activities. A gate installed at the entrance was frequently tampered with and had to be replaced periodically, at times requiring physical rearrangement of the entrance area with heavy machinery. In spite of such intense anthropogenic impact, the cave still boasts a rich fauna. It houses at least ten troglobionts, species that occur only in subterranean habitats and are never found above ground. Two of the species, the Robber Baron Cave Spider, *Cicurina baronia* (Fig. 9.1), and the Robber Baron Cave Harvestman, *Texella cokendolpheri*, exist only in this one cave, and both are listed as federally endangered by the US Fish and Wildlife Service. A number of other species that are not troglobionts are also found in the cave. Some are occasional visitors but many are residents that move between the cave and the surface on a seasonal or daily basis, such as the cave cricket *Ceuthophilus secretus* (Fig. 9.2). Robber Baron Cave has been protected and managed according to a management plan since it was acquired by the Texas Cave Management Association in 1995. However, many populations of its fauna still appear to be in decline since. The cause was encroachment by urban development toward the cave entrance, which severely limited the foraging area of the cave crickets when they left the cave at night to feed on the surface (Taylor et al. 2005). Consequently, the amount of energy the crickets brought back to the cave, in the forms of guano, eggs and newly hatched nymphs when they reproduced and biomass when they died, was insufficient to sustain the food web within the cave.

   The situation at Robber Baron Cave illustrates some of the major issues in the management of subterranean fauna in karst areas. The first issue concerns the meaning of subterranean fauna itself in light of a historically biased research and management focus on only a subset of the subterranean fauna. The second issue concerns the importance of energy flow from the surface to subterranean ecosystems, the central theme of this chapter. The third issue concerns the apparency of different

Fig. 9.1 A *Cicurina* cave spider, displaying the troglomorphic features of reductions in eyes and in body pigmentation as well as elongated appendages. Photograph by Dr. Jean Krejca, Zara Environmental LLC. Used with permission

Fig. 9.2 The cave cricket *Ceuthophilus secretus*. Photograph by Dr. Jean Krejca, Zara Environmental LLC. Used with permission

types of threats to the subterranean fauna and that threats to the paths of energy flow to the underground are usually less apparent than other threats, such as those that directly affect the physical integrity of the subterranean habitats. The last issue illustrated by Robber Baron Cave is the potential resiliency of the subterranean fauna to disruptions of energy flow from the surface because of the metabolic adaptations of many subterranean species. These issues are discussed in turn below.

9.2.1 The Subterranean Fauna

In general, when considering subterranean fauna, most often species that are not adapted exclusively for the subterranean environment come to mind. These adaptations include a suite of features termed troglomorphy by Christiansen (1962), including reduced-to-complete loss of eyes and body pigment, elaborated extra-optic sensory structures, elongated appendages and more slender body forms compared to related surface-dwelling taxa. The endangered harvestman and spider in Robber Baron Cave both exhibit this classic troglomorphic phenotype. Research on and management practices concerning subterranean fauna have and are mainly focused on troglomorphic troglobionts. Less emphasis is placed on non-troglomorphic troglobionts, such as *Spelobia tenebrarum*, a small fly found only in caves over a wide geographic area but exhibits no obvious troglomorphic feature. Other than bats, and, more recently, cave crickets, species that are not troglobionts, ones that also occur in but are not limited to subterranean habitats, have received the least attention. This bias is understandable in light of our long history of fascination with the often bizarre appearance of troglomorphic species, such as the European Cave Salamander, *Proteus anguinus* (Sweet 1986), and the tremendous academic interest in elucidating the mechanisms of the evolution of troglomorphy, dating back to Darwin (Culver et al. 1995; Culver and Wilkens 2000; Culver and Pipan 2009). In addition, the study of troglomorphy may also provide information on the mechanisms of evolutionary loss of features in general, a common phenomenon not exclusive to members of the subterranean fauna; the loss of hearing in moths on islands without bats is just one of many examples (Fong et al. 1995).

The lack of emphasis on non-troglomorphic species in the study and management of subterranean fauna may also partially follow from the tradition of ecological classification of the subterranean fauna into troglobites: obligate cave-dwelling species, troglophiles: facultative-cave dwelling species and trogloxenes: surface species that are occasionally found in caves. According to this scheme, troglobites, rather than troglophiles and trogloxenes, are the more interesting species, with the mindset that trogloxenes and troglophiles are merely troglobites in training and have not yet arrived at their destinations on their evolutionary paths. But as Culver (1982) pointed out, many troglophilic species are very successful in caves, and that many species are often assigned to one of these ecological categories based on morphology instead of ecology, circular reasoning at its most basic. Furthermore,

inherent in these designations is that evolution of subterranean organisms is a linear process, from trogloxene to troglophile to troglobite. However, adaptations to the subterranean environment surely follow multiple paths, with different species evolving different solutions at any one moment, thus what are designated as troglophiles or even some trogloxenes are no more but certainly no less adapted to the subterranean environment than are troglobites; some troglophiles may evolve into troglobites but many may not. Even entire subterranean communities without a troglobitic species may be severely constrained by the subterranean environment (Gunn et al. 2000). The utility of these designations is in doubt (Sket 2008), and they are not used further in this chapter.

