Memoirs of the Museum of Victoria 56(2):591–596 (1997) 28 February 1997
https://doi.org/10.24199/j.mmv.1997.56.55

CONSERVATION OF CAVE FAUNA: MORE THAN JUST BATS

DAVID P. SLANEY AND PHILIP WEINSTEIN

Department of Zoology, James Cook University, Townsville, Qld 4811, Australia

Abstract

Slaney, D.P. and Weinstein, P., 1997. Conservation of cave fauna: more than just bats. *Memoirs of the Museum of Victoria* 56(2): 591–596.

The expansion of biospeleology as a science and caving as a recreational activity have led to a corresponding increase in pressure on caves and their ecosystems. The threats include direct human disturbance from visitation, and indirect modifications to cave habitats and the surrounding environment. Despite the high profile of conservation issues such as the threat to populations of ghost bats, little work has been carried out in Australia to assess the impact of humans on cave ecology. The aim of this study was to briefly review the effects of disturbance on populations of cave invertebrates, and to investigate the impact that sampling may have upon them.

We recorded the weekly total of individuals of each macroinvertebrate species collected over one month of continuous trapping with a variety of methods in Rope Ladder Cave, Fanning River Caves, North Queensland. The results indicated that numbers of pseudoscorpions, cockroaches, rhizophagid beetles, and pselaphid beetles declined significantly over the sampling period. Sampling of cave invertebrates for scientific purposes may therefore have an impact on the population dynamics of cave species, and may consequently affect the ecology of the cave itself. We recommend that the general ecology of organisms in a cave be investigated before any intensive sampling is carried out, and that where possible, sampling with replacement should be used.

Introduction

Cave environments are unique habitats that are suffering from increasing pressures placed upon them. Caves contain a wide range of invertebrate taxa, such as crickets, cockroaches, millipedes, amphipods, isopods, and arachnids. Many of these organisms show morphological modifications (troglomorphies) that are not found in corresponding surface dwelling (epigean) species. Troglomorphies include reduction or loss of eyes, wings, and bodily pigmentation, and attenuation of appendages (Barr, 1968; Culver, 1982, Kane and Richardson, 1985). Many of these species are relicts, having few or no closely related epigean species. Although a large amount of research has been carried out on Australia's temperate caves (Hamilton-Smith, 1967, 1987; Richards, 1971; Eberhard, 1993; Eberhard *et al.*, 1991), few studies have looked at our tropical caves. Not until the early 1980s did entomological studies delve deeper into North Queensland caves. This work led to the discovery of a rich and diverse range of tropical cave fauna including sandflies, plant hoppers, assassin bugs, and cockroaches (Lewis and Dyce, 1983; Hoch and Howarth, 1989a, b, Malipatil and Howarth, 1990; Roth, 1990). One expedition by Howarth and Stone in 1985 recorded over 40 species of cave arthropods from Bayliss lava tube at Undara, seven of which were new species (two represent new genera) and 24 of which were troglobites (Howarth and Stone, 1990). We have discovered further new species, including a pseudoscorpion, and several sibling species of cave cockroaches (Weinstein and Slaney, 1995). Caves are not only important with respect to documenting and preserving biodiversity, but are important for studying adaptation, speciation, and species interactions. They provide us with natural laboratories in which we can frame and test evolutionary hypotheses.

Cave organisms are particularly vulnerable to disturbance as they live within discrete habitats, with isolated island like distributions. Species are particularly vulnerable when endemic species are confined to one or two caves within a karst region. For example, near Chillagoe, Qld, four small limestone towers occur within a 2 km^2 area within which several endemic cave adapted arthropods are found, with some being restricted to single towers (Hoch and Howarth, 1989b). Population sizes are often small, and due to their isolated distribution may exhibit a limited gene pool and restricted gene flow, which may result in severe bottle necks, further increasing their vulnerability (Barr and Holsinger, 1985; Caccone, 1985; Culver, 1986). The small size of caves, compared to surface habitats, also reduces the resilience of such species to disturbance. Disturbances may not only result in the extinction of these organisms, but in the destruction of the unique cave habitat itself. Disturbances can be categorised as either indirect (brought about by modifications to cave habitats and the surrounding environment) or direct (brought about by human visitation to caves).

