

Swiftlets on islands: genetics and phylogeny of the Seychelles and Mascarene swiftlets

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Abstract: Populations on islands are isolated from mainland populations and are thus expected to diverge and speciate from mainland relatives. We investigated the phylogenetic position and taxonomic rank of the Seychelles and Mascarene swiftlets using nuclear (fibrinogen intron 7) and mitochondrial (cytochrome *b*) DNA sequences. Both sequences recovered a placement for these two swiftlets within a group of other echolocating swiftlets (*Aerodramus*). This agrees with previous results based on limited sequences and confirms a split in swiftlets between echolocating (*Aerodramus*) and non-echolocating species (*Collocalia*). The Seychelles and Mascarene swiftlets are 1.0% divergent in cytochrome *b* sequences suggesting they have been isolated for 500,000 years and merit species status as *Aerodramus elaphrus* and *Aerodramus francicus*. The distinctiveness of *Aerodramus elaphrus* and *Aerodramus francicus* emphasizes the need to develop conservation strategies for both of these species.

Key Words: *Aerodramus francicus*, *Aerodramus elaphrus*, Apodidae, cytochrome *b*, fibrinogen intron 7, echolocation

Island populations generally have small population sizes and are therefore often of conservation concern. Island populations are often genetically distinct from related mainland populations, which emphasizes the importance of preserving them. An important component of establishing priorities for conservation is the level of taxonomic distinctiveness of island populations, i.e. whether they are species, subspecies, or lack any appreciable differentiation from mainland relatives. Here we investigate these issues for two island bird species: the Seychelles swiftlet (*Aerodramus elaphrus* [Gmelin, 1789]) and Mascarene swiftlet (*A. francicus* [Oberholser, 1906]), which are endemic to the Seychelles and Mascarenes, respectively.

Swiftlets are small-bodied representatives of the family Apodidae. Members of the genus *Aerodramus* nest in caves and navigate using a crude form of echolocation (Chantler & Driessens 1995; Lee *et al.* 1996). Among swiftlets, which are distributed throughout Australasia and the South Pacific, *A. elaphrus* and *A. francicus* have the westernmost distribution and represent a biogeographic anomaly because no other species of swiftlet occurs within 2000 kilometres. The taxonomic status of these two species has varied among workers. Some authors place all swiftlets in the genus *Collocalia* (Gaymer *et al.* 1969; Chantler & Driessens 1995) while others separate the echolocating swiftlets into the genus *Aerodramus*, thus recognizing two major swiftlet genera (Lee *et al.* 1996). The species status of the Seychelles and Mascarene swiftlets has been questioned by some workers who consider them both subspecies of *A. francicus* (Gaymer *et al.* 1969; Penny 1974). Others separate them

into distinct species (Cheke 1987; Chantler & Driessens 1995; Lee *et al.* 1996). Lee *et al.* (1996) presented evidence from mitochondrial DNA sequences (cytochrome *b*) that *Aerodramus* and *Collocalia* are distinct genera and that the Seychelles and Mascarene swiftlets are genetically divergent species. Clayton *et al.* (1996) showed that the two species also have distinct subspecies of chewing lice (*Dennyus*), further supporting the distinctiveness of the host species. The goal of this study is to expand the genetic evidence from DNA sequences as a further aid to proper classification of the Seychelles and Mascarene swiftlets.

Methods

We extracted and amplified DNA from tissues of three individuals of *Aerodramus elaphrus* and two individuals of *Aerodramus francicus* according to the protocol of Johnson & Clayton (in review). We also extracted DNA from representatives of twelve other swift and swiftlet species including echolocating and non-echolocating species. Using PCR, we amplified both the mitochondrial cytochrome *b* gene and the nuclear β -fibrinogen intron 7 gene for these samples. We sequenced these PCR products and aligned them using the methods described in Johnson & Clayton (in review). We constructed phylogenies using parsimony and PAUP* (Swofford 1998) and performed bootstrap analyses (Felsenstein 1985). We also compared genetic distances between species to estimate the timescale of speciation in swiftlets.

Results

For the mitochondrial cytochrome *b* gene (1037 base pairs), *Aerodramus elaphrus* and *A. francicus* show 1.0% sequence divergence. All individuals of each species cluster together to the exclusion of samples from other species, making each species monophyletic for mitochondrial DNA (Fig. 1). In contrast to the relatively large divergences between *A. elaphrus* and *A. francicus*, sequences among individuals within each species are identical (0.0%). These two species fall within a monophyletic clade of echolocating swiftlets (Fig. 1). *A. elaphrus* and *A. francicus* are each other's nearest relative and the closest relatives (included in this study) to these two species are *A. salanganus* (Streubel, 1848) and *A. spodiopygius* (Peale, 1848), from which *A. elaphrus* and *A. francicus* differ by 2.2 - 2.5%. The cytochrome *b* sequence data support a deep split between echolocating (*Aerodramus* spp.) and non-echolocating (*Collocalia* spp.) swiftlets with 98% confidence in bootstrap replicates (Fig. 1).

These results are also supported by sequences from a nuclear gene for several swiftlet species. A phylogeny derived from fibrinogen intron 7 sequences (920 base pairs) confirms the deep split between *Aerodramus* and *Collocalia* (unpublished data). The nuclear phylogeny also supports the position of *A. elaphrus* and *A. francicus* as each other's nearest living relatives, that are in turn most closely related to *A. salanganus* and *A. spodiopygius*.

