

## Echolocation acuity of the Palawan Swiftlet (*Aerodramus palawanensis*)

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**Abstract** -- Echolocation acuity trials were conducted on Palawan Swiftlets (*Aerodramus palawanensis*) under natural conditions in Palawan, Philippine Islands. Detection of 3.2 mm diameter obstacles was significantly less than for 6.3 mm and 10 mm obstacles. These results are consistent with previous laboratory trials conducted on other swiftlets. They confirm that although echolocation is used for orientation in cave nesting and roosting areas it is unlikely to be effective in detecting their typically small (< 5 mm) food items.

### Introduction

The ability to use echolocation or animal sonar is a widespread and well studied specialization among bats of the suborder Microchiroptera (Griffin 1958, Vincent 1963, Simmons *et al.* 1975, Busnell and Fish 1980). Among birds, echolocation is known only for the Oilbird (*Steatornis caripensis*) a unique cave nesting caprimulgid of northern South America (Griffin 1954, Konishi and Knudsen 1979) and most, if not all, of the widespread species of cave swiftlets (*Aerodramus* sp.) (Medway and Pye 1977) which occur from the western Indian Ocean islands of Mauritius and Reunion eastward to the islands of the southwest Pacific ocean (Sibley and Monroe 1990). The echolocation sounds utilized for orientation by birds are brief bursts or audible clicks lasting for a few milliseconds with a repetition rate of 3-20 clicks per second (Novick 1959, Griffin and Suthers 1970, Medway and Pye 1977, Fullard *et al.* 1993). The frequency range of these clicks is from 1-16 kHz (Medway and Pye 1977, Fullard *et al.* 1993) and there are no ultrasonic frequencies as typically found in microchiropteran pulses (Cranbrook and Medway 1965). The several tests of the acuity of echolocation in *Aerodramus* swiftlets (Griffin and Suthers 1970, Fenton 1975, Griffin and Thompson 1982, Smyth and Roberts 1983) have indicated that it is probably only utilized for flight orientation within caves where they nest and roost and not for foraging. However, most of the tests of swiftlet echolocation acuity have involved small numbers of individuals flying in laboratory conditions or a man-made mine shaft. We

report here similar experiments conducted with the Palawan Swiftlet (*Aerodramus palawanensis*) under natural conditions in a large nesting and roosting cave.

### Methods

These experiments were conducted in the underground river cave in St. Paul River Subterranean National Park, Palawan, Philippine Islands from 14-21 September 1990. The tests were conducted in a side channel off the main cave about 200 m from the entrance. This site was in constant total darkness. The test apparatus consisted of two bamboo poles erected next to the rock walls of the channel and connected by a lowerable rope, ca. 6 mm in diameter, stretched between pulleys. Suspended from this rope were 12 test obstacles consisting of 3.6 m lengths of nylon or manila rope 10 mm, 6.3 mm or 3.2 mm in diameter. The test obstacles (ropes) were centered 30 cm apart which allowed about another 30 cm space on either side between the outermost rope and the rock wall. Depending upon the tidal influenced water level in the cave the test obstacles stopped near the water surface or were about 50 cm above it. Small metal bells were attached to the bottom of each test obstacle as a further aid in detecting contact by a flying bird. Twenty four of twenty six separate trials with the several test obstacles were conducted between 16:45 and 20:00 when large numbers of swiftlets were returning to roosting sites in the cave; two additional trials were conducted from 10:20-11:30. Observations were

made of individual swiftlets which either passed through the apparatus without striking a test obstacle (= a pass), struck a test obstacle (= a hit), or turned back before passing through but after having approached to within approximately 2 m of it (= a turn). Visual observations were made under two sets of conditions. The first was under very low light conditions achieved by reflecting a small incandescent headlamp beam off the ceiling above and slightly back from the test apparatus. This gave just enough light for the swiftlets to be seen and their performance quantified, but not enough illumination to allow them to decrease their utilization of echolocation. Elsewhere in the cave when either bright lights were used or when near the mouth of the cave and natural light was available, we noticed a clear decreased utilization of echolocation. Under these brighter light conditions, but not during the acuity trials, echolocation clicks were reduced in emission rate or were discontinued altogether (personal observation). The second method of observation entailed the use of a battery powered infrared light source to illuminate the test apparatus and the observation of the swiftlets by means of a night vision scope. Again, no diminution of echolocation click emission rate seemed to occur under these conditions. In both observation conditions the birds' performance was thus thought to be strictly on the basis of their ability to detect the test obstacles by echolocation alone.

