Echolocation in Free-Flying Atiu Swiftlets (*Aerodramus sawtelli*)[1]

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ABSTRACT

Vocalizations of wild Atiu Swiftlets (*Aerodramus sawtelli* Holyoak 1974) were recorded as they entered and exited their roost/nesting cave on Atiu Island in the Cook Islands. The echolocation calls of the Atiu Swiftlet resemble those of other *Aerodramus* spp. in their short durations (1–3 msec), peak frequencies (6–7 kHz) and broad bandwidths (3–10 kHz) but are emitted as distinct single pulses rather than the double or multiple clicks typical of most swiftlets. Spectral analyses indicate that the birds do not adjust the peak frequencies of their calls as they fly within the cave and we suggest the bird does not systematically structure the frequency content of its calls. Birds decrease their interpulse periods upon entering the cave and increase them upon exiting, presumably in response to differing light levels. As they land at their roost/nest site, birds emit a train of low interpulse period calls that is occasionally followed by a vocalization that we suggest serves as an announcement to other birds on or near the nests.

Key words: Aerodramus sawtelli; *Atiu Swiftlet; Cook Islands; echolocation; Pacific; roosting behavior; spectral analysis; systematics; tropical birds; vocalization.*

ECHOLOCATION IN BIRDS HAS BEEN DESCRIBED for swiftlets (Apodidae) (Medway 1959, 1962a, b, 1965, 1966, 1967; Novick 1959; Harrisson 1966; Fenton 1975; Medway & Pye 1977; Pye 1980; Coles *et al.* 1987) and oilbirds (Steatornithidae) (Griffin 1953, Pye 1980, Suthers & Hector 1985). In swiftlets, the sounds are broad-band clicks with peak frequencies (PFs) between 1 and 16 kHz that are produced by the birds as they fly in the dark areas of their roost/nest caves. Swiftlets appear to use echolocation only for low resolution target discrimination and do not, like insectivorous bats, garner detailed information from the echoes of their clicks. Swiftlets are diurnal birds with large eyes and use vision to locate their insect prey (Medway 1962b). Bats that emit coherent echolocation calls (*i.e.,* insectivorous Microchiroptera) manipulate the frequencies within their calls to increase the information content of the echoes (Simmons *et al.* 1979). The unstructured, click-like quality of swiftlet signals (Pye 1980) suggests that frequency structure is not an important element in these calls and swiftlets use only temporal information to determine features about their targets.

Echolocating swiftlets, because of their cavernicolous and tropical habits, are difficult to study in the field and only a few of the acoustic studies of these birds have come from free-flying animals (Harrisson 1966, Medway 1967, Fenton 1975). In this paper we describe the acoustic characteristics of echolocation and social vocalizations of wild Atiu Swiftlets, *Aerodramus sawtelli* (known as Kopeka to the people of the Pacific island where this bird lives).

MATERIALS AND METHODS

This study was conducted on the island of Atiu (20°00′S, 158°07′W), in the Cook Islands during late June and early July 1989. Additional observations were made by JHF during a return visit in late May 1992. Atiu Swiftlets night roost and nest in two known caves: Anatakitaki (= Annataketake [Holyoak 1974]) illustrated in Figure 1, and Tu pu rainga, in the upraised ancient coral reef (makatea) that surrounds the central volcanic uplands.

Recordings were made of the birds with a Sony cassette recorder (Professional Walkman WM-D3) and microphone (Type PC-62) (system response sensitivity: 0.5–15 kHz ± 2 dB). The low bird populations of the cave allowed recordings of single
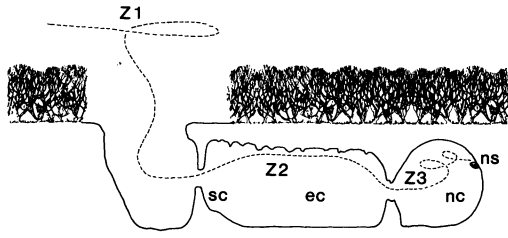
FIGURE 1.   Anatakitaki cave describing the different zones that the birds fly through en route to roosts: zone 1 (Z1)—above canopy; zone 2 (Z2)—entrance chamber; zone 3 (Z3)—deep cave; sc—stalactite columns; ec—entrance chamber; nc—roost/nest chamber; ns—roost/nest sites; dashed line describes typical path of a Kopeka as it flies through the cave.