Indirect disturbance

Deforestation

Clearing of vegetation for timber, mining, and road construction changes local hydrology, and causes severe erosion and increased frequency and intensity of flooding (Lichon, 1993). In NSW and Victoria approximately 60% of the karst regions have had their native vegetation removed or severely modified (Eberhard and Spate, 1995), while in Tasmania, most caving areas are covered by intact temperate forest which is under threat by clearing for the woodchipping industry (Lichon, 1993). Populations of glow worms in Flowery Gully caves, Tasmania, were wiped out as a result of clearing vegetation, an act which made a once permanent subterranean stream become intermittent, in turn lowing the high humidity in the caves required by the glow worms (Lichon, 1993). Clearing of vegetation near caves also removes the major source of nutrient input, dramatically lowering the food available to cave invertebrates.

The exposure of soils surrounding caves caused by clear felling, quarrying, and farming increases the rate of erosion, resulting in high levels of sediment deposition in caves (Kiernan, 1988). High levels of erosion at an Ida Bay quarry, in Tasmania, has caused clay to be washed into surrounding caves (Lichon, 1992). The deposition of clay in cave passages normally containing gravel substrates has led to the loss of cave invertebrates adapted to living in such habitats (Eberhard, 1995). Scouring of organisms from their stream habitat can also occur during periods of flooding (Chutter, 1969), while at Mole Creek Caves, Tasmania, land clearing has resulted in rapid subsidence and collapse of cave systems (Lichon, 1993).

Changing water levels

Flooding induced by land clearance or by the construction of dams can obliterate entire cave communities. Cave communities at Texas in Queensland, Burrinjuck in NSW, Dartmouth in Victoria and Lorinna in Tasmania have all been lost as a result of dam constructions (Eberhard and Spate, 1995). Alternatively, lowering the water table can have a similar effect on cave invertebrates. In Yanchep, Western Australia, groundwater pumping is threatening aquatic cave species (Jasinska and Knott, 1991). In the Naracoorte caves, South Australia, the transpiration from overlying pine plantations has reduced the amount of water seeping into the caves, resulting in cave desiccation.

Quarrying

In addition to changing local flow regimes and increasing sedimentation rates, quarrying of limestone for cement and other building materials (eg marble) often entails the complete destruction of a cave and even entire karst tower systems. Blasting in the vicinity of caves can also cause severe structural damage to them, altering the microclimate within. Limestone operations at Mount Etna, Queensland, have led to numerous caves being destroyed, including ghost bat (*Macroderma gigas*) maternity caves (Eberhard and Spate, 1995), and presumably their associated invertebrate cave communities.

Pollution

Caves are often used for dumping of agricultural, industrial and public waste. The occurrence of sudden large influxes of nutrients (eg dead farm animals) can lead to the introduction of surface invertebrates and allow some cave species to out-compete others, upsetting the delicate ecological balance (Chapman, 1993). From 1900 to 1976 waste and wash water from a cheese factory and abattoir in Yahl, Mount Gambier, South Australia, was discharged into an unconfined limestone aquifer. The effluent contaminated groundwater, resulting in abnormally high nitrate levels in the surrounding limestone karst (Slaney and Ragusa, 1990). At Mole Creek, Tasmania, stock access to karst regions and dairy effluent runoff has increased nutrient levels, resulting in high bacterial populations in cave waters (Lichon, 1993). Pesticides and fertilisers may also be washed into caves from surrounding agricultural land (Chapman, 1993, Lichon, 1993). Cave entrances may not only be blocked by waste but infilled to make way for farming, roads and housing developments. Such blockages lead to a decrease in the amount of nutrient input into the cave ecosystem and result in the depletion or extinction of cave invertebrates (Culver, 1986).

Tourism

Construction of paths and walkways, lighting, gates on cave entrances, and widening of cave entrances for tourism, create a number of problems for cave organisms (e.g., Webb, 1984). These constructions lead to the alteration and loss of habitat, upon which highly adapted organisms depend, by altering cave temperatures, humidities and atmospheric composition (e.g., Pugsley, 1984). Artificial lighting used for tourism can enable the establishment of plants that would not be able to survive in the normal conditions of little to no light. In turn, introduced plants may provide habitat for surface dwelling invertebrates, thus altering cave community composition (Howarth, 1982; Eberhard and Spate, 1995). Construction of gates with low sills have a tendency to trap leaf litter which would otherwise be washed into caves, as has occurred at the entrance to Kubla Khan Cave in Tasmania (Spate and Hamilton-Smith, 1991). Changes to cave microclimates also affect bat maternity sites and associated cave invertebrates (Tuttle, 1979). The placement of air tight doors to control desiccation of speleothems in Alexandra Cave at Naracoorte, South Australia, has wiped out populations of rhaphidophorid cave crickets (Hamilton-Smith, 1987).

