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Guanophilic invertebrate ecology and conservation in caves

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Abstract

Guano in caves is deposited by bats, birds, orthopterans (crickets and grasshoppers), and small mammals, with each type of guano sustaining a unique ecosystem. The most widespread and common guano is that produced by bats and these deposits are generally the largest in volume. Guano deposits are extremely variable, unlike other cave habitats, and consist of numerous micro-habitats differentiated by fluctuating temperature, moisture, and pH. Fresh guano is basic, commonly with a pH of 8.5-9.0 that rapidly becomes acidic (5.0-5.5) with age and depth. Varying water content of guano, due to desiccation with increasing age, also results in a noticeable mosaic of micro-habitats. Both pH and water content control the diversity and density of fungi and bacteria, the trophic basis for many guano ecosystems and essential for breaking down many of the otherwise indigestible faecal products. Arthropod community composition is strongly seasonal, with distinctly different fresh and old guano assemblages. Guano associated communities commonly consist of insects (beetles, flies, cockroaches, springtails, moths and wasps), arachnids (spiders, mites, pseudo-scorpions, whip scorpions and harvestmen), crustaceans (isopods), and nematodes. Species richness is significantly higher at the tops of guano piles than at bases. Increasing species richness positively correlates with increasing pH at bases of piles. Substantial removal of guano, either fresh or desiccated, dramatically decreases or potentially destroys guano associated communities primarily by lack of food but also by disturbance. Compaction of guano deposits, through human visitation, also destroys essential micro-habitats in the upper layers of deposits making them unusable to virtually all organisms. Pollution of groundwater that contacts guano deposits can also adversely affect guano communities by reducing, or completely destroying, natural micro-organism populations. Guano associated communities rely on the adequate protection of guano producing animals, the caves they inhabit to ensure the continual, or seasonal, deposition of fresh guano. These are essential criteria for the conservation of guano communities.

Introduction

The protection of guano communities is important as they contain a very different fauna to other cave communities. These specialised communities provide a snapshot of geologically recent species dispersal, combined with unique opportunities for ecological study of communities in a highly controlled environment. The faunas they contain are fascinating examples of cave life including a wide variety of insects and arachnids (Figs 1-3). Australia alone contains 240 guano associated cave species inhabiting over 60 karst areas and large areas remain to be sampled or recorded making them a significant proportion of our cave fauna (Moulds 2004). The extent of guano faunas remains largely unrecognised in most countries whose caves contain guano deposits as these communities are often overlooked when assessing subterranean biodiversity.

Figure 1. Pseudoscorpions are commonly found in guano deposits in Australian caves hunting small invertebrates. The grasp their prey in their large claws (pedipalps) and poison them using small glands in the end before consuming prey using their jaws (chelicerae) located centrally on the head.

Figure 2. This unusual looking insect is actually a fly from the family Nycteribiidae. This family specialises in being ectoparasites of bats and other mammals. They are commonly found on guano piles in bat caves, having dropped from their host after a blood meal.

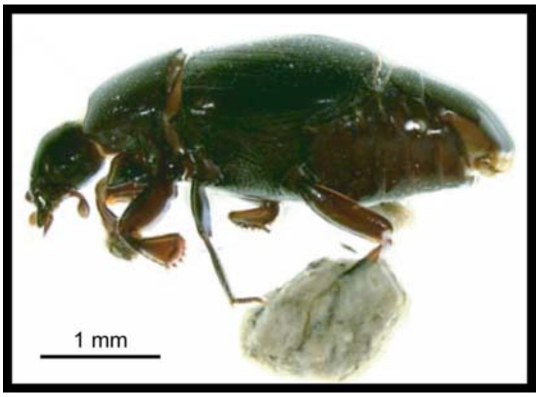

Figure 3. Histerid beetles are predatory beetles found in many guano caves in Australia. They prey upon small mites at the top of guano piles and reach their population peak during summer months.

Guano associated invertebrates are classified according to their degree of guano dependence. This guano dependence is an extra classification on top of the degree of cave dependence (i.e. troglobite, troglophile, etc). Although the extent of guano dependence is often poorly known, microhabitat preferences and associations provide significant information on the ecological and life histories of many taxa. Some subterranean species are known to be associated with epigean (surface) guano deposits and can be classified as guano dependent when found in caves. There are three classes of guano dependence as defined by Gnaspini and Trajano (2000); guanobites, guanophiles and guanoxenes.