The lack of emphasis on non-troglomorphic species may also result from inadequate resource for species identification. Colonization of, and adaptation to, subterranean habitats by surface species are continuous, ongoing processes. Therefore, at any time, the subterranean fauna must consist of a variety of species, many that have successfully adapted to the subterranean environment in different ways but also many more that are recent arrivals. Therefore, the subterranean fauna consists of many more species that are not troglomorphic or are not troglobionts, or both, than species that are troglomorphic troglobionts. Thus identification of both troglomorphic and non-troglomorphic species from any subterranean ecosystem would require a greater commitment of time by more taxonomic specialists than identification of only the troglomorphic species. In addition, troglomorphic species generally exhibit high degrees of endemism (Culver and Pipan 2009). Troglomorphic specimens from different subterranean systems are more likely to constitute new taxa than non-troglomorphic specimens and may enjoy a higher priority for identification by taxonomic specialists. Constraints in money and time are real impediments to a full description of the entire fauna in a subterranean ecosystem. For example, in a 3-year survey of the invertebrate cave fauna of West Virginia, Fong et al. (1994) documented only troglobionts, most of them troglomorphic, because it would have been too expensive and too time consuming to obtain complete taxonomic information on all the species collected.

The lack of emphasis on non-troglomorphic species is unfortunate. Although the traditional view of the pinnacle of adaptation to the subterranean environment is that of troglomorphic species, such as the Robber Baron Cave Spider, many more non-troglomorphic species are also well adapted to this environment and are integral components of subterranean ecosystems. Some of these non-troglomorphic species, such as the cave cricket in Robber Baron Cave, are keystone species that play a critical role in supporting the entire subterranean fauna, including the endangered troglomorphic spider and harvestman, and they do so by serving as biological vectors bringing energy from the surface, or allochthonous energy, into the subterranean ecosystem. Indeed, most of the troglomorphic taxa are effectively energy sinks, while many non-troglobionts, by serving as vectors of allochthonous energy, are effectively proximate energy sources of subterranean ecosystems. Therefore, management practices need to consider all of the taxa in addition to the troglomorphic species and especially their ecological roles in the subterranean ecosystem.

9.2.2   The Importance of Allochthonous Energy

The hallmark feature of the subterranean environment is constant darkness and thus the absence of primary production through photosynthesis. In most underground ecosystems, the base of the food web depends on input of allochthonous energy derived ultimately from photosynthesis on the surface. There simply is no other source of energy for the fauna in subterranean ecosystems except for systems based on chemoautotrophy (see below). As the situation at Robber Baron Cave illustrates, protecting the subterranean fauna requires management practices that maintain the ecological integrity of not only the subterranean system itself but also that of the surface terrane, which is the ultimate source of energy, as well as that of the natural paths of energy flow from the surface into the subterranean system. Management of energy flow in situations similar to that of Robber Baron Cave means ensuring sufficient energy input into the cave to support the underground trophic structure by biological vectors, such as the cave cricket, and by other means.

Management of energy flow also means preventing excessive energy input, particularly in the form of organic pollution. This problem is especially acute in karst areas experiencing heightened intensity of agricultural activity or housing and industrial development. Pollutants, both organic and inorganic, may be toxic by themselves or may alter the chemistry of the subterranean environment so as to pose a direct threat to the fauna (Pasquarell and Boyer 1993; Elliott 2000). For example, Culver et al. (1992) documented the near extirpation of one of only four known populations of an endangered troglomorphic aquatic isopod crustacean, *Lirceus usdagalun*, due to illegal dumping of sawdust into a cave entrance sinkhole in Virginia, USA. Organic pollution may also indirectly affect the cave fauna through excessive nutrient enrichment of the subterranean habitat, which then promotes invasion by surface species that may out-compete and displace resident species (Sket 1999). Of course, such point sources of organic pollution are easier to identify than the nonpoint sources, such as the slow accumulation of pesticides and fertilizers from agriculture runoff that then drain into subterranean systems.

Another form of excessive energy input, affecting mainly caves developed for commercial tourism, is from lighting used to illuminate passages and especially rock formations. Prolonged illumination promotes growth of a lampenflora, plants and algae associated with electrical lighting (Aley 2004). Development of a lampenflora destroys the aesthetic value of the cave itself at best and may enable establishment of invasive surface species and subsequent displacement of the native cave fauna at worst. In large systems where commercialized trails comprise a small percentage of the total passages, lampenflora may not be a major issue, but even then, affected passages are known to have fewer cave species compared to unaffected passages (Culver and Pipan 2009). In small systems, lampenflora may, in concert with other effects of physical alteration of the passages for and from tourism, have a large adverse effect on the cave fauna. Installation of low wattage lighting of appropriate spectra may address this issue but requires a large initial monetary investment.

Frequently, one management practice to protect a subterranean system and its fauna is gating cave entrances to minimize human activity. The assumption is that human activity inside a cave will have a negative impact on the cave fauna. However, Robber Baron Cave still harbors a diverse cave fauna in spite of a long history of high- impact human visitation. The fauna in Robber Baron Cave was in decline because of curtailment of energy flow into the cave due to urban development on the surface, not because of disturbance from human visitation inside the cave. A cave gate is effective in curbing incidences of vandalism, theft of speleothems and out- right malicious attacks on large aggregations of animals such as roosts of bats (Elliott 2000). A cave gate is also an attractive management tool because the gate is a visible, physical evidence that something has been done. It is becoming clear, however, that gating a cave by itself is not an effective tool to protect the fauna in the cave, especially the invertebrates. The design of cave gates has evolved from early ones that actually hindered to modern ones that allow for the movement of vectors of allochthonous energy, such as bats and other small mammals as well as crickets and other insects, between the surface environments and the caves (Elliott 2000). However, as the scenario at Robber Baron Cave shows, if the integrity of the surface ecosystem is compromised and its ability to generate and provide allochthonous energy to support the subterranean ecosystem is diminished, even a perfectly designed gate is ineffective in protecting the community of organisms in the cave. Thus, a thorough understanding of the connections between the surface and the subterranean environments in terms of energy flow is one crucial key to effective management and protection of the fauna.

