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THE FOOD OF THE WHITE-RUMPED SWIFTLET (Aerodramus spodiopygius) IN FIJI

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ABSTRACT

Diptera (flies), Homoptera (planthoppers), Hymenoptera (social insects), Isoptera (termites), and Coleoptera (beetles) were the most numerous prey in 32 food boluses being delivered by parent White-rumped Swiftlets (*Aerodramus spodiopygius*) to their chicks inside two Fijian caves. Numerically the main food items were flies (37%) and planthoppers (33%). Both the season and the habitat over which the birds had been feeding seemed to determine whether flies or planthoppers predominated in a particular bolus sample. Flies predominated in the prey of swiftlets foraging over open country, whereas planthoppers predominated in the prey of swiftlets foraging over both forest and open country.

The number of insects in each food bolus ranged from 47 to 750 ($\bar{x}$ = 236). The average weight of a bolus was 0.225 g (range 0.1-0.43 g). The average length of all prey was 2.48 mm, which is larger than the average length of available prey (1.63 mm). The number of prey species ranged from 2 to 83 ($\bar{x}$ = 30 per bolus). Altogether, 167 species were recorded in food boluses. The White-rumped Swiftlet bred during the wet season, when insects were more abundant.

This study, along with others (largely unpublished), shows for the first time that flies are often the most common insect in the prey of swifts, swiftlets and swallows.

INTRODUCTION

Swifts have been shown to collect more food on fine days than on wet days, although the reasons differ with latitude. Lack (1956) found that, in temperate latitudes, nestling Common Swifts grew more in wing length and weight on sunny warm days than on dull, cold, wet days. He also found that the food boluses fed to chicks contained larger insects on warm days than on wet days. Aerial tow netting showed that flying insects were in greater densities on warmer days and so the swifts could select larger prey (Lack & Owen 1955).

In the tropics, however, Hespenheide (1975) found from tow net sampling that flying insects were at higher densities in wet weather. Despite this, he found that swifts and swallows

1. Took the same average size of insects on both wet and dry days;
2. Caught a greater size range on wet days, probably because the rain reduced their foraging time, forcing them to be less selective;
3. Showed a preference for swarms, when present; and
4. Did not favour flies, presumably because flies manoeuvre better than other insects.

The preference for swarms applied particulary to the larger swifts.

From these findings, Hespenheide suggested that flies are scarce in the diet of all aerially feeding insectivores because they are harder to catch, being more manoeuvrable than other insects. He also proposed that certain behaviour, characteristic of each insect order, caused the average size of prey taken from each insect order to be significantly different.

This paper has two purposes. The first is to show the number, size and identity of the White-rumped Swiftlet's prey in Fiji. The second is to determine whether Hespenheide's findings apply to this swiftlet, which is widely distributed in the tropical south-west Pacific, or to other aerial feeders such as the swifts and swallows, as reported in other studies.

METHODS

In December 1981 and 1983, I studied the food of swiftlets nesting at Nasinu Nine-mile, 9 miles north of Suva. Of the two nesting colonies in separate caves at Nasinu Nine-mile, I chose that in the larger Waterfall Cave, where my longevity studies that had run since 1974 had shown that the birds are disturbed less by the public than those breeding in the smaller colony in Dry Cave.

Birds were captured as they carried their prey to their chicks, mostly in nests built in totally dark sections of the cave. I caught the birds in a butterfly net before they reached their nests because Lack (1956) and Fischer (1958) had found with the Common Swift (*Apus apus*) and the Chimney Swift (*Chaetura pelagica*) that disturbing birds at their nests made some desert.

Whenever a bird had its throat distended with a food bolus, I gently prised open its mandibles using my thumbnail and pencil and, holding the bird upside down, rolled the food bolus out with the pencil.

I collected the food boluses in the wetter of Fiji's two seasons, the season shown by other studies to have more abundant insects. I weighed each food bolus and then preserved it in formaldehyde. In the laboratory, I sorted the prey into orders and into unnamed but distinctive groups, presumably species, and then counted and measured them.

I sampled potential prey by the methods of Hespenheide (1975). The two areas sampled were the 4.3 km along Wainibuku Road from the Suva-Nausori road to near the entrances of Dry and Waterfall Caves, and in Tamavua, 10 km from the cave. The first area consisted of small horticultural farms, together with some young scrub regrowth and occasional trees. Farm crops were mainly pineapples, taro and cassava among scattered coconut trees. The

Tamavua area was a well-vegetated well-spaced residential area with food crops, flowering shrubs, trees and lawns. Swiftlets were feeding down to 0.5 m in both areas and at times were feeding while I was collecting samples in the tow net.

RESULTS

Identity of prey

Flies were found in all food boluses but one and were the most numerous prey in 16 of the 32 boluses taken in December (Table 1). Flies made up 43% of the total sample of 7433 invertebrates. Planthoppers were in all 32 food boluses and were the most numerous in seven of them. Planthoppers made up 24% of the total sample.