Discussion

DNA sequence data can resolve a phylogeny for a group of species, aid in determining species' boundaries, and provide an estimate of the timing of speciation events. Sequence data from independently sorting mitochondrial (cytochrome *b*) and nuclear (fibrino-

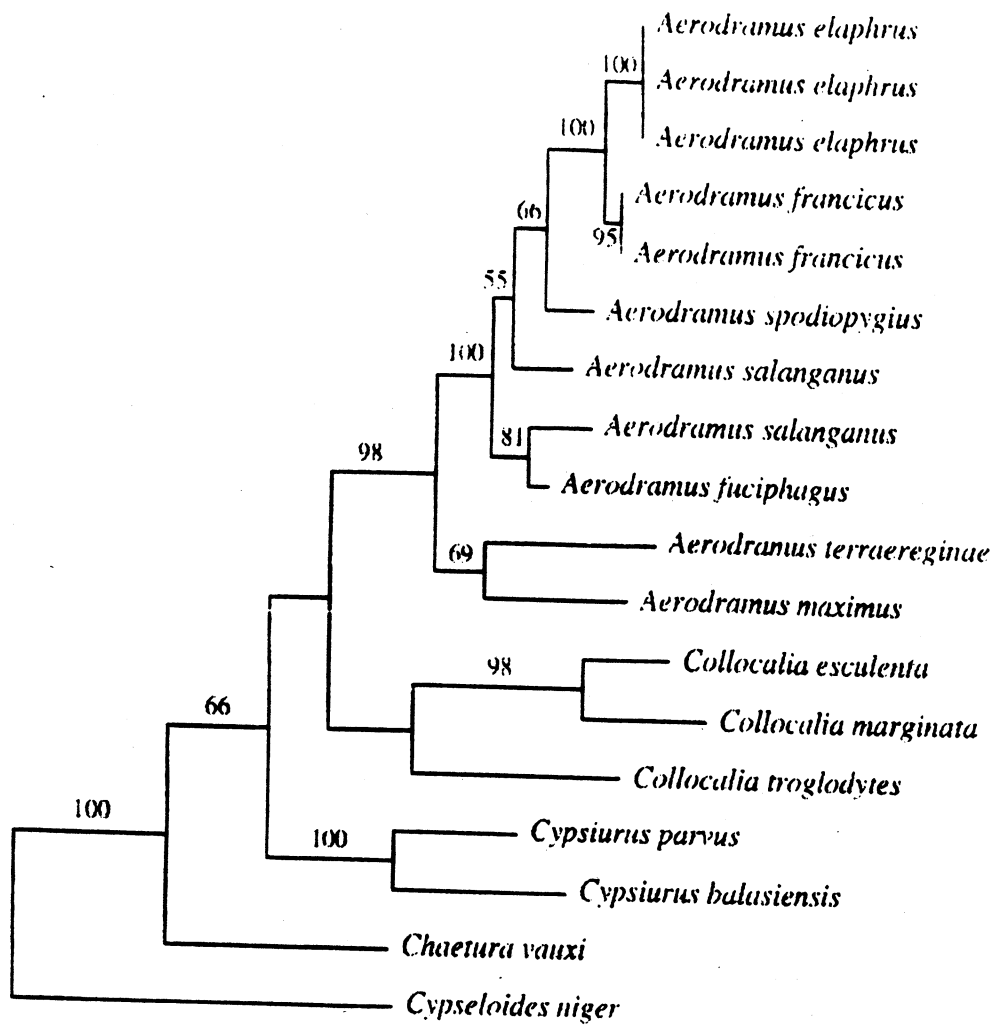


Fig. 1. Phylogeny for swiftlets (*Aerodramus* and *Collocalia*) derived from unordered parsimony of cytochrome *b* sequences, with three genera of swifts (*Cypsiurus*, *Chaetura* and *Cypseloides*) as outgroups. Only *Aerodramus* spp. are capable of echolocation. Branch lengths are proportional to reconstructed changes. Numbers on branches indicate bootstrap support from 1000 replicates. Unlabelled nodes received less than 50% bootstrap support.

gen intron 7) genes and swiftlets supports a pronounced split between the echolocating and non-echolocating species, consistent with the results of Lee *et al.* (1996) based on a shorter cytochrome *b* sequence. Thus, the phylogeny derived from these DNA sequences supports the recognition of *Aerodramus* and *Collocalia* as distinct genera of swiftlets. Two island swiftlets of conservation concern, the Seychelles swiftlet (*Aerodramus elaphrus*) and Mascarene swiftlet (*Aerodramus francicus*), fall within the genus *Aerodramus*, again confirming the results of Lee *et al.* (1996).

Sequences from the cytochrome *b* gene indicate that swiftlets from the Seychelles are identical and 1.0% divergent from swiftlets from Mauritius, which are in turn identical to other individuals on Mauritius. Using a molecular clock calibration for mitochondrial DNA of 2% per million years (Klicka & Zink 1997), we estimate that the Seychelles and Mascarene swiftlets have been isolated from each other for approximately 500,000 years with no gene flow. In addition, we estimate that these island species have been isolated from other swiftlets for approximately one million years, based on the genetic distance to their nearest relatives, but we are not able to determine which island was colonized first. Our data strongly support recognition of the Seychelles and Mascarene swiftlets as distinct species, highlighting the need for conservation efforts directed at both of these unique species.

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