In some subterranean systems, the trophic structure is supported by energy produced within the system from chemoautotrophy and is independent of allochthonous energy derived from photosynthesis. The best documented type of chemoautotrophy is based on the oxidation of hydrogen sulfide, such as in Moville Cave in Romania (Sarbu et al. 1996), which supports a large number of troglomorphic species. Engel (2007) detailed other such chemoautotrophic subterranean systems. The two types of energy sources are not mutually exclusive. For example, Grotta di Frasassi in Italy shows two distinct food webs, one based on allochthonous energy input in the form of bat guano and the other based on energy from chemoautotrophy (Sarbu et al. 2000). Chemoautotrophic systems are largely driven by microbial activity. The topic of management of the subterranean microbial fauna and flora in karst is discussed elsewhere in this volume.

9.2.3   Apparency of Threats

A host of human activities unrelated to the energy base of the subterranean ecosystem in karst areas also affect the underground fauna. Much of these activities causes physical disturbance of the karst terrane. Examples include limestone quarrying, flooding of cave systems as a result of water impoundment behind dams, mining of groundwater aquifers and road building, among others. These activities have severe

consequences for the subterranean fauna because they physically alter the landform at best and can completely obliterate a cave system at worst. The relative intensity and impact of these activities differ in different locations. For example, on a global scale, limestone quarrying is growing at the highest rate in Southeast Asia (Clements et al. 2006). This region is considered a biodiversity hotspot for both surface and subterranean fauna and flora, because the limestone karst in the area is relatively untouched by other human activities and the fragmented nature of the karst terrane in the region promotes endemism. Quarrying activities there have probably resulted in extirpation of numerous species before the species were discovered (Culver and Pipan 2009). Quarrying activities also threaten the cave fauna in much of Australia, especially the Cape Range (Hamilton-Smith and Eberhard 2000; Humphreys 2004), but it is of concern in only some parts of the U.S. (Dasher 2001; Jones et al. 2003). There are many additional threats to the subterranean fauna. Tercafs (2001) gave a detailed discussion of a long list of potential threats to the subterranean ecosystems and the subterranean fauna. Some of the issues raised are especially intractable. For example, Culver and Pipan (2009) reasonably suggested that global warming is a universal threat to subterranean fauna.

Effects of such human activities that pose direct physical threats to subterranean systems and the activities themselves have high apparency because they are usually overt, visible and some may even be well understood. Likewise, point sources of pollution can be identified. This is not to minimize the complex issue of managing karst resources and the subterranean fauna in face of such overt threats. Local, regional and national laws protecting karst resources, especially caves and associated fauna with threatened or endangered status, exist in many parts of the world. Application and enforcement of such laws, however, are often tempered by social and economic realities at the local scale. But clearly all these threats have high apparency, and at the emotional level, at least, people are motivated to action for protecting a subterranean system or its fauna or both when the threats are identifiable and apparent. A good example is recounted by Elliott (2000), who led a 3-month project in 1976 to relocate all 30 species of the entire fauna along with as much cave soil, rocks and woody debris as could be carried from a cave to a nearby abandoned mine because the cave was to be completely inundated from rising water behind a newly constructed dam, and the cave was one of the only two known sites at the time of the rare cave harvestman, *Banksula melones*.

In contrast, how allochthonous energy is made available and delivered to the subterranean fauna is generally not immediately obvious, and disruptions to the delivery of this vital resource to the underground are not readily apparent. As illustrated by the situation at Robber Baron Cave, an understanding of how cave crickets act as the main vector of allochthonous energy revealed the major mechanism by which urban development affected the cave fauna. In this instance, the cause of degradation was not disturbance by increased human visitation or the increased potential of pollution. When the threat has low apparency, such as when cave crickets return less and consistently less energy to Robber Baron Cave as their foraging area becomes smaller and smaller, it may be difficult to understand the issue at hand to begin with, and once it is understood, it may be difficult to garner support to address

the problem than when the threats are highly apparent. This is understandable, because in the first case, support means well-defined action, such as helping to stop quarrying activity toward a certain direction or to reroute a road being built or even to relocate an entire fauna of a cave, but in the second case, it is unclear what support means in terms of specific action for each potential supporter involved. One inherent challenge to management practices for protecting subterranean fauna is first to recognize such threats with low apparency and then to motivate public support to deal with such threats.

9.2.4 Potential Resilience of the Subterranean Fauna

Although not universal, many subterranean species have lower metabolic rates and longer life spans compared to surface counterparts (Huppop 2000), and some may also be adapted to ramp up reproduction during infrequent episodes of increased influx of energy resources (Turquin and Barthelemy 1985). Low metabolic rates and long life spans may allow such species to persist for some period even when the normal paths of energy input have been disrupted or curtailed for a duration. This may be the situation with many of the species in Robber Baron Cave. Encroachment of urban development toward the cave entrance in San Antonio leading to the reduction in energy input from cave crickets has been an ongoing process for a lengthy period, yet the fauna in the cave has persisted, and their persistence may be possible because of this metabolic adaptation. Recognition of this resilience means that recovery of the subterranean fauna is a real possibility, provided that the route of energy input is understood. The documented decline of the fauna in Robber Baron Cave has probably resulted from natural attrition of individuals over time coupled with the lack of recruitment of new individuals from reproduction due to insufficient food. However, now that the critical role of the crickets in this system is understood, increasing the energy flow into the cave by restoring the surface ecosystem to enable expansion of the foraging area of cave crickets should be a long-term management goal. Reversing urban development may even be achievable in light of the number of small dams that have been removed since the severe ecological consequences of such dams are understood and widely publicized. In the meanwhile, management practices that emphasize a gradual increase coupled with periodic jumps in input of energy into the cave system in the future may allow the fauna to recover. Such energy may be artificially augmented, e.g., by establishing protected night time feeding stations for *Ceuthophilus secretus* near the cave entrance.