TABLE 1 — Composition of White-rumped Swiftlet prey in 32 food boluses. 1981 & 1983 combined

Order	No. Where Dominant	% Where Dominant	% Range In All Boluses	$\bar{x}$ % of Samples Where Present $\pm$ SE	No. of Boluses Present in	No. in Total Sample	% Individuals In Total Sample
Diptera	14	37 - 88	0 - 88	37 $\pm$ 4.8	31	3176	43
Homoptera	7	37 - 100	1 - 100	33 $\pm$ 6.2	32	1748	24
Hymenoptera	2	62 - 83	0 - 83	18 $\pm$ 5.5	30	1615	22
Coleoptera	1	53	0 - 53	9 $\pm$ 2.1	28	484	7
Isoptera	1	45	0 - 45	15 $\pm$ 4.1	12	168	2
Heteroptera	0	0	0 - 2	<1.0	7	9	
Trichoptera	0	0	0 - 3	2 $\pm$ 1.0	3	7	
Thysanoptera	0	0	0 - 3	1 $\pm$ 1.0	8	23	
Megaloptera	0	0	0 - 1	1.0	1	3	
Lepidoptera	0	0	0 - <1	<1.0	2	4	1
Psocoptera	0	0	0 - 2	<1.0	4	6	
Ephemeroptera	0	0	0 - 1	1.0	1	1	
Neuroptera	0	0	0 - <1	<1.0	1	1	
Unidentified	0	0	0 - 1	<1.0	7	12	
Aranae	0	0	0 - 8	2 $\pm$ 0.5	17	52	1

Social insects were in 30 of the boluses but were the most numerous in only two boluses. They made up 22% of the total sample. Termites and beetles were the most numerous in one bolus each, but beetles were present more often than termites. Although termites occurred in only 12 of the 32 boluses, they sometimes did so in reasonable numbers (17-43 or 9%-45% of total insects in the bolus). They are available to swiftlets only while swarming, when they are the preferred food. Spiders, although very small, were found in 17 of the 32 boluses.

The 1983 samples, which were collected on two days, had a very different composition. The averages for the six boluses taken on 11 December were 84% planthoppers and only 3% flies (one bolus containing 100% planthoppers). However, in only two of the six boluses collected on 5 December were planthoppers predominant (an average of 59%). Thus the diet of swiftlets cannot be adequately assessed by means of brief and intermittent sampling.

Size of prey

The largest prey found in this study were two adult moths 11 mm long. Two moth larvae 4.5 and 9 mm long were also well above average prey size. Termites were the largest of the common prey, averaging 4.5 mm, then planthoppers (2.5 mm), social insects (2.3 mm), flies (2.2 mm) and beetles

(1.9 mm). The average size of the prey was 2.48 ± 0.11 mm ($\bar{x}$ ± SE), which is significantly greater ($t=6.4$, $p<0.01$, df=39) than that of the prey available (1.63 ± 0.12). The data for total prey was based on the means of all 32 boluses rather than that of each type so that the extreme means of the uncommon types did not swamp those of the majority. The average size of the flies, social insects and beetles was each significantly larger than that available ($t=3.2$-3.5, $p<0.01$, df=27-38).

The average size of the smallest group of insects (beetles) commonly found in the prey was not significantly smaller than that of the flies ($t=1.63$, $p>0.1$, df=54). The flies were not significantly smaller than the Hymenoptera ($t=0.12$, $p>0.1$, df=57), which however were significantly smaller than the termites ($t=9.5$, $p<0.001$, df=40).

The average size of each major insect order found in the boluses, whenever it was predominant in a bolus, was compared with the size of the same order from boluses when it was in the minority. The size of insects from a swarm (arbitrarily decided by Hespenheide to be when more than 20 of a species occur in a bolus) was compared with the size of the same insect order when found in fewer numbers. None of the comparisons were shown to be significant, except that of beetles. In the one bolus where beetles were dominant (54%), their average size of 5.7 mm ± 0.2 was significantly greater than the average of all others (1.7 mm ± 0.09).

A significant difference in size ($p<0.001$) was found between three of the four major insect orders when the two samples, each of six boluses and each taken in December 1983, were compared. These are shown in Table 2. These two groups of samples had three important differences. Those taken on the 5th were collected earlier (1300-1555 hours) than those taken on the 11th 1900-1918 hours). The 5th was largely an overcast day, but the 11th was the fourth consecutive sunny day. Both these differences may be expected to cause those collected on the 11th to be larger (Lack 1956, Hespenheide 1975). In addition, the boluses on the 11th were taken one hour after sunset, when the swiftlets were probably catching dusk-flying insects, which have been shown to be larger than those flying during the day (Lewis & Taylor 1967, Hespenheide 1975). So then, both prey size and prey type show daily changes.

