Encyclopedia of Caves

Third Edition

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Chapter 79

Mammals and birds—vertebrate visitors

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Diversity of species

Although there are no troglobiotic mammals or birds, many species are associated with caves. Comprehensive lists of mammals and birds from caves are generally lacking, but accounts that exist indicate visitation by a diversity of mammal and bird species. For example, a review of vertebrates in caves in the Sonoran and Chihuahuan Deserts of North America identified 67 mammal species that visited caves on one or more occasion (Strong, 2010). Bats composed around one-third of the mammal species observed, and rodents (mice, rats, gophers, squirrels) composed around one-third as well. Larger mammals such as black bears (*Ursus americanus*) and mountain lions (*Puma concolor*) were also observed. In addition, 20 species of birds were reported, including multiple species of vultures, owls, and swallows. Observations of vertebrates in caves were dominated by a handful of species—of the mammals, several bat species were regularly observed, as were porcupines (*Erethizon dorsatum*) and ringtails (*Bassariscus astutus*). Among the birds observed, great horned owls (*Bubo virginianus*) and cave swallows (*Petrochelidon fulva*) were most common.

The frequency with which a species is observed in caves loosely reflects the degree of cave association for that particular species. Many mammal and bird species are *trogloxenes*, or sporadic visitors to caves, who may use the cave temporarily for shelter or foraging. Species that inhabit caves for all or some part of their life cycles but who also spend time on the surface are *subtroglophiles* (Sket, 2008). Subtroglophiles known from the deserts of North America include woodrats (*Neotoma* sp.), porcupines, and cave swallows that have dens or nests in caves, as well as various bat species that roost in caves all or part of the year, including for hibernation.

Mammals and birds associated with caves generally lack obvious morphological, life history or behavioral adaptations that facilitate life underground. Cave-dwelling bats are an exception, as their ability to echolocate enables them to navigate in the dark zone of caves. Similarly, the two lineages of birds most closely associated with caves—the oilbird (*Steatornis caripensis*) and several species of cave swiftlets—echolocate, and are in fact the only bird species known to do so. Oilbirds range through northern South America to Trinidad. They are nocturnal fruit eaters who nest in caves, with colonies reported to contain as many as 20,000 individuals. They have eyes adapted for visual sensitivity and large olfactory organs which likely facilitate feeding at night. Oilbirds use echolocation to navigate within caves rather than when feeding (Brinkløv et al., 2013). Cave swiftlets are distributed across the Indo-Pacific region, and at least 16 species are known to echolocate. They are diurnal foragers who hunt insects on the wing. Cave swiftlet nests are constructed from the bird's own saliva and glued to cave walls. These nests are collected for "bird's nest soup," a billion-dollar industry. The demand for swiftlet nests has led to the extirpation of some cave populations (Sankaran, 2001), as well as the practice of rearing swiftlets in man-made structures (Thorburn, 2015).

Use of caves

Mammals and birds visit and occupy caves for a variety of reasons. These associations may be occasional or regular, and they may vary seasonally, as for species that hibernate in caves. In addition, the strength of these associations may vary across the range of an individual species, depending on the availability of cave habitats, variation in climate, and other factors.

Many endotherms visit caves occasionally, where they may use caves as temporary roosts or refuges by day or night. Such visits are typically limited to the entrance or twilight zone of caves, and may provide relief from extreme environmental conditions. In deserts, caves may provide relief from extreme aridity and access to water sources (Strong, 2010). Caves may also provide relief from extreme daytime temperatures (in hot climates) or nighttime temperatures (in cold climates or at high elevation). In addition, caves may serve as refuges from predators.

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Many mammals forage in caves. Numerous species of mice are found in caves around the world where they may feed on crickets and other invertebrates. In North America, raccoons (*Procyon lotor*) and ringtails commonly forage in caves where they feed on mice, bats, crickets, and crayfish. Raccoon tracks and scat are commonly found in the dark zone of caves.