9.3   Paths of Allochthonous Energy

Allochthonous energy enters subterranean systems via four main paths (Tercafs 2001; Culver and Pipan 2009). The first and most obvious is transport by water. The second is transport by active movement of organisms into caves. Energy also enters

via passive input from gravity or by wind. A less common path is by tree roots projecting into cave passages. The relative importance of these paths differs in different regions and for terrestrial and aquatic habitats.

9.3.1 Transport by Water

The most obvious path of energy from the surface to the underground is via water, as dissolution is how caves are created in limestone karst. Water enters subterranean systems via sinking streams or as percolating water infiltrating vertically through the soil. The quantity and the quality of the energy delivered via these two routes differ in significant ways.

9.3.1.1 Sinking Streams

Surface streams usually sink and become part of a karst subterranean drainage at the contacts between water impermeable rock and soluble limestone. Sinking streams vary greatly in size, from intermittent rills to permanent rivers. The volume of water carried by a sinking stream may vary seasonally by several orders of magnitude. In forested, temperate regions, sinking streams can transport underground a large amount of organic matter in the form of leaves, twigs, branches and even entire tree trunks, known as coarse particulate organic matter (CPOM). However, the energy quality of this CPOM input appears very low. Generally, the CPOM is rapidly processed by shredders, such as some crustaceans and larvae of aquatic insect, into fine particulate organic matter (FPOM) and quickly becomes unimportant in the metabolism of the cave stream organisms (Simon and Benfield 2001, 2002). Furthermore, the aquatic subterranean fauna, such as snails and amphipod and isopod crustaceans, actually depends on energy from the biofilm coating rocks and sediment in the cave stream (Simon et al. 2003). The biofilm consists of a variety of microorganisms as well as organic and inorganic particles embedded within a polysaccharide matrix (Boston 2004), and the biofilm is limited by carbon in dissolved organic matter (DOM), not FPOM (Simon et al. 2003). The importance of sinking streams as an allochthonous energy source therefore depends on the quantity of DOM they transport underground. The quantity of DOM in the surface stream is positively correlated with the duration of processing of CPOM and FPOM by biological agents and mechanical breakdown by physical disturbance of the substratum (Allen and Castillo 2007). However, this duration is also positively correlated with the size of the stream and therefore the velocity or scouring power of the water current. Therefore, a larger sinking stream will bring in more DOM to support the biofilm but will cause physical disturbance of the substratum where biofilms are located, while a smaller sinking stream will have little DOM. Thus, in temperate regions, although sinking streams are the source of a large quantity of particulate organic matter in cave streams, the quality of this organic matter is such that they do not constitute an important source of allochthonous energy for subterranean aquatic fauna.

The large quantity of particulate organic matter delivered underground by sinking streams, however, may not be inert for the subterranean ecosystem. Sinking streams frequently deposit CPOM and FPOM on banks of cave streams, and organic matter is quickly colonized by fungi and possibly bacteria. Although these deposits are spatially and temporally highly heterogeneous within a cave system, most cave organisms are adapted to rapidly seek out and utilize ephemeral resources as they become available (Culver and Pipan 2009). In fact, when searching for terrestrial cave invertebrates, speleobiologists commonly focus their attention first on any available leaves and wood debris left behind by flood water if other organic matter such as guano is absent. Whether these deposits of organic matter and their associated fungal or bacterial colonies constitute a significant allochthonous energy base for terrestrial cave organisms such as springtails, millipeds and beetles that patrol the riparian zone is yet to be quantified. Clearly, this resource is utilized by the terrestrial cave fauna. The unanswered question is whether the absence or reduction of this resource will adversely affect the diversity or the carrying capacity, or both, of the terrestrial cave fauna.

Sinking streams also inject more than particulate organic matter into subterranean habitats. It is common, especially after spring thaws and storm events, to find washed into cave streams numerous individuals of the surface aquatic fauna, such as larvae of aquatic insects, especially of mayflies, caddisflies and stoneflies and even some surface vertebrates such as amphibians and fish. Their biomass, when consumed by resident subterranean species immediately as prey or later when they die, certainly represents a spatially and temporally unpredictable energy resource of high quality directly or indirectly through increased microbial activity similar to fungal colonies on particulate organic matter left on cave stream banks. Possibly, some of the subterranean fauna are stimulated to initiate reproduction by such an influx of high-quality energy, but there is no direct evidence to support this. The relative importance of this resource for the diversity and abundance of the aquatic cave fauna has not been quantified.