We recorded a total of 1554 interactions in the form of 716 passes and hits and 838 turns in test and control observation periods. As all of the swiftlets observed were free-flying and unmarked the total number of separate individuals observed could not be determined; it is quite possible that observations were made of the same individual's performance on more than one day. Many thousands of swiftlets utilized the entire 8.2 km long underground river cave with some nests located at least 4 km from the cave mouth (Coleman 1981). A vastly smaller component of the population including those individuals with nests or roosts in the immediate vicinity of the test apparatus, or which used the channel to reach other more remote side chambers of the cave, were likely to have been observed during our experiments.

The taxonomy and identification of swiftlets, particularly in the field, is very confusing. Recent reviews of the Philippine Island swiftlets (Dickinson 1989, Sibley and Monroe 1990) indicate the presence in Palawan of a swiftlet which can be considered either as an endemic subspecies, *palawanensis*, of the widespread Mossy-nest Swiftlet *Aerodramus vanikorensis* (Dickinson 1989) or an endemic species *A. palawanensis* (Sibley and Monroe 1990). In light of several distinctive aspects of this swiftlet (Collins,

unpublished) and until more definitive information is available, we follow Sibley and Monroe (1990) in giving *palawanensis* full species status. Our observations and prior field work by Coleman (1981) indicate that the swiftlets of the underground river are attributable to this species. This was further confirmed by comparison of museum specimens and a voucher specimen (#7391) housed in the ornithological collections of California State University, Long Beach. This specimen was one of a total of 19 swiftlets, randomly captured in the underground river cave, which were weighed, measured and examined before release, all of which seemed to belong to this single species (Collins, unpublished). Two other non-echolocating species, the Glossy Swiftlet, *Collocalia esculenta* and Pygmy Swiftlet, *C. troglodytes* were seen near the mouth of the underground river cave but were never seen to penetrate beyond the area of natural light (personal observation).

Echolocation acuity and obstacle avoidance were judged by the percent passes and hits of birds flying through the apparatus and also by means of a model formulated by Smyth and Roberts (1983) of a theoretical missile the same width as the wing span of the swiftlets traveling through the test apparatus. This model determines that the probability of a bird striking a test object to be  $k(t+m)/D$  where  $k$  is the number of test obstacles of diameter  $t$  stretched across a passage with a width  $D$ . The width of the missile or wingspan of the swiftlet is  $m$ . The number of obstacle strikes ( $S$ ) compared to the total number of flights ( $N$ ) should be approximately equal to  $k(t+m)/D$  if the bird is flying at random. Thus the ratio ( $R$ ) of  $k(t+m)/D$  over  $S/N$  can be used to indicate the degree of randomness of the swiftlet's flight performance. An  $R$  value equal or close to 1 indicates random flight independent of the obstacles, and a value appreciably greater than 1 indicates avoidance behavior. An  $R$  value below 1 would indicate deliberate collisions with the obstacles or at least a collision rate greater than predicted by random flight. As also noted by Smyth and Roberts (1983) "this method of analysis is independent of the distance between obstacles, or between an obstacle and the side wall, providing such distance is greater than  $m$ ." In our calculations a wing span ( $m$ ) of 28.5 cms was used which is slightly less than the maximum (stretched) wing span (30.16 cm +0.73 SD; Collins unpublished) but more closely approximates the normal wing span of this swiftlet in flight.

