

Phylogenetic relationships of the Papuan Swiftlet *Aerodramus papuensis* and implications for the evolution of avian echolocation

J. JORDAN PRICE,^{1*} KEVIN P. JOHNSON,² SARAH E. BUSH^{3†} & DALE H. CLAYTON³

¹Department of Biology, St. Mary's College of Maryland, St. Mary's City, MD 20686, USA

²Illinois Natural History Survey, Champaign, IL 61820, USA

³Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

The swiftlets (genera *Aerodramus*, *Collocalia* and *Hydrochous*) are unusual among birds in that many species can orientate in complete darkness using echolocation. The position of the Papuan Swiftlet *Aerodramus papuensis* in this group has been uncertain historically, in part due to morphological differences between it and other swiftlets (it has three toes instead of the usual four) and a lack of data on its behaviour (there is uncertainty about whether it echolocates). Here we investigate the phylogenetic affinities of the Papuan Swiftlet using DNA sequence data from two mitochondrial genes, cytochrome *b* and ND2. We present evidence that it is able to echolocate but, unlike previously studied species that use echolocation primarily while flying in caves, *A. papuensis* uses this ability while active outside caves at night. We also provide new evidence for placement of the monotypic Waterfall Swiftlet *Hydrochous gigas*, a species that does not echolocate. Our data provide strong support for a basal relationship between *A. papuensis* and other *Aerodramus* taxa and suggest that this species and *H. gigas* are sister taxa, a relationship that would indicate paraphyly of the genus *Aerodramus*. Our phylogeny provides new insights into how echolocation has evolved in the swiftlets, in particular by indicating higher levels of homoplasy in this trait than was previously thought.

Swiftlets (Apodidae: Collocaliini) are small, insectivorous birds found throughout the Australasian region from the Indian Ocean to the South Pacific. Most species roost and nest in caves, often placing their nests in areas of complete darkness, and are able to navigate using echolocation (Griffin 1958, Medway 1959, Medway & Pye 1977, Koon & Cranbrook 2002, Nguyen Quang *et al.* 2002). This unusual ability to echolocate is found elsewhere in birds only in the Neotropical Oilbird *Steatornis caripensis*, a species that also nests in caves (Griffin 1954, 1958). Unlike the ultrasonic cries of bats, the echolocation clicks of swiftlets are well within the human range of hearing (Cranbrook & Medway 1965), and so presumably do not allow the acuity needed to locate

aerial insect prey. Rather, studies of several species indicate that echolocation is used in swiftlets primarily for avoiding obstacles while flying in darkness when visual cues are not available (Medway 1967, Griffin & Suthers 1970, Fenton 1975, Griffin & Thompson 1982, Collins & Murphy 1994). Most swiftlet species studied to date forage during the day and produce echolocation clicks mostly while flying through the caves in which they roost at night (Chantler & Driessens 1995, Chantler *et al.* 2000).

The Papuan, or Three-toed, Swiftlet *Aerodramus papuensis* is unusual among the swiftlets in several ways. Most notably, it is the only known member of the Apodidae to have only three toes instead of the usual four (Chantler & Driessens 1995, Chantler *et al.* 2000). The hind toe, or hallux, is absent. Previous reports of this little-studied species also suggest that it might be active outside caves at night (Chantler *et al.* 2000), a behaviour not commonly reported in other swifts and swiftlets. Relationships between *A. papuensis* and other swiftlet taxa have

*Corresponding author.
Email: jjprice@smcm.edu

†Present address: Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS 66045, USA.

been unclear, but morphological and putative behavioural differences indicate that this species is relatively distant from the rest. Whether or not *A. papuensis* is capable of echolocation has not previously been described (Medway & Pye 1977, Chantler & Driessens 1995, Chantler *et al.* 2000). Indeed, Nguyen Quang *et al.* (2002) note that echolocation is assumed to occur in all members of the genus *Aerodramus* '... except perhaps in the Three-toed Swiftlet, *Aerodramus papuensis*, a rare species of New Guinea whose ability to echolocate is still unknown.'