birds as they flew into or out of the cave. To avoid frequency artifacts, only those pulses recorded from the bird as it faced the microphone were analyzed (approach phase calls). Recordings were examined with a digital fast Fourier transform (FFT) spectrum analyzer (Nicolet 100A Mini-analyzer) interfaced to an 80286 personal computer with an additional customized FFT program (Dawson & Fullard 1991). Figure 2 illustrates the spectral variables that were measured for the echolocation pulses. Spectral and temporal data from these analyses were tabulated and statistically examined with the computer. Simple linear correlations were performed on the acoustic parameters against the pulse sequence number as birds entered or exited the cave. For all analyses, statistical significance is assumed at $P < 0.05$.
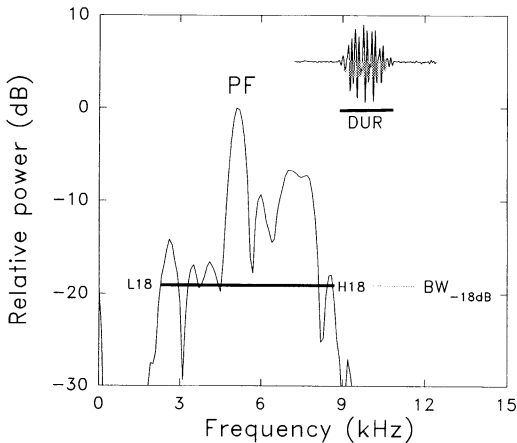

FIGURE 2.   Frequency spectrum and oscillogram (inset) of a Kopeka entrance echolocation call illustrating the parameters measured. DUR: duration (msec); PF: peak frequency (kHz); L18: lowest frequency 18 dB below PF; H18: highest frequency 18 dB below PF; BW_{-18dB}: bandwidth 18 dB below PF.

RESULTS

Most of our observations and all of our recordings of the Kopeka were done at Anatakitaki in the eastern makatea of Atiu. Censuses were taken of the birds as they left in the morning at 0615–0730 and as they returned in the evening at 1800–1915. We estimate that 180–230 birds resided in Anatakitaki at the time of our visit. An examination of the roost sites in Anatakitaki revealed that the birds had not begun nesting during our visits. We collected no voucher specimens since only one species of *Aerodramus* is known from Atiu (Holyoak 1974, Pratt et al. 1987, Tarburton 1990).

Antakitaki is approximately 4.5 m high and 12 m wide at its entrance expanding into an entrance chamber (Fig. 1) that is 26 m long by 4–6 m high by 25 m wide (at its broadest point). From here it narrows into smaller nesting chambers (Fig. 1) where the ceiling drops to 2–3 m high in the furthest reaches. Birds will nest in the lighter portions of the cave (Tarburton 1990), but during our study most roosting birds were in the nesting chambers. The birds' flight entrance to Anatakitaki is at the bottom of a vegetated, 5 m deep bowl and they enter the cave from this depression through vertical passageways formed by 6 columns of stalactites. To enter Anatakitaki, birds descend from the open air above the forest canopy (Fig. 1) into the twilight below the trees. From here they fly through the stalactite passageway into the entrance chamber (Fig. 1) where the light dims quickly. While in the entrance chamber, the birds fly close (50–100 cm) to the ceiling (cf. Harrisson 1966) and continue into the furthest and darkest reaches of the cave to their roosts (Fig. 1). The roost/nest chamber is blocked from the light of the entrance chamber by a series of large columns and turns (not shown in Fig. 1) and, although light levels in the roost/nest chamber were not quantified, our eyes registered complete darkness.