## Results

The duration of each observation period varied according to the number of birds passing the test

apparatus. Thus we have chosen to present data on passes, hits or turns as percentages of the total number of birds observed during each of the observation periods. Before analysis of variance was conducted, the data were arcsine transformed (Sokal and Rohlf 1981). These data were then tested for normality by Lilliefors test and homogeneity of group variance by Box's small sample F approximation for cell counts less than 10; both were not significant (SYSTAT 1990) indicating parametric statistics are appropriate. Since a T-test of within group trials for each of the three test obstacle sizes indicated no significant difference between the percent hits observed under dim light and infrared light ( $T=0.092$ ,  $P>.05$ ) these two types of observation data were pooled in the subsequent analyses.

An ANOVA indicated that there were significant differences between the percent hits for each of the three obstacle sizes ( $F = 13.3$ ,  $P<0.001$ ). Tukey's HSD multiple comparisons indicated that hits of 3.2 mm obstacles was significantly higher than those for both 6.3 mm and 10 mm obstacles while there was no significant difference between the percent hits of the 6.3 mm and 10 mm obstacles. When performance is analyzed as R values (Table 1, Figure 1) all three obstacle sizes appear to be avoided substantially more often than predicted for random flight, although performance with the smallest obstacles is substantially below that for the other two sizes of obstacles. An ANOVA analysis of the percent successful passes through the apparatus also showed a between group significant difference ( $F= 8.85$ ,  $P<0.001$ ). Included in this analysis were 4 control tests in which the number of flights through the apparatus area were counted at a time when the cross rope and test obstacles had been lowered to water level. The percent passes during these control periods were significantly higher than the percent passes for all obstacle tests. However, the control periods should be considered more a measure of the normal rate of swiftlet flight traffic through the test area. Accordingly when compared to the sum of both passes and hits by swiftlets passing through the test

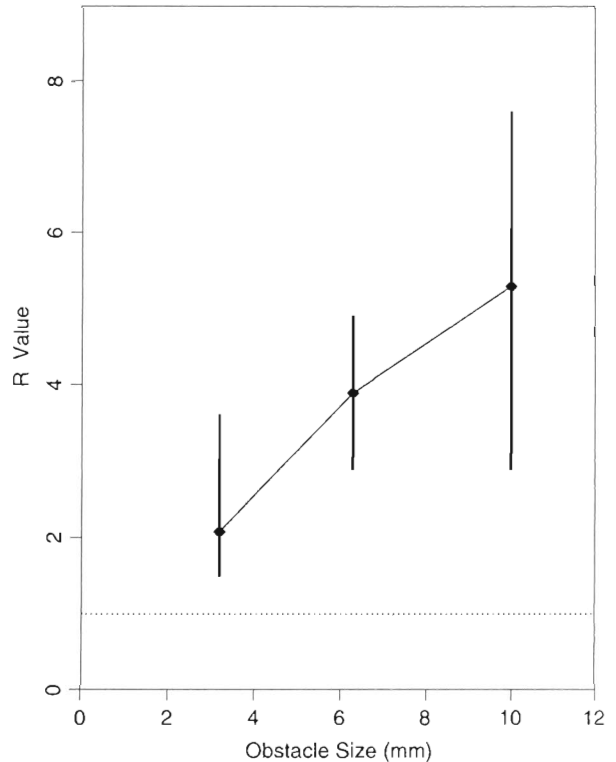


Figure 1. R values for echolocation acuity in Palawan Swiftlets. Random performance ( $R = 1$ ) indicated by dotted line. Vertical bars indicate range; lines connect means. See text for calculation of R values.

apparatus the difference is not significant. Similarly, there was no significant difference between the percent turns without any of the obstacles present and the turns made when all of the test obstacles were in place. This suggests that there was not an appreciable difference in the flight behavior of the swiftlets and the rate at which they passed through the test area either when the test apparatus was in place or when it was not. For turns, this may be due to either the swiftlets having sufficient acoustic acuity and memory to note the presence of an inflatable boat on the water and two bamboo poles leaning against the

Table 1. Results of echolocation acuity trials with *Aerodramus palawanensis*.