The manner in which echolocation has evolved in the Collocaliini is not yet fully understood, in part due to uncertainties about relationships within the group. The swiftlets are typically divided into three genera, *Aerodramus*, *Collocalia* and *Hydrochous*, based on such features as body size, plumage glossiness, nest features and a capacity to echolocate (Brooke 1972, Chantler *et al.* 2000). Recent phylogenetic studies with incomplete taxon sampling using mitochondrial DNA (mtDNA) sequence data are consistent with the monophyly of both *Aerodramus* and *Collocalia* (Lee *et al.* 1996) and that of the Collocaliini (Thomassen *et al.* 2003, Price *et al.* 2004). However, relationships of the single member of the genus *Hydrochous*, the Waterfall Swiftlet *Hydrochous gigas*, have remained unresolved (Lee *et al.* 1996, Thomassen *et al.* 2003), and affinities of several *Aerodramus* species, including *A. papuensis*, have not been analysed previously using molecular data.

Until recently echolocation was thought to have evolved only once in the immediate ancestor of the *Aerodramus* clade. This view was based on the presence of echolocation in all studied members of this genus and a presumed lack of this ability in other genera (Brooke 1972, Medway & Pye 1977, Lee *et al.* 1996, Thomassen *et al.* 2003; but see Marin & Stiles 1993). The recent discovery of echolocation outside of the genus *Aerodramus*, however, in the Pygmy Swiftlet *Collocalia troglodytes* (Price *et al.* 2004), provides strong evidence against this idea. Echolocation has either arisen several times independently in the *Aerodramus* and *Collocalia* clades, or evolved once at the base of the swiftlet tree and was subsequently lost in some taxa. Resolving the phylogenetic position of *H. gigas*, which does not echolocate, could help in resolving the issue (Price *et al.* 2004). Furthermore, given the striking differences between the Papuan Swiftlet and other *Aerodramus* species, an examination of both the position of this unusual species on the swiftlet tree and its potential ability to echolocate is highly warranted.

In this study, we investigate the relationships of the Papuan Swiftlet using sequence data from two mitochondrial genes, cytochrome *b* (*cyt b*) and NADH dehydrogenase subunit 2 (ND2). We present evidence that this species is able to echolocate and, surprisingly, that it uses this ability while active outside caves at night. A new phylogeny for the swiftlets, which includes our molecular data from *A. papuensis* as well as a recently published *cyt b* sequence data from *H. gigas* (Thomassen *et al.* 2003), provides some new insights into how echolocation has evolved in these intriguing birds.

METHODS

A. papuensis individuals for molecular analyses and tape recordings of vocalizations were obtained by S.E.B. and D.H.C. on 18 November 2002, immediately outside the entrance to Losavi Cave (c. 1350 m) near the village of Herowana in Eastern Highlands Province, Papua New Guinea (PNG). Birds were captured in flight using a 30-m mist-net, which was set at 22:00 h on 17 November and taken down at 03:00 h on 18 November. All *A. papuensis* individuals were captured in darkness between 02:00 and 03:00 h. We obtained tape recordings of vocalizations during this period using a Sony WM-D6C stereo cassette recorder and Sony ECM-Z70 electret condenser microphone. Birds were recorded while flying over the vicinity of the net, while struggling in the net and immediately upon release. Vocalizations were similar in all three conditions.

DNA was extracted, amplified and sequenced for the mitochondrial *cyt b* (1058 bp) and ND2 (1078 bp) genes as described by Price *et al.* (2004). These sequences have been deposited in GenBank under accession numbers AY950787 and AY950788, respectively. *Cyt b* and ND2 sequences from other swiftlet taxa and from 15 species of swifts and treeswifts used as outgroups were obtained from Price *et al.* (2004) (GenBank accession numbers AY294424–AY294483 and AY204486–AY294545). We also obtained a *cyt b* sequence from *H. gigas* (1143 bp) from the study of Thomassen *et al.* (2003) (GenBank accession number AY135625). In all, we included mtDNA sequences from 62 individuals representing 40 species and subspecies of swifts and swiftlets.

No significant incongruence was detected between the *cyt b* and ND2 genes using the partition homogeneity test (Farris *et al.* 1994, 1995, Swofford 2002, see also Price *et al.* 2004), so subsequent analyses

combined the two genes. Both parsimony and maximum likelihood analyses of combined *cyt b* and ND2 data were conducted using PAUP* (Swofford 2002). We performed 100 random addition replicate heuristic parsimony searches to find the most parsimonious tree(s), then bootstrapped these data sets using 1000 replicates (Felsenstein 1985). For maximum likelihood, we computed the simplest model that could not be rejected in favour of a more complex model using Modeltest (Posada & Crandall 1998). These tests identified the GTR+I+G model as the favoured one for maximum likelihood analyses. We used ten random addition heuristic searches with TBR branch swapping to estimate the maximum likelihood tree. A maximum likelihood bootstrap analysis was then conducted with 100 bootstrap replicates and NNI branch swapping.