Atiu Swiftlets begin echolocating immediately upon entering Anatakitaki, rapidly reducing their interpulse periods (IPPs) as they fly into the entrance chamber. They continue echolocating within the roost/nest chambers and during brief forays around the cave itself. When they exit the cave they begin echolocating within the roost/nest chambers and continue until they reach the stalactite columns of the entrance chamber. We divided the flight echolocation recordings into entrance and exit sequences and have examined the calls for differences in temporal and/or frequency structure. Although recording the birds inside the cave resulted in substantial

TABLE 1.   *Acoustic characteristics (means ± standard errors) of the echolocation pulses (Fig. 2) of the birds as they entered and exited the Anatakitaki cave. Ten different birds were analyzed for all measurements; number of approaching echolocation pulses = 10.*

Parameter	Entrance	Exit	t
DUR[a]	2.24 ± 0.04	2.41 ± 0.04	−3.14*
IPP[b]	107.1 ± 2.8	186.1 ± 6.4	−11.2*
PF[c]	6898 ± 60	6961 ± 79	−0.63
BW$_{-18dB}$[d]	6052 ± 83	6005 ± 96	0.373

* Significant at the $P < 0.05$ level.
[a] Duration (ms).
[b] Interpulse period (msec).
[c] Peak frequency (Hz).
[d] Bandwidth (Hz) 18 dB below PF.

echo noise, the spectral analysis program we used allowed us to separate the emitted pulse from its echo by means of an operator-controlled cursor positioning feature. A typical echolocation call is illustrated in Figure 2. All of the pulses recorded ($N = 670$) were short clicks (1–3 msec) emitted as distinct single pulses with peak frequencies within the human-audible range of 6–8 kHz and with broad bandwidths (Fig. 2, Table 1). Although our recording system was flat only to 15 kHz, we are confident from the steep high frequency roll-offs in the FFT spectra that no substantial signal energy exists at frequencies above 12 kHz. Echolocation clicks were also detected from birds as they foraged for insects in the failing light of the late afternoon. To our ears these calls were considerably fainter than those heard from clicking birds of equal distance (2–4 m) in the cave and appeared to be emitted as the birds entered the shadows of the bushes they were foraging near.

The temporal and spectral characteristics from the approach phase pulses recorded from ten different birds as they either entered the cave in the evening or exited in the morning were correlated against the bird's relative position in the cave. We believe that these data were not pseudoreplicated since no birds re-entered or re-exited the cave during the recordings. As we were not certain of the position of each bird as it began echolocating, we performed individual correlations on the entrance/exit echolocation sequences of each bird. Neither of the spectral parameters (peak frequency, −18 dB bandwidth) revealed significant correlations in any of the birds as they flew towards the microphone during either their entrances or exits. Analyses made of clicks recorded as the bird flew away from the microphone suggest that higher frequencies are reduced (possibly as a result of the acoustic shadow of the bird's body). In contrast to the spectral data, interpulse periods did correlate to the relative position

of individuals as they entered and exited the cave (Fig. 3). Exiting birds emitted fewer calls in general, and these were significantly longer and had lower interpulse periods than those issued by entering birds.
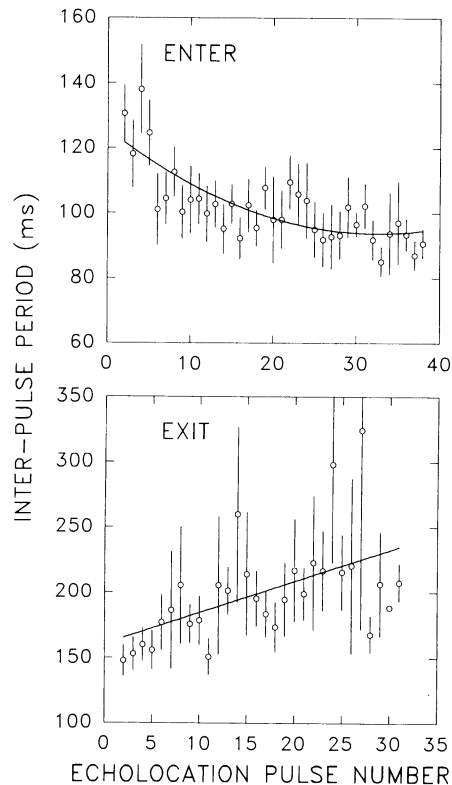