Direct disturbance

Damage to caves and the loss of cave fauna may be caused directly by human visitation. Visits by the general public, caving clubs, and researchers result in the trampling of some cave invertebrates (Spate and Hamilton-Smith, 1991), and the compaction of cave floor sediments occupied by others (e.g., crickets and beetles, Middleton, 1979). At Mount Widderin Cave, Skipton, Victoria, an invertebrate community living on unconsolidated substrate has disappeared as a result of soil compaction by high numbers of human visitors (Spate and Hamilton-Smith, 1991). In addition to soil compaction, walking through cave pools may adversely affect aquatic invertebrates. In Tasmania, rare psammaspid and syncarid crustaceans are confined to such habitats (Eberhard, 1993), and alterations of turbidity in their waters may critically alter their environment. Cave visitors also pose a potential threat to cave invertebrates by introducing organisms from the surface and from other caves which may outcompete and displace the extant cave fauna. Cave visitation may also result in the trampling of plant roots, leading to the loss of root feeding invertebrates and their predators (Howarth, 1982). Cave visitors using acetylene torches may also impact on cave organisms through the toxic calcium carbide by-product of these torches.

Generally, caves as discrete confined habitats tend to have a carrying capacity of visitation, above which level of disturbance collapse of cave communities is likely to occur (Howarth and Stone, 1982, Spate and Hamilton-Smith, 1991). Field data on cave fauna distributions in Hawaiian lava tubes by Howarth and Stone (1982) show that species diversity and population levels are inversely proportional to the level of visitation and human disturbance. Disturbance of bat colonies brought about by human visitation, (particularly by bat researchers !) has contributed to the decline of many colonies (Tuttle, 1979). Bat decline from human disturbance has been observed in central and south-eastern NSW caves (Hall and Dunsmore, 1974). In turn, the loss of bats has led to the loss of endemic guanophilic invertebrates.

Impact of scientific studies

Despite the high profile of conservation issues such as the threat to populations of ghost bats, little work has been carried out in Australia to assess the impact of humans on cave ecology, with no studies on the effect that trapping may have on cave invertebrate populations. Key (1978) and Heath (1987) claimed that there is no evidence of collecting ever affecting a population of insects detrimentally. However, declining populations of the collected Bathurst Copper Butterfly suggest otherwise (Dexter and Kitching, 1993), and we provide evidence in this paper that intensive sampling of cave invertebrates can deplete populations. Culver (1986) stated that worldwide, one of the dangers to cave fauna is the appalling number of species threatened by over-collecting for scientific purposes, but he cites few data to support this statement. With this in mind we analysed past data we had obtained in investigations of tropical cave fauna, to assess the impact that our sampling may have had on populations of cave invertebrates.

During August 1993 we surveyed the macroinvertebrate fauna of Rope Ladder Cave, Fanning River Caves, in tropical north Qld, and recorded the weekly total of individuals of each macroinvertebrate species collected over one month of continuous trapping with four different methods concurrently (pitfall only, baited pitfall, leaf litter dry, and leaf litter wet, with no replacement; Weinstein and Slaney, 1995). Four species were trapped in sufficient numbers to look for trends in their frequency of capture.

Pseudoscorpions, cockroaches, rhizophagid beetles, and pselaphid beetles showed a significant decline in number over the sampling period (from 12, 44, 680 and 18 individuals to 5, 25, 250 and 4 individuals respectively). Given that sampling occurred at the same time of day and that we found no seasonal effects (e.g., periodic rainfall) impacting on these populations during the study period (Weinstein, 1994; Weinstein and Slaney, 1995), the probability of recording a simultaneous decrease in populations of four different species by chance alone is 0.0625 (0.5^4). Thus, the data suggest that our sampling of cave invertebrates adversely affected their numbers.