Because ND2 sequences for *H. gigas* were not available for this study, we used *cyt b* sequences alone to estimate the phylogenetic position of this taxon following two approaches. First, we used the tree(s) recovered in the above parsimony and maximum likelihood analyses as a constraint (i.e. backbone) tree to which we added *H. gigas*, using only *cyt b* sequences in analyses to determine its position. As an additional comparison, we analysed the complete data set of *cyt b* and ND2 sequences under both parsimony and likelihood, coding the ND2 gene as missing data for *H. gigas*.

Spectrograms of *Aerodramus papuensis* vocalizations were generated using Raven sound analysis software (Version 1.1, Cornell Laboratory of Ornithology, NY, USA, sampling frequency = 22.05 kHz, discrete fourier transform (DFT) size = 128 samples, frequency resolution = 248 Hz, time resolution = 5.8 ms, 99% frame overlap). Measurements of these sounds were compared with those measured previously for other swiftlet taxa (Price *et al.* 2004). On the basis of evidence for the presence of echolocation sounds in *A. papuensis*, we reconstructed the evolution of echolocation in the swiftlets by mapping the presence and absence of this character on our molecular phylogeny using simple parsimony in MacClade (Version 4.06, Maddison & Maddison 2003).

RESULTS

We captured 35 birds within a 1-h period from 02:00 to 03:00 h on 18 November 2002. Of these birds, toes were counted on 25 individuals. All 25 had only three obvious toes, but detailed examination of three of the 25 individuals revealed a vestigial

hallux beneath the skin of the tarsus. Eight birds were prepared as museum skin (SEA 392–394, 396), skeletal (SEA 389, 395) or spirit (SEA 390, 391) specimens. Two of these (SEA 389, 395) were deposited in the PNG National Museum; the remaining specimens were deposited in the Museum of Natural History, University of Kansas (voucher number of tissue sample sequenced is SEA 389).

During the previous day, 17 November, S.E.B. and D.H.C. carefully searched all accessible regions within Losavi Cave and found no evidence of *A. papuensis* individuals. No birds were seen or heard and no nests were found. The capture of so many individuals outside the cave later that night suggests that birds had been roosting or nesting nearby, perhaps under overhangs or in small tunnels outside the cave entrance.

Parsimony and maximum likelihood analyses of *cyt b* and ND2 genes, excluding *H. gigas*, resulted in trees that were identical for relationships among *Collocalia* and *Aerodramus* species, including *Aerodramus papuensis*. Placement of *A. papuensis* as the sister taxon to all other *Aerodramus* received strong bootstrap support in all analyses (Fig. 1), with sequence divergences on the combined data set of 8.2–9.5% between *A. papuensis* and its congeners. Inclusion of *cyt b* sequences for *H. gigas* with the backbone tree either constrained (using *cyt b* data only) or unconstrained (using both *cyt b* and ND2) resulted in an identical position for this species as the sister taxon of *A. papuensis*, although this was not well supported in bootstrap analyses. Together these two species form the sister group to all other species of *Aerodramus* (Fig. 1). Phylogenetic relationships of other taxa were similar to those presented by Price *et al.* (2004).

Sounds recorded from *A. papuensis* individuals flying at night (Fig. 2) were similar in their acoustic features to the echolocation sounds recorded in other *Aerodramus* species (Medway & Pye 1977, Suthers & Hector 1982, Thomassen *et al.* 2004) and in the echolocating Pygmy Swiftlet (Price *et al.* 2004). As in these other echolocating taxa, Papuan Swiftlets produced stereotyped double clicks, each of which consisted of two broadband pulses of sound separated by a short pause of 15–22 ms, the second click louder than the first. Recordings of echolocation clicks in other species have generally been made within their roost caves or while birds were flying through the cave entrance at dusk or dawn (e.g. Medway 1967, Fenton 1975, Medway & Pye 1977, Fullard *et al.* 1993, Collins & Murphy 1994, Price