FIGURE 3.   The average ± standard errors IPPs of all the birds recorded as they entered (top) and exited (bottom) Anatakitaki. Birds were recorded ($N = 10$ [ENTER]; $N = 10$ [EXIT]) from the first pulse recorded (echolocation pulse number 1). A second order polynomial regression is fitted to the ENTER data ($r^2 = 0.77$, $P < 0.05$); a linear regression is fitted to the EXIT data ($r^2 = 0.53$, $P < 0.05$).
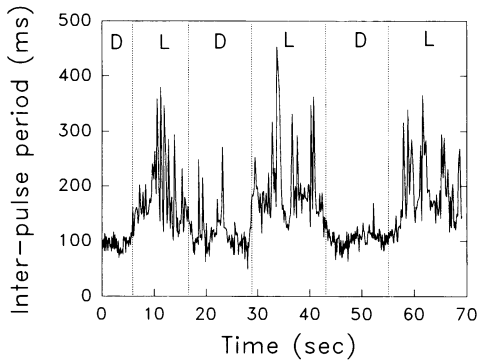
FIGURE 4.   Changes in one Kopeka's IPPs during sequential bouts of light (L) and dark (D) as it flew in the entrance chamber of Anatakitaki cave.

The longest periods recorded for echolocation calls were from birds as they prepared to exit the cavern into the forest light. Although exiting birds emitted significantly longer pulses than entering birds (Table 1), durations were not correlated to the relative position of the bird in either entrance or exit flights.

To examine the effect of cave illumination on the Kopeka's IPPs we released one bird in the Anatakitaki entrance chamber and recorded its calls in the presence and absence of light from a 3 V flashlight (Fig. 4). Once released, the bird circled near the chamber ceiling for 5–7 minutes allowing for six light/dark exposures. Although the clicks emitted during the two conditions were spectrally similar, the bird quickly changed its IPPs when the
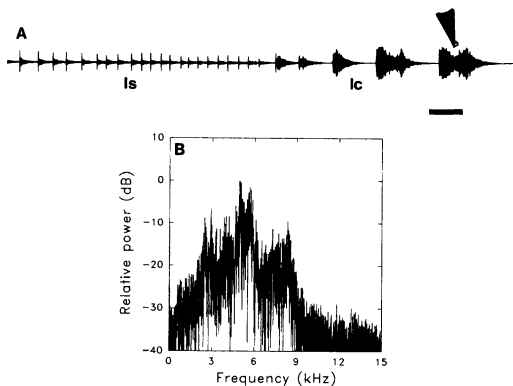

FIGURE 5.   (A) Oscillogram of echolocation landing sequence (ls) and landing call (lc) from a single bird as it approached and landed upon its roost in the deepest section of the cave. (B) Fast Fourier transform frequency spectrum of one of the syllables (marked by arrowhead in A) of the landing call. Scale bar for oscillogram, 250 msec.

light was applied, using significantly longer median periods ($Z = 16.99$, $P < 0.05$).

As birds approached their roost sites in the deepest recesses of the cave (Fig. 1), their echolocation call IPPs rapidly decreased just as they landed. These rapid click sequences were only heard from birds in the cave as they prepared to land so we have labelled them landing sequences (Fig. 5A). While in the nest/roost caves we occasionally heard a distinctive vocalization from birds at the end of their landing sequences. Since we only heard this call from birds in the cave as they approached their nest we have named it the landing call (Fig. 5A). The landing call begins with 2–3 echolocation-like short clicks followed by 3–4 longer (200–250 msec) chirps. Although the landing call sounds more tonal, it also has broad bandwidths with peak frequencies ranging from 5–7 kHz (Fig. 5B). We heard these calls only from birds that were very near their roosts and on 6 occasions when we heard them and illuminated their nest sites, the birds had just landed. Calls that resembled the two-note pattern of the landing call were also heard from birds flying above the tree canopy in the makatea but we were unable to observe the behavior of the birds that were emitting them.

DISCUSSION

The works of Medway (1959, 1962a, b, 1967), Novick (1959), Griffin and Suthers (1970) and Fenton (1975) leave little doubt that the function of the clicks emitted by swiftlets are for echolocation within the dark confines of their caves. The eyes of *Aerodramus* spp. are large and their predation on small insects (Medway 1962b, Medway & Pye 1977) suggests that vision is the swiftlet's prey detection system and their echolocation is of a low resolution kind similar to the tongue clicks of *Rousettus* spp. bats (Sales & Pye 1974). Although the Atiu Swiftlet echolocates mainly within its caves, we detected faint clicks from birds foraging in shadows (*cf.* Harrisson 1966) in the failing light of the evening. These birds were hunting near bushes when their clicks were heard and we propose that extra-cavernicolous echolocation in the Kopeka is also for the detection of obstacles.