The range of 21 White-rumped Swiftlet boluses was 0.1-0.43 g, averaging 0.23 g ± 0.02. A significant correlation was found between the number of insects in a bolus and the weight of a bolus (Spearman rank correlation r_S = 0.66, $p<0.002$, n=21). This, together with a negative correlation (r_S = -0.84, $p<0.001$, n=21) between the number and size of the insects in a bolus, indicates that a bird returns to feed its chicks when it has all it can hold.

TABLE 2 — Average size of common prey (1983 sample in mm)

	5 December	11 December	Difference
Coleoptera	1.45 ± 0.084	2.35 ± 0.236	p<0.001
Hymenoptera	1.70 ± 0.110	3.06 ± 0.425	p<0.001
Homoptera	2.15 ± 0.180	2.86 ± 0.081	p<0.001
Diptera	2.16 ± 0.303	2.81 ± 0.482	N. S.

The almost spherical food boluses were about 6-7 mm in diameter. Some boluses were firm but others fell apart easily, making them hard to measure.

The number of insects in a bolus varied from 47 to 750. The average number for all 32 boluses was 236 ± 32. The 1981 sample averaged 269 ± 44 (n=20) and the 1983 sample averaged 178 ± 36 (n=12).

Combining the data for December 1981 and December 1983, as shown above, hides certain information. Whereas flies were dominant in most of the combined sample of food boluses, they were exceeded by planthoppers in seven of the 11 boluses from the 1983 sample. Further analysis of the numbers of individuals and species in the major orders is shown in Table 3.

TABLE 3 — Frequency of major prey in food boluses ($\bar{x}$ ± SE)

	Individuals 1981[1]	Species[4] 1981[3]	Individuals 1983[2]	Species 1983[2]
Diptera	123.9 ± 31.0	12.4 ± 1.7	58.4 ± 25.4	11.4 ± 3.1
Hymenoptera	71.2 ± 15.9	7.3 ± 1.8	16.3 ± 5.6	7.2 ± 1.0
Homoptera	40.2 ± 12.4	3.9 ± 0.4	84.9 ± 19.4	4.9 ± 1.0
Coleoptera	21.8 ± 4.2	5.6 ± 1.2	5.8 ± 3.0	2.8 ± 1.0
Isoptera	7.9 ± 1.8	0.3 ± 0.1	1.2 ± 0.6	0.3 ± 0.1
Total	269.2 ± 44	32.6 ± 5.2	170.0 ± 33.7	29.25 ± 7.4

NOTE:
1 Numbers in 20 boluses taken 2-24 December
2 Numbers in 12 boluses taken 5,11 December
3 Numbers in 12 boluses taken 2-24 December
4 'Species' is not a named species but is ascribed to individuals that are morphologically similar

The decrease in total insects per bolus between the years was not significant ($t=1.79$, $p>0.1$, df=30, two-tailed). Neither was there a significant change in the number of species within each major order or the total number of species per bolus between the years. This uniformity suggests that further comparative analysis would be valid. Such analysis shows that the decrease in the number of individuals per order in a bolus between 1981 and 1983 was significant ($t=3.09$-3.53, $p<0.01$, df=30) in the social insects, beetles and termites. This decrease was offset by a significant increase in planthoppers ($t=2.23$, $p<0.05$, df=30). The number of flies did not decrease significantly ($t=1.63$, $p>0.1$, df=30).

The number of species found in a bolus varied from 2 to 83 and averaged 29 in 1983 and 33 in 1981.

DISCUSSION

Prey size compared with that of other swiftlets

Prey size has been positively related to the body size of insectivorous birds (Hespenheide 1971, 1975; Dyrcz 1979). The White-rumped Swiftlet, with its light weight and small prey, fits into the general trend. It takes the smallest prey of any apodid so far studied (Table 4).

Table 5 shows that the White-rumped Swiftlet is typical of all aerial feeding birds studied to date (Hespenheide 1975, Waugh 1979) in that it takes larger prey than the average of that available.

