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Arcuate Nest Ridges — a biogenic morphotype associated with cave-dwelling swiftlets

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Abstract: Arcuate Nest Ridges are small (6 – 10cm-wide), arc-shaped, rock ridges that protrude (by some 1 – 2cm) from rock faces where cave-dwelling swiftlets nest. The nests (mainly of the White-nest swiftlet *Aerodramus fuciphagus*) are made of hardened saliva, and strongly glued to high-angle and commonly sheer cave walls and ceilings. The cement-like saliva impregnates the pores of the rock surface under the area of contact of the nest, thus protecting that spot from the condensation corrosion (usually biogenic in origin) that typifies the rest of the open cave wall. Over the centuries of nest-site fidelity the surrounding cave wall corrodes back but the protected arc remains emergent from the rock face, to be used again each nesting season. The number of abandoned nest sites, as indicated by empty arcuate nest ridges, can be used as a conservation tool to monitor effects of harvesting or population decline.

Keywords: Biogeomorphology, condensation corrosion, *Aerodramus*, edible nests, nest-site fidelity.

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Introduction

Recent years have seen a growing interest in biogenic processes and forms that modify the interior of caves, generally documented from caves in equatorial and tropical environments. Examples can be seen both at a large (speleogenic) scale (e.g., elephant "mining" of the cave passages in Kenya: Lundberg and McFarlane, 2006; significant chamber enlargement by condensation corrosion from bats and birds in Borneo: Lundberg and McFarlane, 2012; erosion driven by guano diagenesis: Barriquand *et al.,* 2012) — at a smaller scale (e.g., bell-holes: Lundberg and McFarlane, 2009; spectacularly eroded speleothem blocks: Sala *et al.,* 2023) — and even on a tiny scale (e.g., bat claw and thumb scratches: Merino *et al*., 2019).

In this short note we document a small-scale (~6 – 10cm), emergent, form observed in several of the caves of Borneo, S.E. Asia, associated mainly with the nests of the White-nest swiftlet, *Aerodramus fuciphagus*, and to a lesser extent with nests of the Black-nest swiftlet *Aerodramus maximus*. Although small, these features have some relevance to, and could be used as a tool in, biological management and conservation.

Background

Echolocating swiftlets of the genus *Aerodramus* are widespread in insular southeast Asia, where they frequently take advantage of the predator protection provided by nesting in high-ceiling caves. The nests of the swiftlets are made up of varying proportions of specialized sticky saliva (Chantler and Boesman, 2020) secreted by sublingual glands in the male (Ma and Liu, 2012) that enlarge during breeding (Sankaran, 1998), along with leaves, moss, and feathers. The saliva forms a hard cement that glues the bracket-shaped nest to the cave wall and shapes the nest into a neat cup (Sankaran, 2001). The amount of saliva dictates the stickiness and structural strength of the nests and thus controls the locations within the cave that are suited to the different species.

Mossy-nest swiftlets, *Aerodramus salangana*, produce loosely-woven nests of vegetation that, being minimally bonded, require ledges or cavities for their support (Fig.1). The Black-nest swiftlet, *A. maximus*, makes self-supporting nests of feathers bonded to themselves and to the cave wall by the sticky saliva. Commonly these nests are also built on available pre-existing ledges or concavities on, or in, the cave walls,

***Figure 1**: Two naked nestlings peer over the top of the mossy nest of* Aerodramus salangana*, perched in a shallow elliptical cavity, Stonehorse Cave, Mulu, Borneo.*