Obstacle Size (mm)	trials (N)	Total observations	Passes (%)	Hits (%)	Turns (%)	R Values mean (SD)
3.2	15	433	29.1	28.9	42.0	2.08 (0.61)
6.3	4	208	31.7	10.6	57.7	3.91 (0.93)
10	7	671	27.9	7.3	64.8	5.33 (1.70)
(Controls)	4	242	58.3	—	41.7	—

walls and reacting accordingly, or the normal maneuvering in the chamber, particularly while approaching nests and roosting sites in the vicinity of the test apparatus. We favor the latter interpretation.

## Discussion

A detailed comparison of these data with those presented by earlier workers (Medway 1967, Griffin and Suthers 1970, Fenton 1975, Griffin and Thompson 1982, Smyth and Roberts 1983) is in part confounded by differing methodologies as well as possible interspecific differences. However, the observed differences may be more apparent than real. The electronic technique used by Smyth and Roberts (1983) for detecting obstacle hits for *A. spodiopygius* was more precise than any of the ones used in the other studies. Any contact, including a light brushing by the outer primary feathers of the wing would be scored as a hit. However, Griffin and Suthers (1970) observed that "even in the light [*A. vanikorensis*] avoided obstacles in only about 75% of the trials, probably because gentle touches with the primary feathers caused little discomfort" and that since "the objects were clearly visible, these contacts... must have been due to a failure to dodge the obstacles rather than a lack of sensory information about their location." Field observations of the White-throated Needletail (*Hirundapus caudacutus*) in Australia (Althofer 1937), Vaux's Swift (*Chaetura vauxi*) (Collins 1971) and White-throated Swift (*Aeronautes saxatalis*) (T. Ryan, personal communication) in California confirm that casual contact with naturally occurring environmental obstacles, particularly vegetation, occurs under natural conditions. This may also be a rather routine occurrence in Palawan Swiftlets' natural environment. Thus in experiments of echolocation acuity not all observed hits may indicative of an inability to echolocate the test objects. As noted by Cuthill and Guilford (1990) "successful obstacle avoidance is not simply a function of obstacle perception, but also the accepted collision risk" which can be a graded response and not the all-or-none perhaps implicitly assumed in most studies. Repeated contacts with the abrasive surface of their cave environment could result in an increase in feather wear of swiftlets and a potential impairment of flight. However, none of the swiftlets from the underground river cave examined in this study, all of which had old unmolted outer primaries, showed any pronounced feather wear that could be attributed to this cause (Collins, personal observation). Thus such casual contact would not seem to be particularly detrimental. In the studies of *A. vanikorensis* (Griffin

and Suthers 1970), *A. palawanensis* (this study) and *A. spodiopygius* (Griffin and Thompson 1982) there was some difficulty in analyzing echolocation performance using larger diameter test objects due to the increased inertia of these obstacles and a resultant failure to correctly tally all hits. This was particularly true when this was dependent on visual rather than electronic detection of obstacle movement. In this study, this probably contributed to the elevated performance calculations (higher R values) for swiftlets avoiding the 10 mm test objects as well as the much greater variance in these R values. It is likely that there were also some passes through the test apparatus which involved unobserved minor wing contact with all sizes of test objects and which would have been scored as hits rather than passes by electronic rather than visual methodology. If the rate of observed hits of the test objects in daylight (Griffin and Thompson 1982, Smyth and Roberts 1983) is used as a correction factor (decreasing the percent hits scored electronically) then the data, from the three