TABLE 4 — Prey size of various Apodidae and Hirundinidae

Predator		x̄ Size (mm)	S E	Range	Mode	Source
White-rumped Swiftlet *Aerodramus spodiopygius*		2.48	0.11	0.3-11	-	This paper
Glossy Swiftlet *Collocalia esculenta*		2.6	-	-	-	Waugh & Hails 1983
Mossy-nest Swiftlet *Aerodramus vanikorensis*		3.05	-	c.1.5-12.5	-	Harrisson 1976
Black-nest Swiftlet *Aerodramus maximus*		3.05	-	c.1.5-12.5	-	Harrisson 1976
Barn Swallow *Hirundo rustica*		3.3	-	-	-	Waugh & Hails 1983
Horus Swift *Apus horus*		3.71	0.08	0.8-9.0	2.6-3.0	Collins 1980
Short-tailed Swift *Chaetura brachyura*		4.0	0.07	1-9	3	Collins 1968b
Chimney Swift *Chaetura pelagica*		c.4.0	-	-	<5	Fischer 1958
Common Swift *Apus apus*	Fine	3.5	-	<2-	-	Lack & Owen 1955
	Wet	6.5	-	->10	-	Lack & Owen 1955
Pacific Swallow *Hirundo tahitica*		4.8	-	-	-	Waugh & Hails 1983
House Swift *Apus affinis*		5.09	-	-	-	Waugh & Hails 1983
Chestnut-collared Swift *Cypseloides rutilus*		6.9	0.2	5-10	7-8	Collins 1968b
Black Swift *Cypseloides niger*		8.68	-	2-12	9-10	Collins 1968b
Grey-breasted Martin *Progne chalybea*		10.5	-	-	-	Dyrcz 1984
Mangrove Swallow *Tachycineta albilinea*		15.7	-	-	-	Dyrcz 1984

TABLE 5 — Size of prey of White-rumped Swiftlet (total sample)

	Actual prey			Potential prey		
	x̄	SE	n	x̄	SE	n
Diptera	2.21	0.11	31	1.64	0.14	9
Homoptera	2.47	0.10	32	-	-	-
Hymenopera	2.38	0.15	29	1.80	0.10	9
Isoptera	4.50	0.19	11	-	-	-
Coleoptera	1.85	0.17	26	1.26	0.05	7
Trichoptera	3.06	0.65	5	3.3	-	1
Thysanoptera	1.49	0.14	11	1.38	0.03	4
Megaloptera	2.67	-	1	-	-	-
Lepidoptera	9.00	-	2	3.4	-	2
Psocoptera	3.45	0.61	4	3.3	-	1
Neuroptera	1.50	-	1	-	-	-
Ephemeroptera	3.00	-	1	-	-	-
Heteroptera	2.47	0.29	6	2.0	0.26	4
Unidentified	2.28	0.34	5	-	-	-
Araaidae	1.67	0.12	17	4.5	-	1
Total	2.67	0.11	32	1.63	0.12	9

Hespenheide (1975) expected that the average size of each insect order in a swift's prey would be significantly different from that of the other orders. He derived this by assuming that the different orders of insects have different average flight abilities and that the birds spend about the same amount of energy in capturing any given prey item. Hespenheide (1975) found some evidence for these expectations in the prey of other swifts. However, this study shows evidence to the contrary in that swarming insects can negate both of Hespenheide's assumptions. An insect is seldom using or likely to use its full flight capabilities (in terms of high speed and manoeuvrability) while swarming, and an aerial predator will expend less energy in procuring a bolus of any high-density collection of insects.

The food bolus

Since Bartels (1931) demonstrated that the Alpine Swift fed its chicks infrequently with large boluses of food, such feeding behaviour has been shown for other Apodidae. The wet weight of the White-rumped Swiftlets' food boluses varied about as much (0.1-0.43 g) as those of the Common Swift (<0.7-2.5 g, Lack & Owen 1955), although less than those of the Edible-nest Swiftlet (*Aerodramus fuciphaga*) (0.13-1.08 g, Langham 1980) and the Chimney Swift (*Chaetura pelagica*) (0.2-0.9 g, Fischer 1958).

The average number of insects in a bolus (236) is much larger than the 94 average of 10 boluses from the same species in Queensland (Smyth 1980). From this one could predict (assuming that the above correlations between size and number of insects in a bolus hold) that the Queensland subspecies takes larger prey than the Fijian subspecies does. This is expected (Bergmann's rule) as the Queensland subspecies *A. s. terraereginae* is much larger (12.2 g) than Fijian birds (8.1 g). In the Edible-nest Swiftlet, which is similar in size, the prey numbered 100 to over 1200, with an average of more than 500 per bolus (Langham 1980). The much larger Common Swift usually has 300-1000 prey in a bolus, but the recorded range is 58-1500 (Lack & Owen 1955).

The number of species in a bolus varied from 2 to 83 and averaged 29 in 1983 and 33 in 1981. This is about half the number of species found in similarly sized samples from the stomachs of Short-tailed Swifts (Hespenheide 1975), perhaps because fewer species are available in Fiji than in Panama and Costa Rica, as one would expect by Fiji's small area and isolation. However, the average number of species taken by the White-rumped Swiftlets is lower than might be because 21 of the 24 birds apparently fed at swarms (as defined by Hespenheide 1975). The highest number of species in a bolus is only nine less than the highest in the Short-tailed Swift. One swiftlet had fed at six swarms and another at only two swarms, neither taking any other species. Five of the birds fed on fewer than 10 species to produce a bolus — a characteristic proposed for the larger swifts (Hespenheide 1975). The 24 boluses contained 167 species, of which 67 were flies, 44 social insects, 23 beetles, 18 planthoppers, 11 spiders, 5 each of sap-suckers (Heteroptera) and thrips (Thysanoptera), 2 book lice (Psocoptera) and 1 termite. An additional 29 species were taken in the tow net.