9.3.1.2 Percolating Water

Precipitation reaching the ground surface and not utilized by plants can move laterally and form streams or lakes, or infiltrate vertically through the soil. Water percolating through the soil will accumulate dissolved material, and more importantly, dissolved organic carbon (DOC) resulting from decay of vegetation and metabolism of soil organisms, as well as microbes and other organic compounds adsorbed onto soil particles. In karst areas, the transition zone between the soil and the underlying limestone is a potentially vast network of minute cavities and channels, termed the epikarst, which can retain a large volume of water (Williams 2008). Epikarst water percolating further downward through fractures in the limestone can intersect cave passages, forming water drips from cave ceilings. The epikarst has a tremendous storage capacity. Thus, it is common to find water dripping from cave ceilings even if the local surface terrane has experienced a prolonged dry period. Indeed, water in

the majority of small headwater streams in a subterranean drainage basin likely originates from the epikarst rather than from sinking streams.

Drip water from the epikarst contributes DOC to cave streams (Simon et al. 2007). Although the concentration of DOC in drip water is usually low, it may be the only source of organic carbon available to support the biofilm, which in turn, is the foundation of the aquatic food web in cave streams (Simon et al. 2003). Furthermore, the large number of water drips in cave passages point to the delivery of a potentially vast quantity of DOC over time from the epikarst to cave streams. Epikarst water is potentially a highly significant source of allochthonous energy for the aquatic subterranean fauna, especially at small, upper level headwater cave streams.

Examination of drip water also reveals a diverse assemblage of organisms, including bacteria, small crustaceans, microarthropods and even archaeannelids (Pipan 2005; Pipan and Culver 2005), indicating that the epikarst is the primary habitat for many species and is likely an ecosystem in itself. Fong and Culver (1994) show that in a large subterranean drainage basin, diversity of aquatic crustacean species is highest at smaller, upper-level headwater streams and decreases towards larger, lower-level streams. They attributed the higher diversity of headwater streams in part to a higher rate of influx of epikarst species, because the upper-level headwater streams are closer to the epikarst and because there are more upper-level headwater streams than larger streams in any drainage basin. Recent biological surveys in caves with an emphasis on water of epikarst origin have yielded many new species of copepod and amphipod crustaceans (Fong et al. 2007, Holsinger JR pers. comm.). The scenario is thus one of a constant rain of epikarst water delivering not just DOC but also animals into cave streams. Knapp and Fong (1999) and Fong (2003) examined the temporal variation in the population size of an amphipod crustacean, *Stygobromus emarginatus,* in a headwater cave stream and suggest that movement of organisms between the epikarst and the uppermost reaches of some cave streams is an active, dynamic process in addition to the passive downward rain of animals trapped in ceiling drips. Whether these animals of epikarst origin constitute a significant input of allochthonous energy to cave streams in the form of biomass is unclear. Simon et al. (2007) and Culver and Pipan (2009) conclude that the energy input in terms of numbers of organisms from ceiling drips, consisting mostly of copepod crustaceans of 1 mm or less in body size, is insignificant compared to the quantity of DOC in drips. This conclusion does not take into account the possibility of active movement of potentially large numbers of organisms of large body size, up to 10 mm in body length for *S. emarginatus* in the Knapp and Fong (1999) study, between the epikarst and the cave stream via means other than drips. My experience from collecting live amphipods from cave streams is that *S. emarginatus* must be separated immediately from *Gammarus minus*, another amphipod of about the same body size whose primary habitat is the cave stream, because most specimens of *S. emarginatus* would be quickly eaten by *G. minus* if both are left in the same container. Thus, it is reasonable to assume that *S. emarginatus*, which likely originates from the epikarst, is a high-quality energy source for *G. minus* in the cave stream habitat itself. In general, whether the biomass of organisms of epikarst origin

is or is not a significant component of the allochthonous energy input in addition to DOC from the epikarst, the importance of epikarst water as a source of energy for the aquatic cave fauna cannot be overemphasized.

9.3.1.3   Humidity

Although the previous sections emphasize the role of water as a vector of energy into subterranean systems, the presence of water itself is obviously vital to the cave fauna. This is self-evident for the aquatic cave fauna. Many terrestrial cave species show a reduction in the thickness of the cuticle. The interesting question of whether this is an adaptation to the high humidity of caves or an adaptation to metabolic economy or simply a result of relaxed selection is not yet settled. In any case, a thinner cuticle clearly results in increased water permeability and thus a heightened sensitivity to desiccation (Howarth 1980). Some cave beetles in both North America and Europe have elaborated, specialized organs functioning as humidity detectors (Peck 1977; Accordi and Sbordoni 1978), ensuring that they can seek out areas of high humidity and suffer low rate of water loss. Thus, water entering subterranean systems either from sinking streams or the epikarst also serve to maintain a high humidity in cave passages, which is vital to the survival of some, if not most, of the terrestrial cave fauna. Again, it is common experience among speleobiologists that both the diversity and abundance of the terrestrial fauna are lower in drier than in moister cave passages.

9.3.2   Transport by Movement of Animals

A variety of animals actively move in and out of caves from the surface environment. Some are accidental or occasional visitors to caves, such as snakes, raccoons and wood rats, while others migrate between the cave and the surface on a daily or seasonal basis, such as the cave crickets, in Robber Baron Cave, and bats. To different extents, all these animals bring energy resources from surface habitats into caves, but, clearly, bats and crickets are major vectors. The quantity and type of resources brought into caves differ among different groups of organisms.

Guano deposited by animals in caves after foraging outside is a major mechanism of energy delivery. In Mammoth Cave, for example, sources of guano range from animals such as unpredictable raccoons to highly predictable cave crickets, and each type of guano is associated with different specialized communities adapted to differences in ease of physical processing and assimilation of the guano (Poulson 2005).