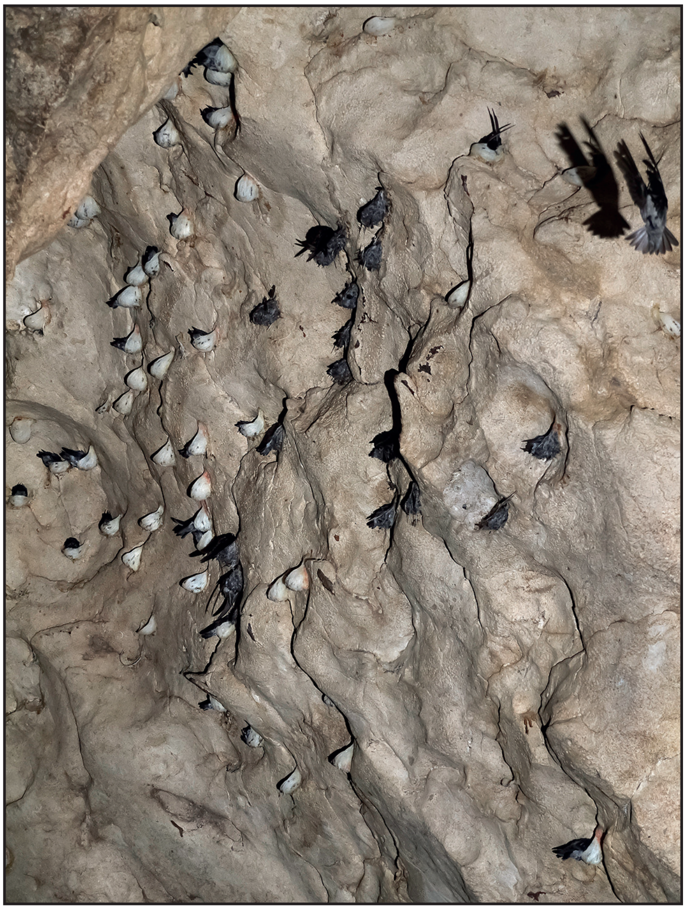

***Figure 2**: Black nests of* Aerodramus maximus *and white nests of* Aerodramus fuciphagus*, Simud Putih, Gomantong, Borneo. Both nests show the distinctive bracket or half-cup shape clinging to the wall, but the black nests are generally on slight indentations of the surface, while the white ones are attached to the more sheer faces.*

but they have enough structural integrity that they can be free-hanging and thus constructed on very high-angle cave walls and ceilings (Fig.2). The White-nest swiftlet, *A. fuciphagus* (Fig.2) builds nests almost entirely constructed from their salivary excretions (Koon and Cranbrook, 2002). These nests can be attached to relatively smooth, very high-angle to overhanging cave walls and ceilings, and do not rely on pre-existing ledges; they are also the prime target of the lucrative edible-nest harvesting industry (Sankaran, 2001; Koon and Cranbrook, 2002).

The features described here, which we have named "Arcuate Nest Ridges", develop as a direct consequence of the nest building (see explanation below) of the White-nest swiftlet and, less commonly, the Black-nest swiftlet. They can be seen at the base of active nests, and, where nest sites are no longer used, the ridges give evidence of former nest sites.

The Arcuate Nest Ridges: description and process of formation

The ridges are the same width as the nests — about 6 – 10cm — and curve upwards in a shallow arc following the shape of the nests — up to about 3 – 4cm on either side (each looking like a small rocky smiley face without eyes).The extent to which they stand proud of the general rock face varies, the largest that we have seen protrude by about 1.5cm. Their distribution follows the distribution of nests — often in lines or *en echelon*. Figure 3 shows white nests in Gomantong Cave, Sabah, Borneo, where each nest sits on a small arcuate nest ridge, but several other nest ridges are no longer occupied. This may be indicative of a formerly more extensive occupation.

The process of formation (Fig.4) is as follows. On a virgin surface, White-nest swiftlet nest-building probably begins on random, slight protuberances on otherwise smooth and high-angle walls where they have little competition from other swiftlet species. The nests are curved semi-spherical bracket shapes (Sankaran, 2001). Hardened saliva at the point of contact of the nest with the wall cements the nest to the rock. This coats the rock, impregnating the uppermost millimetre or so of the rock face with hardened cement, which in turn protects that particular spot from the general erosion of the rest of the rock face.

The rest of the rock face is subject to condensation corrosion, especially in chambers with large populations of bats or birds. This type of corrosion is characteristic of caves with regular exchanges of air and alternations of temperature. When the temperature of the cave walls is below the dew point of the cave air, water will condense on the surfaces, dissolve the CO_2 in the cave atmosphere and thus become aggressive to limestone (Dreybrodt *et al*., 2005; Merino *et al*., 2019). Biogenically-mediated condensation corrosion (Audra *et al*., 2016, 2022; Bruxelles *et al*., 2016) occurs where water vapour in contact with the rock is rendered aggressive to calcium carbonate through the metabolites of macro-organisms (for example, dense populations of bats or birds roosting in close contact with the rock: Lundberg and McFarlane, 2009, 2012) or micro-organisms (for example, microbial degradation of guano: e.g., Merino *et al*., 2019; Barriquand *et al*., 2021, 2024).