Past studies have also indicated that sampling may have adverse effects on cave populations, with pitfall trapping reducing cave beetle populations (Peck, 1975, 1976). All that may be required to extinguish the local population of a cave dwelling species is the careless or accidental desertion of a pitfall trap (Vandel, 1965; Howarth, 1982). A single trap in a restricted area may not only trap a species to extinction, but may subsequently affect the ecology of the cave itself through changes in the population dynamics of the surviving cave fauna. A possible way of minimising such impacts is to sample with replacement, or if trap sites are to be left in situ for an extended period of time, to use a 'trap' which allows for the free movement of individuals. We have designed a survey tool which meets both of these requirements (Slaney and Weinstein, in press). A wet leaf litter trap (which simulates nutrient influx into dry tropical caves during monsoonal rains) maintains the viability of organisms, thus allowing their release back into the cave environment following identification and counting. Because this trap is not only conservation friendly but is also more effective and more efficient than other sampling techniques (Weinstein and Slaney, 1995), we recommend it as the survey tool of choice in these fragile ecosystems (Slaney and Weinstein, in press).

Implications

Compared with the USA, Australia is extremely depauperate in numbers of caves (Jennings, 1983). Despite this, Australian caves are of international significance, containing a diverse range of cave organisms. Cave habitats in Tasmania are amongst the richest temperate cave communities (Eberhard and Spate, 1995), while tropical caves in Western Australia and Queensland have an exceptional abundance of cave species (Humphreys, 1993, Howarth, 1988). Legislatively only Tasmania and Western Australia recognises cave invertebrates as important, but even then only on a species by species basis (New, 1984; Eberhard and Spate, 1995; Humphreys, pers. comm.). The formulation of conservation policies/strategies for protecting cave invertebrates is difficult due to the lack of taxonomic and ecological data. The lack of such data is obviously not a problem unique to caves, but is a major shortfall which threatens the conservation of Australia's invertebrate fauna on the whole (New, ms.). Caves more than most other ecosystems can play an important role in making both the public and policy makers aware of this problem, as they tend to have a relatively high local profile (e.g.,Jenolan Caves, Undara Lava Tubes, and Chillagoe Caves, all of which are rich in cave fauna and provide important local landmarks).

One of the problems facing cave researchers is determining whether insect species are rare, as they are often difficult to observe due to camouflaging adaptations, the cryptic microhabitats in which they live (cracks or rock piles), and the inaccessibility of the cave in the first place. Further, individuals within each population may be able to find refuges from which they can continually recolonise other cave regions, thus demonstrating patchy distributions both in space (location) and time (seasons). Howarth (1983) stated that there is a requirement for experimental ecological studies to determine what factors limit cave species distribution, what are the significant perturbations, and how these disturbances affect cave communities. For example, long term ecological research is required to establish methodologies for distinguishing between short term population fluctuations and longer term irreversible changes (Howarth and Ramsay, 1991).

Generally, biologists recognised that insect species are endangered to the extent that their habitats are endangered, and that their conservation can be accomplished only by conserving their habitats (Key, 1978). With cave ecosystems the surface and subsurface drainage basins are coupled, forming a highly integrated unit (White *et al.*, 1995), and the conservation of cave fauna would thus be best achieved by protecting the cave ecosystem and the surrounding catchment area (not just around the cave entrance) from the sorts of disturbances we have outlined in this paper (including scientists!). We recommend that ecosystem stability and vulnerability to disturbance, as well as the general ecology of organisms in a cave, be considered before any intensive sampling is carried out. We further recommend that any sampling be done with replacement using techniques similar to our own leaf litter traps (Slaney and Weinstein, in press). For cave communities where direct visitation is having an effect on populations of cave species, access must be restricted, and tourism should be established only in caves with few species. Where possible, caves immediately adjacent to such tourist caves should have restricted access to allow organisms to retreat into a readily available refuge.

The faunas of many caves which are under threat either directly or indirectly have not been investigated at all, and may never be discovered without detailed taxonomic and ecological studies. Caves are a unique biological resource with both scientific and cultural importance, especially for invertebrates. We must not neglect the biodiversity and conservation value of these habitats, always bearing in mind that conservation strategies can only be as sound as the research upon which they are based (New, ms.).

References

Barr, T.C., Jr., 1968. Cave ecology and the evolution of troglobites. *Evolutionary Biology* 2: 35–102.