In addition to guano, another important mechanism of energy delivery into caves by cave crickets is the laying of eggs in caves. As detailed below, some beetles have become specialized cricket egg predators, relying only on cricket eggs during parts of the year.

9.3.2.1 Bats

Many bat species forage outside at night and return to caves during the day, often forming large roosts, both in the tropics and the temperate regions. Many species also form large seasonal aggregations in caves, either as maternity colonies or winter hibernation colonies. The dominant form of resource they produce inside caves is guano. Caves harboring large bat colonies can receive an impressive amount of guano. About 20 million Mexican free-tailed bats, *Tardarida brasiliensis*, deposit 5×10^4 kg of guano per year in Bracken Cave in Texas (Barbour and Davis 1969). Even smaller colonies, such as the 3,000 gray bats, *Myotis grisescens*, forming a maternity colony in Cave Springs Cave in Arkansas produce 9 kg of guano each year (Graening and Brown 2003). The importance of bat guano as a high-quality energy resource for cave invertebrates, especially in the tropics, is underscored by the existence of whole communities specializing in bat guano with complex trophic structures and many species showing different degrees of troglomorphy (Deharveng and Bedos 2000). The importance of bat guano as an energy source for the fauna in a temperate zone cave is illustrated by an inadvertent experiment in Shelta Cave in the City of Huntsville, Alabama, as described by Elliott (2000). The cave harbored a large colony of the gray bat, *M. grisescens*, as well as a rich and abundant aquatic invertebrate fauna including three species of crayfish and a shrimp along with amphipod and isopod crustaceans. Because of potential threats from encroaching urban development, the National Speleological Society bought the property around the cave entrance, and the entrance itself was gated in 1968 to protect the cave and its fauna. Unfortunately, the bats abandoned the cave within 2 years, partially because the gate was ill-designed for transit by bats and because of accelerated urban development, and did not return even after a bat-appropriate gate was installed in 1981. The subsequent demise of the aquatic cave invertebrate fauna was well documented in a series of studies (see Summary in McGregor et al. 1997). It is impossible to tease apart the specific effect of the absence of bats and the diffuse effects of increasing urban development, such as nonpoint source pollution, on the decline of the cave fauna; but the sudden cessation of a once reliable influx of a high-quality energy resource in large quantity in the form of bat guano is very likely a major contributing factor. Recently, Fenolio and Graening (2009) documented a large congregation of the aquatic isopod crustacean *Caecidotea macropropoda* in a cave in Oklahoma. They estimated 10,000–15,000 individuals forming a mat in a pool that was 3 m in diameter and less than 10 cm at the deepest point. The cave has accumulated much guano deposited by a seasonal maternity colony of the gray bat, *M. grisecens*, and the pool bottom was covered with decaying bat guano. They also cited previous work indicating this isopod was extremely abundant back in 1982 in this cave, and that tens of thousands of the cave flatworm, *Dendrocoelopsis americana*, were observed in the same cave in 1950. Clearly, the bat guano in this temperate zone cave has supported highly abundant populations of at least two aquatic troglomorphic species for a long time.

   In situations where bat guano is scattered rather than concentrated, no specialized guano community exists and the guano is certainly utilized by the usual cave

fauna. The importance of this scattered resource, similar to particulate organic matter on cave stream banks, however, has not been quantified.

Bats, of course, leave more than just guano in caves. Bodies of dead bats and some newborn bats fall onto cave floors, and underneath large bat roosts especially in the tropics, they are quickly consumed by scavengers that are part of the guano communities (Deharveng and Bedos 2000). Where bats do not form concentrated colonies and specialized guano communities are absent, it is assumed that dead bats represent a spatially and temporally unpredictable, high-quality energy resource utilized by the subterranean fauna.

9.3.2.2 Bats and White-Nose Syndrome

Since it was first noticed in early 2006 in a cave in Northern New York, a fungus has devastated winter hibernation colonies of several bat species in the Northeastern U.S. (Blehert et al. 2009) and has subsequently spread to other states. This disease is termed bat white-nose syndrome (WNS) because the white fungus appears most prominently on the noses of infected bats. The fungus is identified as *Geomyces destructans*, a new species genetically related to but is morphologically distinct from other species of the wide-spread genus *Geomyces* (Gargas et al. 2009). Although the origin of WNS is unknown, its effect is dramatic, killing up to 75% of bats in infected sites (Blehert et al. 2009). Appropriately, there are much ongoing research and management concerns targeting WNS. Management practices are focused primarily on monitoring of unaffected sites to detect the spread of WNS, and on prevention of the spread of WNS to new sites via restriction of human traffic, although there is no evidence indicating any new WNS infestation directly resulting from movement of humans (Aley 2010). Management of WNS is reasonably concentrated mainly on bats in caves. However, Aley (2010) indicates that the other members of the cave fauna must not be neglected. Because bats are important vectors bringing in allocththouous energy into caves, the drastic reduction in bat population sizes means that the invertebrate cave fauna in infected caves will probably also suffer from the effects of WNS well into the future. Management of WNS should include practices that recognize the fauna of the entire subterranean ecosystem in addition to the bats. A possible management practice to buffer the invertebrate cave fauna in infected caves may involve artificially supplying energy into these caves in the form of guano harvested from laboratory colonies of small mammalian insectivores such as shrews.

