The diet of the White-rumped Swiftlet (*Aerodramus spodiopygius*) in Queenslands's savannah.

M.K. TARBURTON

P.O. Box 595, Apia, W. Samoa

Abstract Homoptera (planthoppers), Diptera (flies), Hymenoptera (social insects), and Isoptera (termites) were the most numerous prey in 45 food boluses being delivered by parent White-rumped Swiftlets (*Aerodramus spodiopygius chillagoensis*) to their chicks inside six Chillagoe caves. The main food items were planthoppers (47%) and filies (24%), by frequency. The number of insects in each food bolus ranged from 7 to 587 (x = 149). The average weight of a bolus was 0.33 g (range 0.11 - 0.62 g.). The average length of all prey was 3.6 mm, which is larger than the average length of available prey (2.2 mm). The number of prey "species" ranged from 2 to 83 (x = 40) per bolus. A total of 317 invertebrate "species" were recorded in food boluses. The White-rumped Swiftlet breeds during the wet season, when insects are generally accepted as being more abundant. However, the density of potential prey is shown to be significantly lower than that taken during the breeding season in Fiji.

Introduction

The White-rumped swiftlet (A. spodiopygius assimilis) takes flies as its most common prey in some seasons in rainforest habitats in Fiji (Tarburton 1986a). Because published studies (Hespenheide 1975, Lack 1956) had not shown flies to be the dominant taxon in the prey of other swifts, it appeared worthwhile to make a comparative diet analysis of this species where it feeds in different habitats and climates. In Fiji this species feeds over rainforest with high rainfall throughout the year. At Chillagoe, Queensland, Australia the same species feeds over savannah habitat where eight months of the year are usually very dry. These are some of the factors which might alter the type and size of the prey taken over the savannah at Chillagoe.

This comparison of the diet of *A. s. chillagoensis* in Australia and A. s. assimilis in Fiji is directed at clarifying the relationship of body size to prey size and whether or not climate and the available food base are determining factors in diet composition.

Methods

During December 1985, January and December 1986 and January 1987 I studied the food of *A. s. chillagoensis* nesting at Chillagoe, Queensland, Australia (17°S, 144°E). Food boluses were taken from adults caught by a sweep net in narrow sections of caves as they delivered food to their nestings. Boluses were taken from Guano Pot, Gordale Scar Pot, New Southlander, Crack Pot, Keef's Cavern and Golgotha Cave. The approximate locations of these caves are shown in Tarburton (1988), and the methods for collecting and measuring potential prey samples are described in Tarburton (1986a).

During December 1983, January 1984, December 1985 and January 1986, I sampled potential prey of *A. s. assimilis* by attaching a sweep net to a vehicle in similar fashion to Hespenheide (1975).

However, because A. s. chillagoensis rarely fed below 8 m I could not sample the air they were feeding in with the net mounted on a vehicle. Instead, I sampled their potential prey by placing the same net as used in Fiji on a five m pole and then I stood on the top of limestone outcrops (Suicide & Spring towers as well as tower number 5126 in Chillagoe township) or on the tank stand at the rear of two Queensland National Parks & Wildlife homes. Swiftlets often fed at these locations and were doing so while some of the samples were being collected. Nine samples were collected in a similar manner in Fiji. Samples were taken by swinging the net through the air in circular and figure of eight motions for five minutes and were spread thoughout daylight hours. This sampling may have been biased by my being able to sample above the tree canopy only where rocky outcrops or other protrusions occured. It could well be that the plant lice were on the plains, which may have been inadeguately sampled.

Statistical reporting is based on mean measurements and their standard errors and is shown in text and tables as $\bar{x} \pm$ se. The data for determining the size of all prey were based on the means of all 45 boluses used in the study rather than that of each taxon so that the extreme means of some of the uncommon types did not swamp those of the majority. Whereas Table 2 shows the actual minimum and maximum sizes of all potential prey netted, those few measurements that were above or below the size that the birds were found to have taken were not used in calculating the average of available prey. It is assumed that insects smaller than the minimum size caught are 'selected against' for perceptual or energetic considerations, and that the one insect that was larger than the maximum caught by the birds sampled, would be too large for the bird to handle.

Results

Identity of prey

Planthoppers were found in all but one of the 45 food boluses and were the most numerous in 18 of them (Table 1) making up 47% (3102 individuals) of the total sample of 6583 invertebrates. Flies were found in 42 of the food boluses, and were the most numerous prey in 11 of them making up 24% of the total sample. Social insects were in 44 boluses and

Table 1. Composition of White-rumped Swiftlet prey in 45 food boluses: Chillagoe, 1985-7

Order	No. of boluses present in	Boluses where dominant	% where dominant	x % ± SE (Range) of occurrence, where present sample	No. in total Sample	% Individuals in total
Homoptera	44	18	36 - 100	$37 \pm 4.0 (0-100)$	3102	47
Diptera	42	11	38 - 56	21 ± 2.7 (0 - 56)	1556	24
Hymenoptera	44	13	42 - 97	27 ± 3.0 (<1 - 97)	1175	18
Isoptera	13	3	48 - 98	$28 \pm 8.8 (0 - 89)$	155	2
Aranae	30	0	0	$4 \pm 0.6 (0 - 12)$	272	4
Heteroptera	23	0	0	$4 \pm 1.4 (0 - 33)$	185	3
Coleoptera	23	0	0	$3 \pm 0.6 (0 - 9)$	112	2
Thysanoptera	10	0	0	<1 (0 - 1)	16	<1
Lepidoptera	6	0	0	2 ± 1.1 (0 - 7)	11	<1
Phasmatodea	1	0	0	<1 (0-<1)	1	<1
Unidentified	1	0	0	<1 (0-<1)	1	<1

Table 2. Composition sizes of prey items in boluses of White-rumped Swiftlet and potential prey items in sweep net samples.