***Figure 3**: White nests of* Aerodramus fuciphagus*, in Simud Putih, Gomantong, Borneo. Each nest sits atop an arcuate nest ridge, but several of the ridges are no longer occupied by nests, the most obvious marked with an arrow (perhaps indicative of a reduced population).*

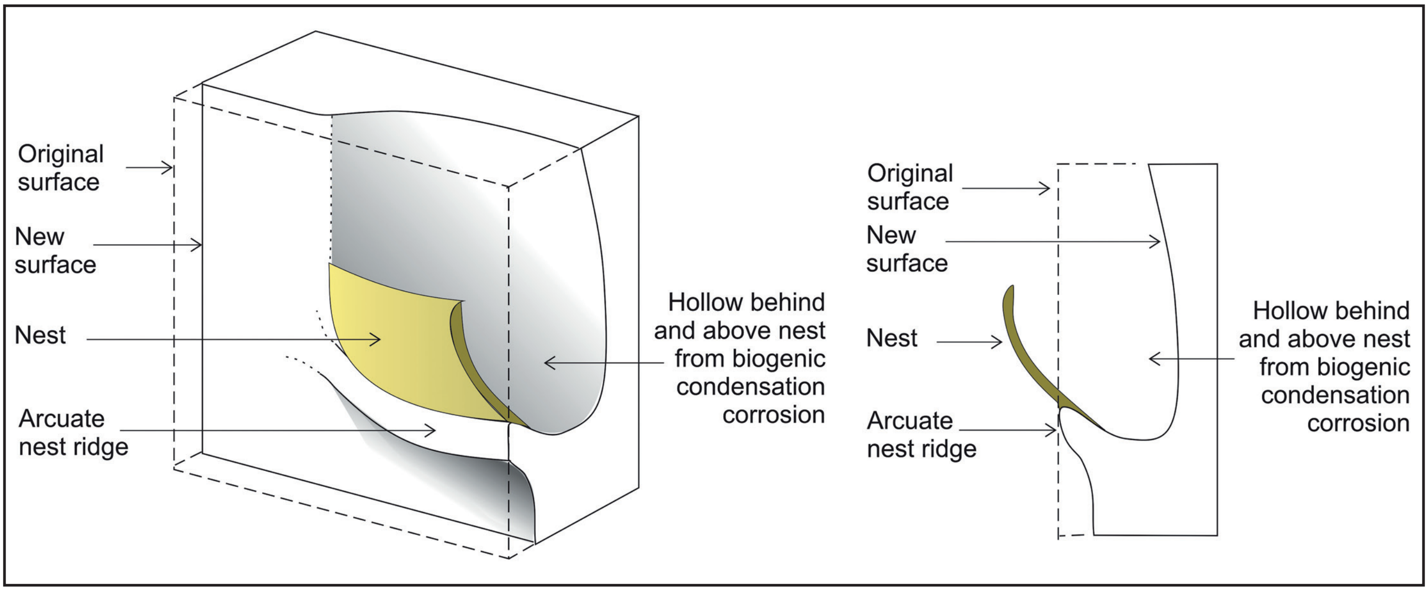

Figure 4*: The process of formation of the Arcuate Nest Ridges, 3D block diagram, and cross-section.*

It has been demonstrated that such biogenic erosion can be significant in caves with high, and spatially concentrated, vertebrate biomass (e.g., Lundberg and McFarlane, 2009, 2012). This, perhaps in addition to meteorologically driven condensation corrosion, causes generalized wall retreat (shown in Figure 4 where the "Original surface" has retreated to the level of the "New surface").

In addition to this, biogenic condensation corrosion is more concentrated in the immediate vicinity of the nests: respired water vapour and carbon dioxide from nesting birds induces biogenic condensation corrosion of the wall adjacent to the nest, producing a concavity (Fig.4). The combination of: 1) salivary cement protecting the arc of rock at the point of contact of the nest; 2) the generalized wall retreat of the chamber; and 3) the more-focused condensation corrosion behind and above the nest sculpts an arcuate ridge of protected rock at the nest-wall interface (Fig.4).