The above results show that only in one bolus, dominated by beetles, was the average size significantly different from the average for insects of the same order in all other boluses. In this case the beetles in the beetledominated bolus were larger than in all other boluses. This is the reverse of that expected if a bird feeding on a swarm is less selective, as Hespenheide (1975) proposed. As only two of the 50 beetles in the bolus were below the mean size of beetles in all other boluses, this bolus seems to have resulted from nothing more than the chance location of a swarm of larger than average beetles.

Taxonomic comparison between available prey and captured prey

For the most valid comparison between potential prey as sampled by the tow net and actual prey from the food boluses, both samples should be collected in the same season. Although this means ignoring the mass of data from 1981, I have chosen to do so because several of the 1983 net samples were taken at the same time as the swiftlets were capturing the insects in the food boluses. On several occasions swiftlets were foraging in the same air space and at the same time as the net samples were being taken. The resulting data are shown in Table 6.

TABLE 6 — Taxonomic proportions of prey compared with aerial invertebrates

Order	$\bar{x}$ % in Tow Net (Dec 83)	$\bar{x}$ % in Food Boluses (Dec 83)	$\bar{x}$ % in Homoptera Dominated Boluses	$\bar{x}$ % in Diptera Dominated Boluses
Diptera	66.9 ± 4.5	25.7 ± 8.3*	8.0 ± 3.6*	61.0 ± 8.5
Homoptera	3.8 ± 0.6	58.0 ± 9.8*	77.8 ± 7.0*	18.5 ± 6.4+
Hymenoptera	11.1 ± 3.5	9.9 ± 2.9	8.9 ± 4.3	11.7 ± 2.1
Coleoptera	15.9 ± 4.7	2.5 ± 1.0-	0.7 ± 0.3*	6.2 ± 1.7+
Isoptera	0	1.6	2.5	0
Trichoptera	0.1	0.2		
Thysanoptera	1.2	0.2		
Lepidoptera	0.7	0		
Psocoptera	0.1	0.3		
Heteroptera	1.1	0.2		
Ephemeroptera	0.2	0		
Unidentified	1.3	0.2		
Araneae	0.1	1.3		

NOTE: * Shows significant difference to tow net samples (p_t <0.001).
+ Shows significant difference to tow net samples (p_t <0.05).

Because two planthopper species (both Delphacidae) formed a clear majority in 8 ot the 12 boluses and only one of these species was rarely taken in the net, the birds with an abundance of planthoppers had apparently spent much of their foraging time in some other habitat than that sampled. Further confirmation of this is given by the significant difference between the percentage of flies in the boluses having mostly planthoppers and the percentage of flies in the tow net samples (t=4.4, p=<0.01, df=10) and no significant difference between the percentage of flies, social insects or beetles in boluses dominated by flies and the percentage of them in the tow net samples. Taken together, these data suggest that the birds with predominantly flies in their food boluses had been feeding in the open habitats that I had sampled with the net, whereas those with predominantly planthoppers had been feeding over the forests (which I did not sample with the net) to the west of the caves.

Of the fly species in the net samples, a similar proportion was found in the fly-dominant boluses (44%) and the planthopper-dominant boluses (47%). This similarity may mean that the swiftlets feeding on planthoppers foraged over the fly-rich open habitats as well as over the planthopper-rich forests. This is confirmed in that the planthopper-dominant boluses contained a larger percentage (43%) of fly species not found in the fly-dominant boluses than the small percentage (24%) of fly species found only in the fly-dominant boluses. This conclusion is consistent with my observation that the swiftlets periodically feed in the open habitat on their way to the forest. It is also consistent with the finding that a greater number of insect species fly over forest, which has a greater diversity of plants than open habitat (Hespenheide 1975, Waugh & Hails 1983).

It is interesting that the average percentages of the three most common insect orders taken in the net are each very close to those taken in Costa Rica and Panama with a similar net by Hespenheide (1975). The largest deviations from any of his results (which varied by season and location) are flies 8.2%, social insects 8.5% and beetles 9.4%. The main interest in this comparison arises from two phenomena. The first is that it would seem unusual for oceanic islands such as Fiji to have a similar proportion of flying insect groups to a region that is attached to two large land masses. The second is that, whereas the two swifts and the swallow studied in Central America did not make proportionate use of flies, the most common insect order, the White-rumped Swiftlet, did in Fiji.

The most common group of flying insects available to Fijian swiftlets was the flies. Hespenheide suggested that flies are more manoeuvrable than most insects and that this helps explain their infrequent occurrence in the prey of large swifts in particular and in aerial predators in general.