The fact that swiftlets did not adjust the peak frequencies of their clicks as they entered or exited the cave suggests that they do not systematically manipulate the spectral design of their clicks in response to changing light levels. The birds, however, exhibit marked changes in their click IPPs as they fly through their cave, likely from the differing

resolution requirements of the birds. Similar to insectivorous bats increasing their pulse rates as they approach targets, Kopekas emit shorter IPPs upon encountering darker situations where obstacles become harder to see. The shortest IPPs recorded came from birds in complete darkness that were about to land on their roosts (cf. *Steatornis* [Pye 1980] and *A. spodiopygia* [Coles et al. 1987]). These landing sequences resemble the terminal sequences emitted by insectivorous bats as they close with their prey (Simmons et al. 1979).

There are, to date, no reports of the social vocalizations or their function in *Aerodramus* spp. and our description of the landing call is qualitative in the absence of detailed behavioral observations. Since the landing call was only issued in the cave as birds approached their roosts, we suggest that this call serves as a warning announcement to individuals on or near the nest (both sexes share in nest-brooding in swiftlets [Medway 1962a]). The Atiu Swiftlet nest, like those of Asian species (Medway & Pye 1977), consists of vegetable matter fastened onto the bare wall face and collisions with resident birds could prove fatal for nestlings. Tarburton (1990) reports that a major cause of nestling mortality on Atiu results from the birds falling out of their nests. The fact that a similar two-note call was heard from birds outside the cave suggests that this vocalization may be a general agonistic signal that also serves in-flight social functions.

To date, only one other swiftlet has been described as emitting single clicks (*Aerodramus maximus* [Medway & Pye 1977]) and those of the Atiu Swiftlet are unique in their distinctly single nature (the oscillograms of *A. maximus* presented in Medway & Pye [1977] suggest these could be of a multiple click design). Single clicking may represent an inherent flexibility in the vocalization mechanism of *A. sawtelli* allowing these birds to avoid pulse/echo overlap. When aerially feeding bats approach their targets, they characteristically commence a "terminal" echolocation sequence, one in which the durations and IPPs of the emitted pulses become shorter and their intensities fainter. Alternatively, double clicking may allow individuals to discriminate their echolocation calls from those of others during crowded flights by means of the specific durations of their intra-doublet times (P. Faure pers. comm.). The low cave population densities of the Atiu Swiftlet may have rendered this requirement unnecessary. The geographically closest swiftlet to the Kopeka whose echolocation has been quantified prior to our study is *A. spodiopygia*, who produces a double click (single pulses are occasionally produced by *A. spodiopygia* [Suthers & Hector 1982], but these were under surgical conditions) and the single pulse design of *A. sawtelli* may indicate a change in eastern Pacific swiftlets. If so, we predict that the Marquesas Swiftlet, *A. ocistus*, also uses a single pulse design in its echolocation.

Like many *Aerodramus* spp., the taxonomy of *A. sawtelli* is poorly defined (Pratt 1986) and its relationship to the echolocating Marquesas Swiftlet, *A. ocistus* and the putatively nonecholocating Tahiti Swiftlet, *A. leucophaeus,* unsure (Pratt et al. 1987, Holyoak & Thibault 1978, Sibley & Monroe 1990). The subspecific rank for *A. sawtelli* from *A. leucophaeus* (Holyoak 1974, duPont 1976, Mayr & Vuilleunier 1983) seems unlikely considering the different echolocation abilities of the two birds. Until detailed phylogenetic analysis becomes available, we suggest that *A. sawtelli* is a distinct species, limited to Atiu Island. Regardless of its precise taxonomic state, the Atiu Swiftlet numbers only 360–460 birds and should be considered potentially endangered since only two breeding caves are known.

ACKNOWLEDGMENTS

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