Guanobites are animals that require the presence of guano for survival. They will only feed on guano and will not use other food sources within caves. Although guanobitic species are occasionally found on other substrates in caves as they move between discontinuous guano deposits, they do not feed or reproduce on these other substrates.

Guanophiles use guano resources opportunistically and are able to complete their entire life cycle using the guano substrate. Guanophiles will however utilise other cave food resources when available and do not have to rely upon guano to feed or reproduce.

Guanoxenes will exploit a guano resource for feeding or reproduction but require other substrates within a cave to complete their life cycle. Guanoxenes can be either troglobites, troglophiles or trogloxenes.

Sources and diversity of cave guano deposits

Cave guano deposits from specific sources can each possess a unique assemblage of species (Horst 1972; Poulson 1972). Throughout the world's biogeographic provinces different species are responsible for being the most important guano producers. The most widespread and common guano is that produced by bats and these deposits are generally the largest in volume. The spatial and temporal deposition of bat guano differs between tropical to temperate caves. Cave-dwelling bats in temperate regions show an annual cycle of occupancy over summer months when pups are born, before colonies disperse to cooler, wintering caves where they enter torpor. This annual cycle results in large amounts of guano deposited over summer months and then a cessation of guano input for approximately seven months. In contrast, tropical caves generally show constant bat occupancy and less congregation of individuals due to warmer ambient temperatures. Many bat populations in tropical latitudes are commonly nomadic, resulting in roaming colonies varying their location in an irregular and non-seasonal fashion (Gnaspini and Trajano 2000). This results in non-continuous guano deposition. The diet of bats (either haematophagous, insectivorous, frugivorous, or nectarivorous) also influences the composition of guano piles and hence the associated guanophilic communities (Gnaspini 1992; Ferreira and Martins 1998; Ferreira and Martins 1999).

Birds are common guano producers in the northern parts of South America, the Caribbean and tropical caves of south-east Asia. Cave-dwelling birds nest in the dark zone, providing an important energy resource for many cavernicolous animals. Swiftlets (Aerodramus spp) nest in the entrance and dark zones of tropical caves in south-east Asia, northern Australia and the Pacific and are insectivorous (Medway 1962; Koon and Cranbrook 2002). These birds also support a range of guanophilic species in the caves of Christmas Island (Humphreys and Eberhard 2001). Richards (1971) reported that droppings from several species of birds nesting in the entrance zone of Nullarbor Plain caves support a wide variety of cavernicolous animals.

Rhaphidophorid crickets are often important producers of guano in temperate caves such as those of the Nullarbor Plain, Australia (Richards 1971) and Mammoth Cave, Kentucky (Poulson 1992). The sometimes large populations of these crickets can accumulate sizeable guano deposits in caves. Cricket guano has a low calorific value as the crickets eat predominately decomposing organic material and have a high assimilation rate (Studier et al. 1986). On the Nullarbor Plain these deposits are important as few other food resources exist because the low mean rainfall limits organic flood debris and bat populations are generally small. Rhaphidophorid guano is also utilised in Mammoth Cave, Kentucky, where it is widely dispersed through the cave system (Howarth 1983). The large and ubiquitous rhaphidophorids within entrance zones of Mammoth Cave provides the largest energy input supporting the majority of the terrestrial animals found in the system (Poulson 1992).

Small mammals such as cave rats (Neotoma spp) are often significant guano producers in temperate zones of North America. Cave rats navigate using urine trails (Howarth 1983) and commonly deposit a few to tens of faecal pellets at once, depending on the season, approximately 0.1g in size (Poulson 1992). These high energy faecal deposits are exploited by specialised consumers and predatory species before being utilised by generalist consumers.

Guano microhabitats

Guano deposits form a mosaic of different microhabitats, on scales ranging from a few centimetres to tens of metres (Figure 4). Guano varies spatially and with depth in its moisture content, pH, degree of compaction and temperature. All these variables combine to create different micro-organism sub-communities, that subsequently affect the arthropod assemblage at each microhabitat.

Figure 4. Guano pile from the maternity chamber of Bat Cave, Naracoorte showing the numerous microhabitats occurring in a single guano pile as well as fungi growing on some areas. The pile is 1m wide at the base.

Moisture content and pH are closely linked as they are controlled primarily by the distribution of fresh guano, characterised by moist basic conditions. The tops of guano piles, that are subject to active deposition by bats roosting above are generally extremely moist with water content up to 90% by weight (Moulds 2003). These active guano piles are also extremely basic, due to the high ammonium content of fresh guano, and often reach levels of pH 9.5 or above. This contrasts with areas of older guano found away from tops of active piles which are dry (moisture content 10-15%) and acidic (pH 4.0-5.0) (Moulds 2003).