He cited studies of six species of large swifts that took a small range of prey species with flies not a major component. He reasoned that, because the larger swifts have greater foraging ranges than smaller swifts, they may specialise on insects in mating or dispersal swarms. However, there are two problems with this argument. The first is that some studies (seven of which have not been previously published) have shown that flies can be the predominant prey of large swifts. Table 7 shows that flies have dominated in the studied diets of eight species, three of which were large swifts. By comparison, the social insects were found to be dominant in the prey of 11 species, planthoppers dominant in the prey of three species and beetles dominant in the prey of two species.

The second problem is that, if flies were more difficult to capture and the difficulty increased with the size of the swift, as proposed by Hespenheide, there should be a good negative correlation between the weight of the swift and the percentage of flies in its diet. There is however only a low negative correlation between the predator's weight and the proportion of flies in the prey for the 37 studies in Tables 7 and 8 that provide numerical data as percentages (r_s= 0.28, $0.10>p<0.05$). It would appear that, regardless of the size of the predator, swifts, treeswifts or swallows do not show any preference for or against flies. The birds presumably take what is available, giving preference to swarms or other high-density concentrations, which are just as likely to

TABLE 7 — Percentage composition (numerically) of major prey of swifts

	Hymenoptera	Homoptera	Coleoptera	Isoptera	Diptera	Bird's Weight	Sample Size	Source
Philippine Spinetail								
Chaetura celebensis	99	-	-	-	-	180	14	Morse & Laigo 1968
Alpine Swift								
Apus melba	4th	-	3rd	-	1st	100	-	Arn 1945
	14	-	54	-	23	100	6	Arn 1945
White-collared Swift								
Cypseloides zonaris	94	<1	2	0	1	98	2	Rowley & Orr 1965
San Geronimo Swift								
Panyptila sanctiheronymi	-	-	-	1st?	-	57	2	Carr & Dickinson 1951
Black Swift								
Cypseloides niger	c.14	c.37	7	1	c.31	46	6	Rathbun 1925
	100	-	-	-	0	46	-	Collins & Landy 1968
Common Swift								
Apus apus	6	66	8	-	17	43	24	Lack & Owen 1955
	3rd	1st	4th	-	2nd	43	-	Koskimies 1950:25
	-	31	-	-	57	43	13	Collins pers. comm.
Zimmers Swift								
Cypseloides cryptus	-	-	-	-	0	39	1	Collins pers. comm.
White-throated Swift								
Aeronautes saxatalis	1st	-	2nd	-	-	33	2	Hespenheide 1975
	3rd	-	2nd	-	1st	33	21	Bent 1940
Fork-tailed Swift								
Apus pacificus	1st	5th	2nd	-	3rd	30	40	Litvinenko 1972
	97	-	-	-	<3	30	-	Chiba 1968
	1st	-	-	-	-	30	-	Lea & Gray 1935

TABLE 7 — continued

	Hymenoptera	Homoptera	Coleoptera	Isoptera	Diptera	Bird's Weight	Sample Size	Source
Horus Swift								
Apus horus	17	41	6	19	8	27	-	Collins 1980
House Swift								
Apus affinis	78	-	10	-	4	27	1	Waugh & Hails 1983
Cayene Swift								
Panyptila cayennensis	-	-	-	-	64	24	1	Collins pers. comm.
Chimney Swift								
Chaetura pelagica	-	-	1st	-	2nd	24	12	Warren 1890:183
	3rd	2nd	-	-	1st	24	-	Fischer 1958
White-rumped Swift								
Apus caffer	1st	4th	2nd	5th	-	22	-	Moreau 1942
Chestnut-collared Swift								
Cypseloides rutilus	51	0	0	49	0	20	4	Collins 1968a
White-tipped Swift								
Areonautes montivagus	-	-	-	-	35	20	11	Collins pers. comm.
Vaux Swift								
Chaetura vauxi	-	1st	-	-	-	18	-	Davis 1937
	-	-	-	-	31	18	10	Collins pers. comm.
Short-tailed Swift								
Chaetura brachyura	29	2	8	5	42	18	17	Collins 1968a
	82	-	11	-	4	18	6	Hespenheide 1975
Grey-rumped Swift								
Chaetura cineriventris	-	-	-	-	27	16	7	Collins pers. comm.
Band-rumped Swift								
Chaetura spinicauda	55	-	25	-	4	14	-	Hespenheide 1975
Neotropical Palm Swift								
Reinarda squamata	-	-	-	-	53	10	6	Collins pers. comm.

Note: 1st = most common, 2nd = second most common, etc.