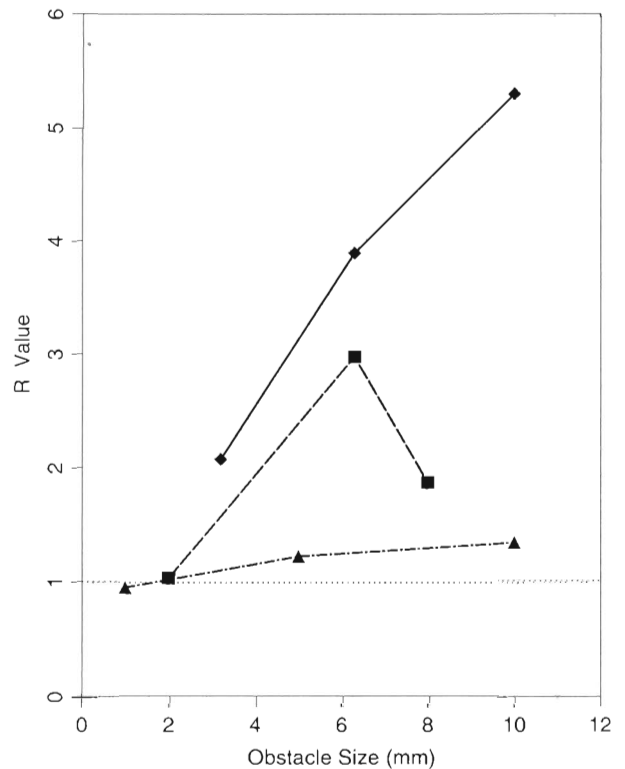


Figure 2. R values for echolocation acuity in three swiftlets: Palawan Swiftlet = solid line (this study); Mossy-nest Swiftlet = dashed line (calculated from Griffin and Suthers 1970); White-rumped Swiftlet = broken line (recalculated from Smyth and Roberts 1983). All lines connect means.

studies from which calculations of R values can be made, show a much greater degree of agreement (Figure 2). In all three studies R values close to 1 ( $R=0.5$  to  $1.5$ ), or significantly lower R values than for larger objects, are noted for test obstacles less than 5-6 mm and higher R values for obstacles larger than this. This strongly suggests that the echolocation ability of *Aerodramus* swiftlets shows rather little interspecific variation and that test results from laboratory studies as well as ones done in natural cave settings are in general agreement. This is perhaps to be expected considering the great degree of similarity in the *Aerodramus* swiftlet echolocation signals examined to date (Medway and Pyc 1977, Fullard *et al.* 1993). Of particular interest would be acuity studies of the Black-nest Swiftlet (*A. maximus*) which is the only swiftlet so far documented as producing a single rather than double-click echolocation pulse (Medway and Pyc 1977). A well developed kinesthetic or spatial memory would seem to be a necessary supplement to the echolocation capacities of swiftlets making daily flights of up to several kms to the back recesses of their nesting caves as well as intricate maneuvers to reach the numerous side chambers utilized in the underground river cave (personal observation). Further investigations of this potentially highly developed sensory capacity in swiftlets would seem appropriate particularly in light of the neurological changes associated with echolocation which have already been documented (Hollander 1974, Cobb 1968).

As pointed out by Smyth and Roberts (1983), despite any remaining differences in the data obtained in the several studies of echolocation acuity of swiftlets, it is clear that it does not begin to match the exceptional capacities of the microchiropteran bats to detect various objects in their environment as well as minute prey items (Simmons *et al.* 1975, Busnel and Fish 1980). Similarly, since the majority of the food items taken by these swiftlets is below the 5-6 mm size of objects which they can locate through echolocation (Harrison 1971, Smyth 1980, Collins, unpublished) it is extremely unlikely that echolocation plays any role in the food gathering of these diurnal foraging swiftlets. This study supports the previous interpretation that echolocation in *Aerodramus* swiftlets is only used to orient flights within their nesting and roosting caves.

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which enabled this research to be conducted. Special thanks to Captain Cousteau for his enthusiastic interest in our efforts to better understand the echolocation abilities of these swiftlets in Palawan. Comments by R. Bray and D. Bradley improved earlier drafts of this paper.

**Riassunto** - Sono state condotte nelle isole Filippine prove di ecolocazione della Salangana di Palawan (*Aerodramus palawanensis*). La discriminazione di ostacoli con diametro di 3.2 mm è risultata inferiore a ostacoli con diametro rispettivamente di 6.3 e 10 mm. I risultati ottenuti sono in accordo con dati di laboratorio effettuati su altre Salangane e confermano che con ogni probabilità l'ecolocazione è utilizzata nell'orientamento nei siti di riproduzione e riposo, ma non nella ricerca del cibo rappresentato da artropodi di piccola dimensione (<5 mm).

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