Closer associations with cave habitats are observed in species that use caves for nesting or dens. Many birds that nest in rocky crevices, cliffs, or under overhangs will nest in cave entrances when they are available. For example, the Eastern Phoebe (*Sayornis phoebe*) commonly nests in cave entrances in North America, and also nests in similar non-cave locations. Similarly, Allegheny woodrats (*Neotoma magister*) form dens in rocky crevices in boulder fields and talus slopes; when available they commonly nest on ledges in caves. Many bat species roost in caves, and some bat species form maternity colonies in caves. Depending on the species, maternity colonies range in size from a handful of bats to millions, as in the case of Mexican free-tailed bats (*Tadarida brasiliensis*) in Bracken Cave, Texas. Nesting in caves may provide relief from extreme environmental conditions. For example, Andean hillstar hummingbirds (*Oreotrochilus estella*) nest in caves at high elevations (~4000 m) in the Andes of Peru. At night the cave is not as cold as the surface, reducing the energetic cost of regulating body temperature (Pearson, 1953).

Many bat species, and other mammals such as black bears, hibernate in caves during the winter in temperate, or colder, regions (Tøien et al., 2011). Hibernation involves lowering body temperature, slowing respiration and heart rate, and decreasing metabolic activity. This extended period of torpor conserves energy reserves during the winter months when food is limited. Hibernating individuals undergo periodic arousals, where the body temperature returns to normal.

Cave ecology

As birds and mammals move between surface and cave habitats they transport resources from the surface to caves. These resources are typically in the form of guano, but can also be dead bodies (from individuals that die in the cave), nesting materials, or food. In resource-poor caves these resources can compose a significant portion of the carbon moving into the cave. By moving to the surface to feed and then returning to caves, cave crickets move resources into caves in a similar manner. The importance of this resource transfer to cave communities is evident in the attraction of troglobionts to guano, and in the effective use of food baits to attract cave invertebrates.

Caves with large populations of birds or bats can see significant accumulations of guano. It is estimated that Mexican free-tailed bats deposit 50,000 kg of guano per year into Bracken Cave, Texas (Iskali and Zhang, 2015). Caves with significant guano deposits often exhibit communities of guano-associated organisms that are distinct from communities found in other caves in the region that lack such guano deposits. It has been suggested that the characteristics of the guano itself (in terms of quantity, type, and seasonality of deposit) are more important than the cave environment in determining these guano-specific communities, as similar guano-specific communities can be observed in other guano-rich, non-cave environments (Ferreira et al., 2007). The volume of guano deposited, as well as the seasonality of deposition and the spatial distribution of guano throughout the cave, will vary depending on the mammal or bird involved.

The resources transferred into caves by mammals or birds are not limited to guano. Some mammals actively transport plant materials into caves—woodrats (*Neotoma* spp.), for example, build nests from plant materials, and also assemble middens of sticks, green vegetation, and fungi. Owls that roost in caves regurgitate undigestible material as owl pellets, and oilbirds regurgitate seeds.

Most organisms associated with caves will not move far in their lifetime, leading to caves being described as "islands" for their resident populations. Mammals, particularly bats, and birds that frequent caves can move from one such island to another. As they move between caves across tens or hundreds of kilometers, mammals and birds can serve as vectors for parasites and microorganisms such as viruses, bacteria, and fungi. The importance of such transfers has become evident as *Pseudogymnoascus destructans*, the fungus that causes White-Nose Syndrome, spread across North America over the past dozen years. Humans can similarly serve as vectors for microorganisms between caves.

Human impacts and conservation

Humans have visited caves for millennia, as evidenced by cave art and the remains of early humans and other hominins found in caves and rock shelters around the world. More recently, human alteration of cave and surface environments has led to declines in many cave-associated mammals and birds. Changes in land cover around caves, disturbance of cave populations (particularly of bat maternity colonies and hibernacula), overexploitation of cave resources (such as cave swiftlet nests), and emerging infectious diseases (such as White-Nose Syndrome) are all impacting cave species. Declines in cave-associated mammals or birds can be expected to impact cave ecology due to associated declines in resource transfers from surface to cave.