TABLE 8 — Percentage composition (numerically) of major prey of swiftlets and swallows

	Hymenoptera	Homoptera	Coleoptera	Isoptera	Diptera	Weight	Sample Size	Source
Purple Martin								
Progne subis	2	0	68	0	20	51	c.10	Johnston 1967
Grey-breasted Martin								
Progne chalybea	75	0.3	-	-	5	33.5	65	Dyrcz 1985
	32	1	41	0	3	51	c. 9	Johnston 1967
House Martin								
Delichon urbica	-	50	-	-	-	19.8	-	Bryant 1975
Barn Swallow								
Hirundo rustica	82	-	6	2	8	19.5	-	Waugh & Hails 1983
Pacific Swallow								
Hirundo tahitica	59	-	7	2	31	17.8	-	Waugh & Hails 1983
Black-nest Swiftlet								
Aerodramus maximus	60	-	-	27	<1	15.9	-	Harrisson 1976
Rough-winged Swallow								
Stelgidopteryx	69	-	23	-	4	13.7	4	Hespenheide 1975
ruficollis	31	-	-	-	33	15.75	-	Beal 1918
Bank Swallow								
Riparia riparia	33	8	14	-	27	14.6	-	Beal 1918
	6	24	3	-	32	14.6	-	Stoner 1936
	5	13	11	-	69	14.6	-	Waugh 1979
White-rumped Swiftlet								
Aerodramus spodiopygius	7	27	12	-	51	12.2	10	Smyth 1980
	26	15	8	3	46	8.2	20	This study
	10	48	3.5	0.5	36	8.2	12	This study
Mossy-nest Swiftlet								
Aerodramus vanikorensis	60	-	-	27	<1	11.3	-	Harrison 1976
Indian Edible-nest Swiftlet								
Aerodramus unicolor	-	c.80	c.10	-	-	c.11.0	-	Ali & Dillon 1980
Edible-nest Swiftlet								
Aerodramus fuciphaga	41	15	-	-	8	10.8	-	Langham 1980
Grey-rumped Swiftlet								
Aerodramus francica	-	-	-	-	49	c.10	2	Collins pers. comm.
Glossy Swiftlet								
Collocalia esculenta	48	15	-	-	26	8.3	-	Hails & Amirrudin 1981
	55	12	34	2	2	8.3	-	Waugh & Hails 1983
Mangrove Swallow								
Tachycineta albilinea	94	3	3	0	<1	14.5	2	Ricklefs 1971
	20	-	-	-	26	-	-	Dyrcz 1984

be flies as any other group. This is not surprising because many flies congregate at feeding or mating sites and so attract feeding swifts, swiftlets and swallows.

To explain the greater dominance of social insects over beetles in prey taken than in prey available, Hespenheide pointed out that the social insects tended to congregate more and so the birds could presumably find such concentrations. There is a similar disproportion in the prey of the White-rumped Swiftlet and the same reasoning could apply. My observations of feeding swiftlets flying in 10-30 m diameter circuits confirms that they do feed on insects that are swarming or in other high-density concentrations.

Hespenheide (1975) found that swifts and swallows preferred the larger catchable prey of the range they could manage. If the same holds for swiftlets, flies, the most abundant but second smallest prey taken of White-rumped Swiftlets in Fiji, could not be taken because of their size alone. Flies must be chosen because they are easier to catch and/or more abundant.

Tow net samples taken in Costa Rica and Panama consistently demonstrated that, although flies were 70-75% of airborne insects, they were only 4% of swift prey in the comparable wet season (Hespenheide 1975). Hespenheide presumed that the flies were harder to catch than other prey. If this is true of flies in Fiji, either the White-rumped Swiftlet is better able to catch flies than the swifts, swallows and other swiftlets whose prey contains few flies or the other kinds of flying insects are far less abundant in Fiji than in Central America and Malaysia. The latter cannot be so because the taxonomic proportions of the Fijian tow net samples (Table 9) are very like those of Central America. So perhaps the White-rumped Swiftlet has greater ability in securing more manoeuvrable prey, although, as Tables 3 & 4 show, it is not alone in this ability.

A likely alternative for flies being chosen, other than their being easier to catch or more abundant, is that in Fiji they occur in high density in small areas. In Central America, flies may not have been in swarms or swarms of larger prey may have been more attractive to the swifts and swallows.

Published comments suggest that mosquitoes are fewer in Fiji than elsewhere because the swiftlets hunt them tirelessly (Wood & Wetmore 1926, Sibson *in* Belcher 1972, Allison 1978/79). I doubt these statements because mosquitoes were 2.5% (21/852) of free-flying insects but only 0.58% (43/7433) of the swiftlet's prey. In addition, four of the six places I have lived at or visited within the range of the swiftlet had large numbers of mosquitoes.