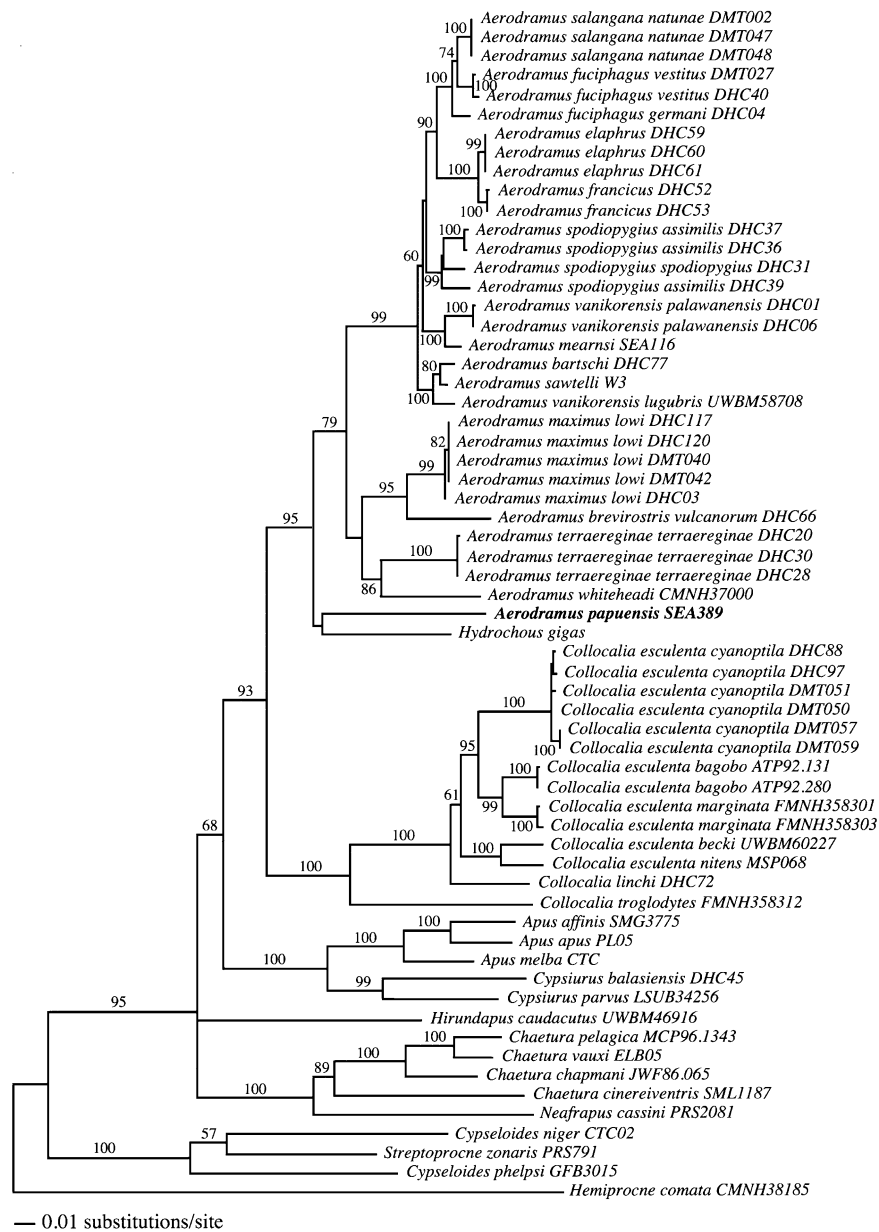


Figure 1. Most likely tree ($-\ln L = 17\,444.605$) resulting from combined unconstrained likelihood analyses of *cyt b* and ND2 sequence data using the GTR+I+G model with substitution rates A–C = 0.393, A–G = 13.588, A–T = 0.512, C–G = 0.188, C–T = 6.262, G–T = 1.000; base frequencies A = 0.330, C = 0.404, G = 0.065, T = 0.201; proportion invariant sites = 0.502; and shape parameter for the gamma distribution = 1.215. The sequence from the ND2 gene for *Hydrochous gigas* was counted as missing data. Numbers on branches indicate support from 100 bootstrap replicates (bootstrap values < 50% are not shown) and branch lengths are proportional to the number of substitutions.

et al. 2004). Our finding that *A. papuensis* uses echolocation while flying outside so late at night is therefore somewhat unusual.

Reconstructing the presence of echolocation on our maximum likelihood tree (Fig. 3) shows the ancestors of the *H. gigas/A. papuensis* clade, those of

the genus *Collocalia* and all ancestors shared between them as being equivocal for this character state. Echolocation has either been lost several times since its original appearance, been gained several times independently, or some combination of these possibilities.