9.3.2.3 Crickets

Large aggregates of cave crickets of the family Rhaphidophoridae are commonly encountered just inside cave entrances, especially during the warmer months, in many parts of the world (Culver and Pipan 2009). They move out at night to forage on the surface under appropriate temperature and humidity conditions and may

range up to 100 m from the cave entrance, return before dawn and stay in caves during the day (Taylor et al. 2005; Lavoie et al. 2007). These crickets are omnivorous, feeding on a variety of foods and bring energy resources into subterranean systems in two main forms: guano and eggs. Poulson (1992) shows that cricket guano is the major energy base for many terrestrial cave invertebrates in Mammoth Cave, Kentucky. Cricket guano is likely the critical energy base for the invertebrate community in Robber Baron Cave. In particular, cricket eggs are extremely important resources for a number of cave beetles in the U.S. During the reproductive season, cave crickets insert their eggs with their ovipositors in holes up to 10 mm deep in sandy substrate. Several species of cave beetles, including *Rhadine subterranea* (Mitchell 1968), *Darlingtonea kentuckensis* (Marsh 1968) and *Neaphaenops tellkampfi* (Kane et al. 1975), are specialized predators equipped to dig up the cricket eggs and consume the contents. The importance of eggs of the cave cricket, *Hadenoecus subterraneus*, as an energy source for *N. tellkampfi* is illustrated by the following: Firstly, the average dry weight of a cricket egg, at 2.26 g, is about 67% of the average dry weight of an entire beetle (Studier 1996); secondly, after consuming a single cricket egg, it takes about 50 days for a beetle to return to its prefeeding weight (Griffith and Poulson 1993); lastly, cricket eggs are the only food available to the beetle during the cricket egg-laying season (Kane and Poulson 1976). Without doubt, in this situation, any reduction in egg production by *H. subterraneus* will have a detrimental effect on the abundance of *N. tellkampfi*.

The crickets leave more than just guano and eggs in caves. It is not uncommon to encounter dead crickets covered in fungi within cave passages. Certainly, these are utilized by other cave organisms, although the quantitative importance of this resource to the cave fauna is unknown. In addition, the newly hatched and very young cricket nymphs may be important prey for predators such as cave spiders and adults and larvae of other cave beetle species as well as cricket egg specialists. There is no evidence that any of the subterranean species in Robber Baron Cave specialize on cricket eggs. It is very likely, however, that newly hatched and very young cricket nymphs are important prey for the endangered harvestman and spider in the cave.

9.3.3 Passive Transport by Gravity or Wind

Some openings to subterranean systems, such as open air pits, sinkholes and cave entrances located at the base of steep slopes, can receive large amounts of leaves and other plant material or aerially dispersing arthropods by gravity and wind. Most of this fallout usually accumulates near the openings, but depending on the geometry of the opening, some of this fallout may be blown deep into the subterranean system. There has been little research to quantify or to determine the quality of this potential resource for the terrestrial subterranean fauna. The quality of the plant matter as an energy source will depend on how rapidly it is colonized by fungal and bacterial decomposers, which, for any given temperature, should be positively

correlated with the moisture content of the fallout material. In temperate regions with ample precipitation, a high rate of colonization is expected, but the high moisture content and, thus, the tendency to form clumps and the heavy weight of this material should reduce the distance it can be blown further underground. Thus, the delivery of this material deeper into the subterranean system in temperate regions will depend more on actions of other agents, such as flowing water or active movement of organisms that have initially utilized this resource near the opening. In arid regions, this relatively dry and light-weight material may be blown far underground by wind but a low rate of colonization by decomposers and thus low energy quality is expected.

Aerially dispersing arthropods may be a better source of high-quality energy fallout in arid regions. Ashmole and Ashmole (2000) estimated 40 mg in dry weight of arthropods per m^2 per day falling on a volcanic field underlain by a vast expanse of mesocaverns. They suggest that terrestrial species occupying mesocaverns, including many with troglomorphic features, actively forage for such fallout on the surface when physical conditions are favorable, such as lower temperature and thus higher relative humidity during the night than during the day.

Although some animals labeled as accidentals become trapped after having actively moved into caves, many do fall into caves due to real accidents. It is not uncommon to find at the base of vertical cave entrances emaciated but living, decomposing carcasses, and bones of small vertebrates such as frogs and snakes to large ones such as foxes or deer or even cattle. These are temporally unpredictable, high-quality energy resource in large quantity, but there is no published study examining their relative importance in the energy budget of the subterranean fauna.

9.3.3.1   Fallout and Phreatic Habitats

There is indirect evidence supporting the importance of fallout for a population of the cirolanid isopod crustacean, *Antrolana lira*. This species inhabits phreatic waters under the Shenandoah Valley in the Eastern U.S.A. (Holsinger et al. 1994) and may be captured with baited traps placed in wells or in caves with access to the water table. The population sizes are small, with ten or usually fewer individuals captured per sampling attempt at most of the 19 sites where it has been collected, including several sites where only one specimen has ever been collected in spite of repeated sampling attempts (Hutchins and Orndorff 2009; Hutchins et al. 2010). The exception is at Steger's Fissure, where the estimated population size is two to three orders of magnitude higher than at other sites (Fong in prep.). The Steger's Fissure site is also the only site where the water table is open to the surface, with two vertical, 1 m diameter openings at the base of a rock outcrop next to a steep hillside allowing leaves and other organic material to fall in. The surface of the water table is about 5 m below the opening and is usually obscured by a mat of plant material, including tree branches. This isopod seems an opportunistic predator preying on any organism that falls in rather than utilizing the copious amount of plant fallout material. Collins and Holsinger (1981) found remains of insect cuticles in the gut contents of several