Because the swiftlets show a high degree of nest-site fidelity over generations (Sankaran, 1998, 2001), the repeated cycles of nests built on the same spot continue this erosion protection over centuries. These ridges are typically obscured to some extent by new, active, nests, but can become apparent following nest harvesting, or in situations where over-harvesting of the nests has reduced or eliminated the local population of swiftlets. We are not the first to observe these features: Sankaran (1998, 2001) mentions in passing that old nest sites can be identified by: "… *shallow indention in the cave wall shaped like the nest cup, and probably caused by repeated nesting by swiftlets at the same site over several decades or centuries*".

The amount of saliva in individual nests will vary with the amount of bonding required and thus with the angle of the slope and texture of the rock face. The amount of saliva (in combination with location fidelity) dictates where the arcuate ridges will develop. Whereas the ridges are most commonly associated with white nests, we can expect ridges to develop with some black nests where these are on higher-angle or smoother surfaces with fewer useful support ledges (Fig.5).

Significance to the ecosystem and conservation

The ridge is created by the continued presence of birds and repeated building of nests on the same spot. The ridge then becomes a slightly more favourable spot, providing a little more support and thus slightly reducing the resources needed for nest building. This is a very minor example of an organism modifying its environment indirectly — perhaps not as dramatic as niche construction (e.g., Lundberg and McFarlane, 2016; Phillips, 2016) — but, in its own small way, helpful to the success of the organism.

The relevance to conservation is that the number and distribution of abandoned nest ridges can be used to monitor harvesting levels, and/or reductions in populations. This would be very simple to do using repeated photography from the same fixed viewpoint over time. The one obvious limitation in many caves — the height of the ceilings and the limits of providing sufficient lighting for photography — could be resolved by the use of high-resolution LiDAR scanning (McFarlane *et al*., 2015).

Arcuate ridges are a relatively minor phenomenon on the spectrum of biogenic modification of caves, but their value lies in their potential to identify the former extent of swiftlet nesting (and hence population size). This is particularly valuable in the face of the collapse of many *A. fugiphagus* populations subjected to intense nest over-harvesting (e.g., Gausset, 2004; Hobbs, 2004).

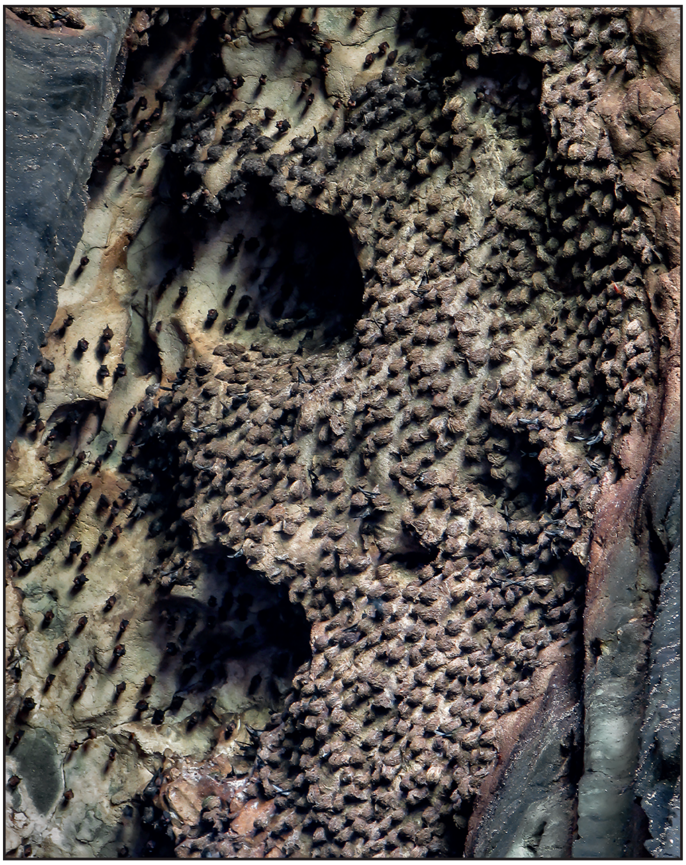

Figure 5*: Looking up to black nests crowded together on a steeply sloping ceiling in Gomantong Cave, Borneo. The isolated dark forms to the left are individual hanging bats.*

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