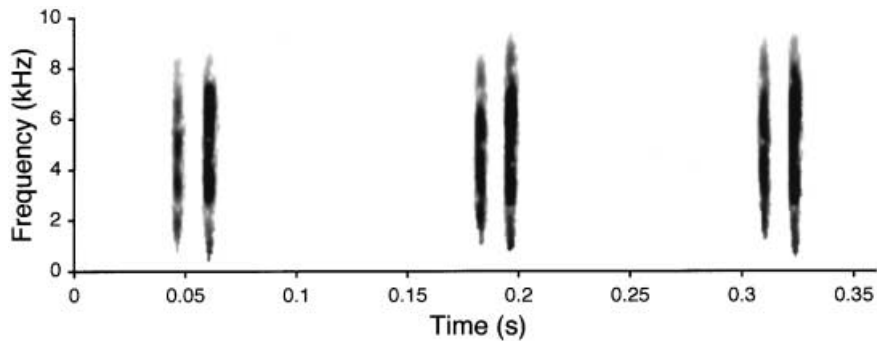


Figure 2. Spectrogram of double clicks produced by *Aerodramus papuensis* while flying outside of Losavi Cave, Papua New Guinea, between 02:00 and 03:00 h, 18 November 2002.

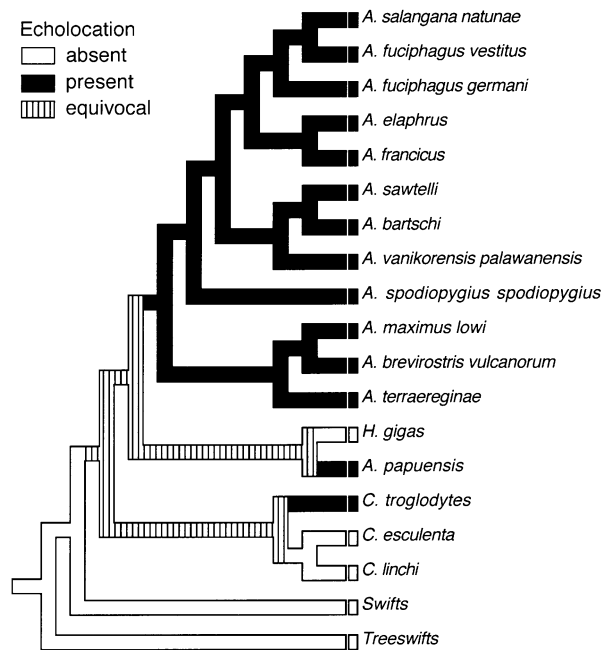


Figure 3. Echolocation reconstructed onto the maximum likelihood phylogeny of the swiftlets. The presence or absence of echolocation in taxa other than *Aerodramus papuensis* and *Hydrochous gigas* are taken from Price *et al.* (2004).

DISCUSSION

The Papuan Swiftlet *Aerodramus papuensis* has been considered conspecific with *A. whiteheadi* in the past (Chantler *et al.* 2000). Our results do not support this taxonomy. Rather, analyses of two mitochondrial genes using a variety of methods show *A. papuensis* as relatively distant to all other *Aerodramus* taxa. Similar to previous molecular studies of swiftlet phylogeny (Lee *et al.* 1996, Thomassen *et al.* 2003, Price *et al.* 2004), our results provide strong support

for monophyly of the swiftlets (Collocaliini) and for the placement of *Aerodramus* and *Collocalia* as separate clades. Our finding of a sister relationship between *A. papuensis* and *Hydrochous gigas*, however, was surprising. Previous studies not including *A. papuensis* have suggested paraphyly of the genus *Aerodramus* by placing *H. gigas* within that clade (Lee *et al.* 1996, Thomassen *et al.* 2003); however, none of these previous results was well supported. Our placement of *H. gigas*, although also not strongly supported, is nevertheless the first to show this species at a consistent position using multiple analyses. Including ND2 sequence data in addition to *cyt b* will surely help in resolving the position of this enigmatic swiftlet.

Distant molecular relationships between both *A. papuensis* and *H. gigas* in comparison with other swiftlet taxa are consistent with a variety of morphological and behavioural characters in which these birds are unique among the Collocaliini. For example, *A. papuensis* is the only swiftlet that has three toes instead of four. It is also one of the few species in this group reported to use echolocation while active outside of caves at night (although nocturnal activity has been reported in at least one other swiftlet, *Aerodramus unicolor*, Chantler *et al.* 2000). Similarly, *H. gigas* is much larger than most *Aerodramus* and *Collocalia* swiftlets (approximately 37 g vs. 14 g and 6.5 g, respectively; Lee *et al.* 1996) and is the only species that nests behind or near waterfalls (Medway & Wells 1976, Chantler & Driessens 1995, Chantler *et al.* 2000). Our finding that these two species are each other's closest relatives was not predicted by morphology or known behaviours but was nevertheless supported by our molecular data (Fig. 1).