We generally lack baseline data about population sizes and the distribution of cave-associated species, which hinders any assessment of long-term population trends. For even the best studied species, such as the Gray bat (*Myotis grisescens*) and Indiana bat (*Myotis sodalis*) of North America, data about population sizes extend back only a few decades, leaving us to speculate about population sizes centuries, or millennia, ago. This lack of information leaves many fascinating questions about prehistoric patterns—How large were bat populations in the Americas prior to human arrival? How did cave bears (*Ursus spelaeus*) or other now-extinct Pleistocene megafauna impact cave ecology? —largely out of reach.

With cave-associated species often spread widely across karst environments, successful conservation efforts have focused on key population centers. Gray bats are a notable example. As more than 90% of all Gray bats hibernate in one of a dozen caves, increased protection of those hibernacula, as well as maternity colonies, contributed to a population recovery over several decades. Similar efforts contributed to the stabilization of declining populations of the Indiana bat. For species that are more widely distributed across the landscape, focusing on such key population centers is not possible. In the Allegheny woodrat, a major population decline across the northern half of its range in the Eastern United States appears to be related to deforestation, human disturbance, and changing forest composition. Such regional-scale effects are difficult to manage or mitigate (Ford et al., 2006).

An emerging conservation issue involves bats and human health. In recent years it has become clear that bats are reservoirs for a tremendous diversity of viruses. Factors likely contributing to this are bat species diversity (more than 1000 species), large population sizes and roosting habits, long life spans, and their ability to fly (connecting geographically distinct populations) (Calisher et al., 2006). Bats have long been recognized as a reservoir for the rabies virus, although the transfer of rabies from bats to humans is exceedingly rare. More recently, bats have been recognized as hosts for other viruses that have infected humans, including the Hendra and Nipah viruses. Molecular evidence also indicates bats host viruses similar or identical to those causing the emerging infectious diseases SARS and MERS (Memish et al., 2013; Hu et al., 2017). Whether bats have a central or peripheral role in these diseases remains to be determined (Moratelli and Calisher, 2015). To minimize the chance of viral spillover between species, epidemiologists urge minimizing contact between wild populations and domestic animals and humans. In addition, the surveillance of viruses in bat populations may identify particular viruses and geographic regions of concern for emerging infectious diseases.

Open questions and new tools

An understudied collection of questions regarding mammals and birds that visit or reside in caves can be grouped under the framework of "movement ecology" (Nathan et al., 2008). Open questions for nearly all of these species involve aspects of the movement of individuals—when and why do they visit caves, as well as how organisms move and navigate between caves and within cave environments. Organismal movements between and within caves may vary by time of day (as for nocturnal or diurnal species), by season (as for species that hibernate in caves, or for those that use caves for maternity colonies), or across the range of a single species. These daily, seasonal, and regional variations in the movement of organisms into and out of caves undoubtedly affect cave ecology.

Fortunately, there is a growing capacity to collect data about the movement and activity of species associated with caves. One promising tool is camera trapping, as cameras can be set up and left in caves or cave entrances for extended periods of time to monitor activity with minimal disturbance to the cave environment. Camera traps have been used to monitor cave entrances, where they can collect information about the diversity and activity of species visiting caves (e.g., Baker, 2015), and can be used in deeper cave environments as well (Fig. 1). Challenges of using camera traps in caves include potential theft of cameras, securing a camera to prevent it being overturned by animals, and situating the camera to capture an informative field of view.

FIG. 1 Image acquired by camera trap in a cave in Tennessee, USA, showing an encounter between a raccoon (*Procyon lotor*) and an Allegheny woodrat (*Neotoma magister*).

Smaller and more sophisticated GPS loggers are a second tool with potential to reveal much about the movement of animals into and out of caves. In one example, a recent study tagged oilbirds with loggers as they left Humboldt Cave in northeastern Venezuela (Holland et al., 2009). The loggers recorded each bird's location across the next several days. This information was downloaded from the logger when the bird returned to the cave. Oilbirds were found to forage as far as 70 km from the cave, returning to the cave around every third day after spending the intervening nights roosting in trees in the rainforest. This information has implications for the conservation of oilbirds, their role as seed dispersers in tropical forests, and their impact on cave ecology. Further advances in such technology should facilitate studies of other regular or occasional cave residents, providing similarly important insights.

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