Barr, T.C., Jr. and Holsinger, J.R., 1985. Speciation in cave faunas. *Annual Review of Ecology and Systematics* 16: 313–37.

Caccone, A., 1985. Gene flow in cave arthropods: a qualitative and quantitative approach. *Evolution* 39: 1223–1235.

Chapman, P., 1993. *Caves and cave life*. Harper and Collins: London.

Chutter, F.M., 1969. The effects of salt and sand on the invertebrate fauna of streams and rivers. *Hydrobiologia* 34: 57–76.

Culver, D.C., 1982. *Cave life: evolution and ecology*. Harvard University Press: Cambridge.

Culver, D.C., 1986. Cave faunas. Pp. 427–443 in: Soulé, M.E. (ed.), *Conservation biology: the science of scarcity and diversity*. Sinauer Assoc.: Sunderland.

Dexter, E.M. and Kitching, R.L., 1993. The Bathurst Copper, *Paralucia spinifera* Edwards & Common. Pp. 168–170 in: New, T.R. (ed.), Conservation biology of Lycaenidae (butterflies). *Occasional Paper of the IUCN Species Survival Commission No.* 8.

Eberhard, S. M., 1993. *Survey of fauna and human impacts in the Jenolan caves reserve*. Jenolan Caves Research Trust, NSW.

Eberhard, S. M., 1995. *Impact of a limestone quarry on aquatic cave fauna at Ida Bay in Tasmania*. NPWS, Hobart.

Eberhard, S.M., Richardson, A.M.M. and Swain, R., 1991. *The invertebrate cave fauna of Tasmania*. Report to the National Estate Office, Canberra.

Eberhard, S.M. and Spate, A., 1995. *Cave communities*. NSW NPWS submission to the Endangered Species Unit of the Australian Nature Conservation Agency.

Hall, L.S. and Dunsmore, J.D., 1974. A survey of cave dwelling bats. *Australian Speleological Federation Newsletter* 64: 9–10.

Hamilton-Smith, E., 1967. The Arthropoda of Australian caves. *Journal of the Australian Entomological Society* 6: 103–118.

Hamilton-Smith, E., 1987. Karst creatures: the fauna of Australian karst. *Australian Ranger Bulletin* 4(3): 9–10.

Heath, A.C.G., 1987. Collect or conserve — the entomologist's dilemma. *New Zealand Entomologist* 9: 4–10.

Hoch, H. and Howarth, F.G., 1989a. Reductive evolutionary trends in two new cavernicolous species of a new Australian cixiid genus (Homoptera: Fulgoroidea). *Systematic Entomology* 14: 179–196.

Hoch, H. and Howarth, F.G., 1989b. Six new cavernicolous cixiid planthoppers in the genus *Solonaima* from Australia (Homoptera: Fulgoroidea). *Systematic Entomology* 14: 377–402.

Howarth, F.G., 1982. The conservation of cave invertebrates. *Proceedings from the International Cave Management Symposium, Murray, KY, 1981*: 57–64.

Howarth, F.G., 1983. Ecology of cave arthropods. *Annual Review of Entomology* 28: 365–389.

Howarth, F.G., 1988. Environmental ecology of North Queensland caves: Why there are so many troglobites in Australia. *Australian Speleological Federation 17th Biannual Conference preprints, Lake Tinaroo, December 1988.*

Howarth, F.G. and Ramsay, G.W., 1991. The conservation of island insects and their habitats. Pp. 71–107 in: Collins, N.M. and Thomas, J.A. (eds), *The conservation of insects and their habitats*. Academic Press: London.

Howarth, F.G. and Stone, F.D., 1982. The conservation of Hawaii's cave resources. Pp. 94–99 in: Smith, C.W. (ed.), Hawaii Volcanoes National Park. *Proceedings 4th Conference in National Science*. Cooperative National Park Study Unit, University of Hawaii Manoa: Honolulu..

Howarth, F.G. and Stone, F.D., 1990. Elevated carbon dioxide levels in Bayliss cave, Australia: Implications for the evolution of obligate cave species. *Pacific Science* 44(3): 207–218.

Humphreys, W.F., 1993. The biogeography of Cape Range Western Australia. *Records of the Western Australian Museum, Supplement* 45.

Jasinska, E.J. and Knott, B., 1991. The importance of caves at Yanchep, Western Australia. *Proceedings* *from the 18th Biennial Conference of the Australian Speleological Federation*: 55–57.