The degree of compaction varies throughout large guano deposits, with areas of high deposition being more compact primarily due to increased moisture content weighing down guano pellets. Away from concentrated depositional areas guano deposits are more aerated allowing different micro-organisms to live.

The temperature of guano piles increases with depth due to decomposition and Harris (1970) reports increases of 15ºC and 19ºC at 5 and 15 cm below the surface respectively.

The relative size and moisture content of faecal pellets is important in determining the succession of fungi that is able to grow. Low humidity results in rapid desiccation of fresh guano, severely reducing fungal growth as many of the opportunistic phycomycetes found on fresh guano are susceptible to drying out (Poulson 1992; Poulson and Lavoie 2000). The substrate that faeces are deposited on is also important, as the amount of leaching is determined by its porosity. Highly porous areas such as sand banks remove nutrients allowing fungi to dominate deposits, while on non-porous surfaces nutrients will concentrate at the interface in low oxygen conditions encouraging bacteria, nematodes and specialist mites (Poulson and Lavoie 2000).

The ecology of guanophilic invertebrate communities

Guano deposits contain a very different faunal community compared with other cave environments due to the almost unlimited supply of available energy (Poulson 2005). Guano associated communities commonly consist of insects (beetles, flies, cockroaches, springtails, moths and wasps), arachnids (spiders, mites, pseudoscorpions, whip scorpions and harvestmen), crustaceans (isopods), and nematodes. Very few consumers within guano communities eat guano directly as it is composed predominately of chitin (insect exoskeletons) and bat hair in the case of the cave-dwelling insectivorous bat populations found in Australia. Instead, many invertebrates eat the succession of bacteria, fungi and yeasts that grow on the guano and help to break it down into useable components (Martin 1977). The vast majority of guanobitic and guanophilic invertebrates are mycetophagous (fungus eating). The diversity of micro-organisms found on guano is immense but unfortunately poorly studied. Common taxa found in south-eastern Australia feeding on fungi are anobiid beetles, numerous fly larvae and guano mites (Moulds 2004). Arthropods that prey upon these consumers include spiders, pseudo-scorpions, beetles and opiliones. Specialised parasites and parasitoids are also active in many guano ecosystems. Braconid wasps (Hymenoptera) are found in many Australian guano caves and parasitise moth larvae (Monopis spp.). The larvae of the minute guanobitic beetle Derolathrus sp. are parasitised by small myrmarid wasps. Parasitic relationships in guano ecosystems are generally poorly understood and further research will undoubtedly reveal many more examples.

Species richness (the number of different species) is significantly higher at tops of guano piles than at bases and shows a strong correlation with increasing moisture content of guano. At the tops of piles there is also generally an increase in food availability as micro-organisms are more diverse and abundant. The bases of guano piles show a trend of increasing species richness with increasing pH. Generally the number of different species is reduced when guano is dry and acidic. The species most commonly found in these microhabitats are specialised mycetophages (fungus eaters), and despite the lower diversity, abundances of such species can be very large.

Threats to cavernicolous guano associated invertebrate communities

Guano associated invertebrate communities rely on the adequate protection of guano producing animals and the caves they inhabit, ensuring the continual or seasonal presence of fresh guano. Removal of guano for use as a nitrogen rich fertiliser can also dramatically impact on invertebrate populations as habitat is destroyed, and microhabitats altered, impacting on the bacteria and fungi that form the base of guano food webs. The compaction of guano deposits reduces the surface area and aeration of guano, essential for the survival of quiescent species and larvae residing below the surface of guano. Compaction can make guano unusable to bacteria and fungi. All these criteria are essential to the conservation of guano communities.

Protection of bat colonies

The protection of bat breeding and over-wintering sites is perhaps the most important and obvious step in the protection of guano associated arthropod communities. Breeding and over-wintering sites provide the largest, most continuous and predictable input of guano that is essential to the establishment of diverse and permanent guano communities. Numerous published articles are available concerning the protection of cave-dwelling bats and their habitat and I shall only deal briefly with this subject. A recent review of bat friendly gates has been published by Elliot (2005). The restriction of human visitation to known bat maternity sites during birthing periods is vital to minimise impact. Disturbance of pups in the weeks after birthing can result in increased mortality from falling and consequently minimal disturbance is crucial in maintaining bat population sizes (Murray and Kunz 2005).