Our maximum likelihood phylogeny suggests several possible scenarios for the evolution of echolocation

in the swiftlets (Fig. 3): (1) this ability arose once in the ancestor of the swiftlets and was subsequently lost in *H. gigas* and in the lineage leading to *Collocalia linchi* and *C. esculenta*; (2) it evolved at least three times independently in *A. papuensis*, *C. troglodytes* and ancestors of the rest of the genus *Aerodramus*; or (3) some combination of the previous two scenarios. Simple parsimony does not resolve which of these possibilities is most likely.

Based on acoustic features, however, the orientation clicks of *A. papuensis*, *C. troglodytes* and most *Aerodramus* species are notably similar in comparison with sounds of other echolocating birds, a pattern that could indicate homology. In particular, the former taxa use double clicks with similar intraclick intervals (15–20 ms, Price *et al.* 2004), whereas oilbirds (Griffin 1958) and at least two other *Aerodramus* species (Medway & Pye 1977, Fullard *et al.* 1993) generally produce single clicks. Evidence suggests that all swiftlets and oilbirds have the capacity to produce both single and double clicks (Suthers & Hector 1982, 1985, Thomassen *et al.* 2004), so this similarity is not due solely to physiological constraints on click design.

Furthermore, evolutionary losses of complex character traits such as echolocation are often thought to be more likely to occur than independent gains (Omland 1997, Cunningham *et al.* 1998), so it seems plausible that echolocation arose once and was lost twice on the swiftlet tree as opposed to alternative scenarios (e.g. gained three times, gained twice and lost once, etc.). Mapping echolocation onto our maximum likelihood phylogeny with losses made even slightly more likely than gains (losses 1.1× more likely) resolves the ancestor of the Collocaliini as having echolocation and supports the idea that this ability was lost in two separate lineages. These reconstructed patterns are altered, however, if *H. gigas* is moved to a position as sister taxon to all *Aerodramus*, a topology that favours the independent appearance of echolocation in *Aerodramus* and *C. troglodytes*. More phylogenetic data on *H. gigas* and additional methods of ancestral state reconstruction (e.g. Pagel *et al.* 2004) will be needed to help solidify our understanding of the evolution of echolocation in these birds.

Echolocation presumably evolved in the swiftlets as an adaptation allowing birds to roost and nest in caves, away from most visually orienting predators or competitors (Fenton 1975, Medway & Pye 1977). The nesting ecology of swiftlet taxa, where known, is generally consistent with this idea. Nests of previously studied echolocating species, such as *Collocalia*

troglodytes (Price *et al.* 2004) and a variety of *Aerodramus* taxa (Chantler & Driessens 1995, Chantler *et al.* 2000), are found most often in complete darkness within caves (but note that the *A. brevirostris vulcanorum* in Fig. 1 was one of several nesting in broad daylight in a volcanic crater in Java; D.H.C. pers. obs.). Non-echolocating species, by contrast, generally nest in areas exposed to daylight. For example, *Collocalia esculenta* and *C. linchi* nest on a variety of vertical substrates, including cliff faces, buildings and cave entrances (Fenton 1975, Chantler & Driessens 1995), and the aptly named Waterfall Swiftlet *H. gigas* builds its nests behind or near waterfalls (Medway & Wells 1976). If these species had cave-nesting, echolocating ancestors, the loss of echolocation with the movement of these lineages out of caves suggests a cost to this ability, most likely in the form of developmental investments for the neural and structural specializations necessary for orientation by sound (Suthers & Hector 1982). The historical loss of echolocation would make sense in *H. gigas*, as the loud waterfalls near which it nests are especially ill-suited environments for echolocation.

The nesting habits of *A. papuensis* remain unknown. However, our inability and the inability of previous investigators (reported in Chantler *et al.* 2000) to find nests of this species despite previous surveys of caverns, including Losavi Cave (M. Tarburton pers. comm.), suggests that, like *H. gigas*, this species might not nest inside caves. If so, the adaptive significance of echolocation in this bird would present somewhat of a mystery. Has echolocation been retained in this lineage from cave-nesting ancestors, and if so, why? The breeding and roosting behaviours of *A. papuensis* are subjects that clearly warrant further investigation.

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