Jennings, J.N., 1983. A map of karst cave areas in Australia. *Australian Geographical Studies* 21: 183–196.

Kane, T.C. and Richardson, R.C., 1985. Regressive evolution: an historical perspective. *National Speleological Society Bulletin* 47(2): 71–77.

Key, K.H.L., 1978. The conservation status of Australia's insect fauna. *Australian National Parks and Wildlife Service, Occasional Paper* 1.

Kiernan, K., 1988. *The management of soluble rock landscapes: an Australian perspective.* Speleological Research Council: Sydney.

Lewis, D.J. and Dyce, A.L., 1983. Phlebotomine sandflies (Diptera: Psychodidae) from caves in Queensland, Australia. *Journal of the Australian Entomological Society* 22: 223–231.

Lichon, M., 1992. Recent history and issues surrounding the saving of Exit Cave, and future options. *Illuminations* 1: 17–22.

Lichon, M., 1993. Human impact on processes in karst terranes, with special reference to Tasmania. *Cave Science* 20(2): 55–60.

Malipatil, M.B. and Howarth, F.G., 1990. Two new species of *Micropolytoxus* Elkins from northern Australia (Hemiptera: Reduviidae: Saicinae). *Journal of the Australian Entomological Society* 29: 37–40.

Middleton, G.J., 1979. Wilderness caves of the Gordon-Franklin River system. *University of Tasmania, Centre for Environmental Studies Occasional Paper* 11.

New, T.R., 1984. *Insect Conservation — an Australian perspective.* Dr.W.Junk: Dordrecht.

New, T.R., ms. Taxonomic focus and quality control in insect surveys for habitat conservation. *Journal of the Australian Entomological Society.*

Peck, S.B., 1975. A population study of the cave beetle *Ptomaphagus hirtus* (Coleoptera; Leiodidae; Catopinae). *International Journal of Speleology* 7: 303–326.

Peck, S.B., 1976. The effect of cave entrances on the distribution of cave inhabiting terrestrial arthropods. *International Journal of Speleology* 8: 309–321.

Pugsley, C., 1984. Ecology of the New Zealand Glowworm, *Arachnocampa luminosa* (Diptera: Keroplatidae), in the Glowworm Cave, Waitomo. *Journal of the Royal Society of New Zealand* 14: 387–407.

Richards, A., 1971. An ecological study of the cavernicolous fauna of the Nullarbor Plain, Southern Australia. *Journal of the Zoological Society of London* 164: 1–60.

Roth, L.M., 1990. A revision of the Australian Parcoblattini (Blattaria: Blattellidae: Blattellinae). *Memoirs of the Queensland Museum* 28(2): 531–596.

Slaney, D.P. and Ragusa, S., 1990. Denitrification in bacterial cultures and soil microcosms. *Centre for Groundwater Studies Report* No. 26, CSIRO: Adelaide.

Slaney, D.P. and Weinstein, P., in press. Leaf litter traps for sampling orthopteroid insects in tropical caves. *Journal of Orthoptera Research.*

Spate, A.P. and Hamilton-Smith, E., 1991. Caver's impacts — some theoretical and applied considerations. *Ninth Akcma Conference*: 20–30.

Tuttle, M.D., 1979. Status, causes of decline, and management of endangered grey bats. *Journal of Wildlife Management* 43: 1–17.

Vandel, A., 1965. *Biospeleology.* Translated by B.E. Freeman. Pergamon Press: Oxford.

Webb, R., 1984. Drovers Cave, Western Australia: cave destruction through management. Pp. 41–48 in: Pilkington, G. (ed.), *Proceedings of the 14th Biennial Conference of the Australian Speleological Federation.* ASF: Sydney.

Weinstein, P., 1994. Behavioural ecology of tropical cave cockroaches: preliminary field studies with evolutionary implications. *Journal of the Australian Entomological Society* 33: 367–370.

Weinstein, P. and Slaney, D.P., 1995. Invertebrate faunal survey of Rope Ladder Cave, North Queensland: a comparative study of sampling methods. *Journal of the Australian Entomological Society* 34: 233–236.

White, W.B., Culver, D.C., Herman, J.S., Kane, T.C. and Mylroie, J.E., 1995. Karst lands. *American Scientist* 83: 450–459.