Removal of guano

Fresh guano contains the highest species richness of all guano in temperate caves (Moulds unpublished data) and its removal stops the succession of bacteria and fungi crucial to the lowest trophic levels of the food web. Substantial removal of guano, either fresh or desiccated, dramatically decreases or destroys guano associated communities, primarily by reducing available food but also via excessive disturbance. Limited removal of guano, if conducted without disturbance to bat colonies, may not prove detrimental to guano invertebrate communities but should be avoided or discouraged whenever possible as critical levels of removal can be reached without warning.

Destruction of microhabitat

Compaction of guano deposits through human visitation destroys essential micro-habitats in the upper layers of deposits making them unusable to virtually all organisms. Compaction of guano deposits results in dramatically reduced surface area slowing or halting breakdown of chitin and other major guano constituents by bacteria and fungi. This is catastrophic to guano invertebrate communities as these organisms form the base of the food web making nutrients available to mycetophages and their predators.

Compaction is the largest factor in the destruction of all sedimentary and organic cave floor microhabitats. This form of degradation is directly associated with the amount of human traffic through a cave. Constant disturbance removes habitat and therefore causes the loss of taxa from sections or sometimes completely from caves. Compaction is most commonly seen in tourist caves where relatively large numbers of people access the same areas. A case study in Alexandra Cave at Naracoorte showed some taxa are notably absent when compared with a similar habitat found in non tourist sections of the same cave (Moulds unpublished data). This is also seen in nearby Blanche Cave where the only cavernicolous fauna is found in small, inaccessible areas protected from compaction. There is a marked difference between the abundance of fauna in low traffic caves, even those used for ‘adventure caving’, compared with most tourist caves at Naracoorte primarily due to compaction of habitat.

Other threats

Pollution of groundwater that contacts guano deposits can also adversely affect guano communities by reducing, or completely destroying, natural micro-organism populations. Encouraging suitable epigean landuse to allow natural hydrology processes is essential in maintaining species richness as this is directly linked to the moisture content of substrates.

Maintaining natural cave airflow is important to all cave-dwelling communities as desiccation of subterranean habitats is potentially destructive to all hypogean communities. The premature desiccation of guano reduces the amount of micro-organism succession that can take place as described above and therefore limits the arthropod communities that can utilise the resource. The majority of cavernicolous and guanobitic taxa are hydrophilic (water-loving) and require a moist habitat to survive so abnormal flows of dry air can rapidly kill large populations of cave invertebrates. Guano communities in arid habitats contain less water- dependant species and are generally far less abundant and transient in their distribution (Moulds 2005).

Management of guanophilic invertebrate communities

Management within parks and reserves

The conservation of guano associated cave communities within managed parks and reserves is easily achieved in most cases due to the highly specific nature of the habitat concerned. Bat sites are generally easily identified and access is commonly already restricted. In such cases track marking should be maintained where any regular access is required to minimise compaction and disturbance of guano microhabitats. This is especially important for irregular roost sites located in tourist caves where small but important guano deposits can support invertebrate communities.

Due to the unpleasant smell and health issues (Histoplasmosis) associated with guano deposits the general public are not inclined, nor should be encouraged, to enter cave areas regularly occupied by large bat colonies. Fortunately, this lack of popularity greatly assists the survival of guano invertebrate communities. Hydrology and airflow regimes should be maintained as close as possible to normal to avoid excessive or abnormal drying of guano deposits.

Management outside conservation areas

In Australia caves on private land or freely accessible public land that contain bat colonies are most commonly wintering sites. These sites often engender little interest by owners. Appropriate education by local caving groups or nearby cave managers is the best way to ensure these sites are protected and undisturbed.

In areas where caves are situated away from actively managed sites or on freely accessible land, discouraging visits by casual tourists should be a primary concern for conservation of bat sites and hence guano deposits and their faunas. Interpretive signs at entrances explaining the needs of bats (and caves) are an effective way to keep most casual visitors away. This can reduce traffic significantly as most visitors are simply curious rather than vandals.

Conclusions

Guano in caves is an important energy resource for a wide variety of organisms and is deposited by many animals. The management and conservation of guano associated invertebrate communities is not complex or difficult in most cases. The protection of bats which ultimately support these unique ecosystems is essential but also the different guano microhabitats. Removal or compaction of guano can result in a loss of vital micro-organisms that are the basis of most guano food webs.

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