specimens. Raw shrimp is the usual bait used to trap *A. lira*, and my experience at this site is that two shrimp abdomens, each about 8 cm in length and 2 cm in diameter, may attract about 200–300 specimens, and the bait pieces are usually completely consumed after 2 h. There is no other prey for *A. lira* as it coexists in this system with only one other crustacean, the amphipod *Stygobromus stegerorum*, which is only 3 mm in length compared to up to 15 mm for *A. lira*. The large population size of *A. lira* at this site, and only at this site, is probably a result of occasional fallout of high-quality energy resource in the form of surface organisms, effectively raising the carrying capacity at this site by orders of magnitude compared to other sites where fallout is absent. Because phreatic waters are extremely nutrient-poor (Culver and Pipan 2009), fallout, when available, may be a critical source of energy for organisms inhabiting this habitat.

9.3.4 Tree Roots

Tree roots commonly penetrate into shallow caves, usually in the form of long strands of aerial roots hanging from cave ceilings. Condensation forming on the roots from the highly humid cave air is a source of water for the trees, and this is especially important in arid regions. In some situations, such as lava tube caves, tree roots are the only stable source of high-quality energy for cave organisms (Howarth 1983). A variety of cave invertebrate specialists feeding on these aerial roots, including planthoppers, terrestrial isopods and even a moth have been described from lava tube caves in Hawaii, the Cape Verde Islands and the Canary Islands (Howarth 1972; Oromi and Martin 1992; Hoch et al. 1999). These specialists are in turn preyed upon by other cave organisms. Thus tree roots form the critical energy base supporting a whole ecosystem of diverse organisms in many lava tube caves (Stone et al. 2005).

In some shallow caves in parts of Australia, with low air humidity and little soil moisture, cave streams are an important source of water for some trees. Aquatic roots of these trees penetrate into the cave stream, forming dense, compact mats of fine rootlets. A diverse assemblage of organisms depend on the energy supplied by these root mats, including amphipods, isopods, leeches, and even fish (Jasinska and Knott 2000). Root mat communities generally support more species with higher abundances than communities based on aerial roots (Jasinska et al. 1996).

9.4 Conclusions

It is unsurprising that, except for those based on chemoautotrophy, subterranean ecosystems are ultimately dependent on the surface ecosystem for energy. That they are intimately connected to surface ecosystems in myriad ways is less obvious. Effective management of the subterranean fauna thus requires holistic approaches

that emphasize these continuities between the surface and the subsurface. Maintenance and protection of the physical integrity of the subterranean environment is obviously an important management practice, yet this must go hand in hand with the same for the surface environment and the paths that connect them.

The extent of the surface environment that must be comanaged with the subterranean environment will depend on the nature of the regional setting. In situations where sinking streams provide the main input of organic material into the subsurface, the scale of focus must be at the level of the drainage basin. It is uncommon, however, that an entire surface drainage basin in a karst area is protected and extremely rare that one is protected as part of a plan to manage the associated subsurface ecosystem. Curiously, as pointed out above, maintaining the integrity of a surface drainage basin may be less important for the aquatic subterranean fauna but more so for the terrestrial subterranean fauna that patrol the riparian zone for organic matter carried in by sinking streams.

In situations where the main input into the subterranean ecosystem is via vertical movement of water, the focus of protection must be at the scale of the recharge area of the epikarst. The epikarst is beginning to be recognized as a subterranean ecosystem in itself with a community of endogenous species. It is also documented to be the major source of dissolved organic carbon needed to support the biofilm which is the base of the food web for the aquatic subterranean fauna, especially in small, upper-level cave streams. The physical extent of the recharge area of an epikarst zone is difficult to delineate; however, at the very least, one or more epikarst zones must map onto the subterranean drainage basin as indicated by surveyed cave passages underneath. Fortunately, extensive archives of such information exist and should be available to resource managers.

In arid to semi-arid regions, animals, such as bats and crickets as discussed above, are the major vectors of energy to the underground. The importance of bats is well recognized, especially for tropical and semiarid subterranean ecosystems. There is evidence indicating bat guano may also be an important energy source in some temperate zone caves. The importance of crickets is beginning to be documented. More studies similar to that of Taylor et al. (2005) are needed to understand the foraging areas of crickets and fully appreciate their role in supporting subterranean ecosystems. Clearly, many organisms may serve similar roles in different settings, and the physical extent of the connected surface environment will differ. The one constant is the integrity of the entrance to the subterranean systems, such as cave entrances. Cave entrances are also potential points of conflict among different management goals, such as ones focused on protecting archeological, geological, historical or other resources by keeping humans out with a gate ill designed for transit by energy vectors.

Of course, the mechanisms of energy transfer, as discussed, for any one setting are not exclusive to each. All the different paths of energy transfer linking the surface and the subsurface likely occur in any one setting but differ in relative importance. Because some of these paths often have low apparency, recognizing the important links that may be impaired for a given situation is critical to the creation of management plans to protect subterranean fauna at risk. Repairing any such

impacted energy links may be extremely effective management practices in light of the metabolic adaptation of the subterranean fauna. Their low metabolic rates may allow some of them to persist for a period of interrupted energy input and slowly recover upon restoration of the normal energy flow. Once a subterranean system has been quarried away or drowned behind an impoundment, it is gone and unrecoverable. However, the potential resilience of some subterranean fauna to restricted energy input means that many of the impacted communities have a likelihood of recovery. Karst resource managers just need to recognize the situation and make it apparent.

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