Food abundance and the timing of breeding

Some evidence suggests that the dry season is a better breeding time than the wet season for birds that feed on the wing. Hespenheide (1975) noted that the swallows and most other insectivorous birds nest in the dry season. He also suggested that, although in the wet season the density of flying insects is higher in cloudy but dry periods and ants and termites seem to swarm most, the more frequent rains must reduce the bird's foraging time. In Asia, the Edible-nest Swiftlet (Langham 1980), the Black-nest Swiftlet and the Mossy-nest Swiftlet (Medway 1962) hatch most eggs during the dry period November to March.

However, such is not always the case. The Indian Edible-nest Swiftlet *Aerodramus unicolor* (Abdulali 1942), the Pacific Swallow and the Glossy Swiftlet *Collocalia esculenta* (Waugh & Hails 1983) produce most of their first broods with the onset of the monsoon rains in May.

In Fiji, the White-rumped Swiftlet also breeds during the season of heavy rainfall. Nests are built in September and October, corresponding with an increase in rainfall (Table 9). I suspect that increase to be the trigger because the increase in both rain and nest building occur so soon after August, the driest month of the year. Laying in November and early December corresponds with a further increase in rainfall. The high level of rainfall continues to April and so covers the period that young are being fed in the nest and the critical period during which the young are learning to feed themselves on the wing.

TABLE 9 — Monthly rainfall averages in millimetres — Koronivia Research Station (1950-1979)

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
367	300	399	359	239	183	171	154	204	221	305	296	3198

Further evidence that there is an increase in the number of flying insects during the wet season in Fiji is the high correlation (r_s = 0.8) between date and the number of insects caught in the aerial tow net during December. The raw data were 5 December 10 insects, 6 December 97 insects, 9 December 68 insects, 11 December 265 insects, 15 December 162 insects. Confirmation of this trend is needed from net samples taken in every month.

Although flies were dominant in most of the combined 1981 and 1983 boluses, that does not prove that this swiftlet specialises in flies. If I had taken more boluses in 1983, the overall result would probably show planthoppers as predominant because, as Table 10 shows, planthoppers made up 48% and flies only 36% of the total 1983 sample.

TABLE 10 — Composition of White-rumped Swiftlet prey

Order	% boluses dominant in		% boluses present in		% of total sample	
	'81	'83	'81	'83	'81	'83
Diptera	60	36	100	91	46	36
Homoptera	20	64	100	100	15	48
Hymenoptera	10	0	95	91	26	10
Coleoptera	5	0	95	73	8	3.5
Isoptera	5	0	40	27	3	0.5
					98%	98%

Inadequate sampling or a real change in prey composition over time has led several workers to make generalisations which later study has shown to be incorrect. The large range of foods in boluses collected at the one time from this and other studies demonstrates how sampling could give biased results. The abundance of various insects can fluctuate greatly for various reasons such as current and past insect density, disease, predation, climate, and responses in prey or plant food species (Bos & Rabbinge 1976, Dixon & Barlow 1979, Anderson & May 1980, Barlow & Dixon 1980, Randall 1982). Such fluctuations are likely in many insects and will restrict the choice of prey for aerial feeders.

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SHORT NOTE

Seasonal song development of a North Island Kokako

The song of a male North Island Kokako (*Callaeas cinerea wilsoni*) was periodically listened to 10 times between April 1981 and June 1982 at Puketi State Forest, Northland. This bird, affectionately referred to as the 'pet bird', is known by Forest Service staff to have inhabited a ridge with large kauri (*Agathis australis*), pate (*Schefflera digitata*), makamaka (*Ackama rosaefolia*) and heketara (*Olearia rani*) for at least the last seven years. His song was recorded in October 1979 by John Kendrick, Wildlife Service. When we played this recording back to the 'pet bird' during each visit, he responded instantly and excitedly. He either ran or hopped quickly through the undergrowth or flew, with laboured flapping, a distance of up to 100 metres to the nearest perch, 10 metres or so above the tape recorder. He puffed himself up and broke into a chorus of chattering and song accompanied by wing beating. It soon became obvious that his wide repertoire was 'programmed': he was able to join his own song exactly, along with the wing-flapping sequences, in complete synchronisation with the tape. Often he was a fraction of a second ahead of the taped version.

The only variable part of the song was the number of *ko* syllables at the end of the song sequence. This part varied through the seasons as follows:

April 1981	*kawl kawl ka ko . . . ko . . . ko*
May, June, July	*kawl kawl ka ko . . . ko*
October, November	*kawl kawl ka ko . . .*
December, January	*kawl kawl ka*
May, June 1982	*kawl kawl ka . . . ko . . . ko . . . ko*

Song is primarily under the control of sex hormones and is in general concerned with the reproductive cycle (Thorpe 1984, Singing *in* Thomson, A.L., A new dictionary of birds, Nelson). The variable aspect of this bird's song is therefore probably related to differing levels of testosterone in the blood as the breeding season progresses. Oliver (1955, New Zealand birds, Reed) noted that the main laying period for Kokako is November-December.

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