		Bolus prey			Potential prey		
Taxon	mean	Range	х %	mean	Range	х %	
Homoptera	2.29 ± 0.15	(1.0 - 10.0)	37	1.87 ± 0.14	(1.0 - 2.6)	5	
Diptera	2.46 ± 0.13	(1.0 - 9.0)	21	2.05 ± 0.18	(0.8 - 8.5)	39	
Hymenoptera	3.62 ± 0.27	(1.0 - 10.0)	27	1.93 ± 0.20	(0.4 - 7.0)	41	
Isoptera	6.94 ± 0.60	(3.8 - 10.0)	8	-	(3.2 - 9.0)	2	
Araneida	2.38 ± 0.11	(1.0 - 5.5)	3	-	2.0	<1	
Coleptera	1.84 ± 0.10	(1.0 - 3.3)	2	2.04 ± 0.02	(1.0 - 6.0)	5	
Heteroptera	3.02 ± 0.19	(1.5 - 8.0)	2	-	(1.7 - 2.2)	2	
Thysanoptera	1.39 ± 0.17	(1.0 - 2.0)	<1	1.03 ± 0.04	(0.8 - 1.5)	6	
Lepidoptera	-	(4.0 - 9.0)	<1	-	9.0	<1	
Phasmotodea	-	9.0	<1	-	-	<1	
Blattodea	-	-	<1	-	7.0	<1	

were the most numerous in thirteen boluses. They made up 18% of the total sample. Termites were the most numerous in three boluses, but beetles, plant bugs (Hemiptera) and spiders were present in more boluses than were termites.

Thirty-one percent (1,669) of the 5,334 insects taken from 24 boluses in the 1985/86 season consisted of just three "species" of jumping plant-lice of the family Psyllidae. The total of 298 species for that season was made up of 90 Hymenoptera, 75 Diptera, 54 Araneida, 36 Homoptera, 25 Coleoptera, 11 Heteroptera, 3 Lepidoptera, 3 Isoptera, and 1 Thysanoptera. The following season in 21 boluses, one species of Phasmodea was found and only 19 new species from the other families were observed in the prey. This took the two year total of prey species to 317.

Size of prey

The largest prey found in this study were three termites and a wasp (a social insect), each 10 mm long. The next largest prey were 9 mm long and included four wasps, a moth, a fly and the only mantid in the sampled prey. Termites were the largest of the common prey, averaging 6.4 mm, then social insects (4.2 mm), plant bugs (3.0 mm), flies (2.5 mm), spiders (2.4 mm) and planthoppers (2.4 mm). The average size of all prey from the 45 boluses was 3.64 ± 0.24 mm (x ± se), which is significantly greater (t_{77} =3.89, p< 0.001), than that of avilable prey (2.4 ± 0.2).

While the average size of prey in each major taxon was not significantly greater than the average size of potential prey (except for the Hymenoptera where $t_{78} = 15.2$, P< 0.001), the data in Table 2 clearly shows the captured prey to be consistently larger than the available prey. The average size of available prey for the two years was 2.43 ± 0.2 (n = 35) which is significantly smaller than the captured prey ($t_{77} = 3.89$, P< 0.001). A comparison of the maximum and minimum lengths of potential and actual prey (Table 2) shows that although prey items smaller than 1 mm are available, these swiftlets do not take them. Termites and moths smaller than 3.5 mm are not common in either available or captured prey.

Abundance of potential prey

In the 1985/6 season the sweep-net samples (n = 19) of available prey at Chillagoe caught an average of 9.4 \pm 1.6 (n = 19) insects of the size range found to be taken by the birds (1-10 mm). In the following season, which was much drier than the previous season, the average number caught was 5.4 \pm 1.4 (n = 21). This was significantly less (t₃₈ = 2.1, P< 0.05) than the previous season.

The food bolus

The weight of 32 White-rumped Swiftlet boluses ranged between 0.11 - 0.62 g averaging 0.33 g ± 0.02 . The number of insects in a bolus varied from 7 to 587. The average number for all 45 boluses was 146 ± 21 . 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 of Whiterumped Swiftlets, Chillagoe (mean \pm se)

	No of	No. of
Order	Individuals	Species ^(a)
Homoptera	71.0 ± 16.0	5.0 ± 1.0
Diptera	35.0 ± 7.0	11.0 ± 1.0
Hymenoptera	26.0 ± 3.0	11.0 ± 1.0
Araneida	6.0 ± 2.0	4.0 ± 1.0
Heteroptera	4.0 ± 2.0	1.0 ± 0.2
Coleoptera	3.0 ± 1.0	2.0 ± 0.4
Isoptera	4.0 ± 1.0	0.4 ± 0.1
Total	149.0 ± 21	32.0 ± 4.0

(a) Species' is not a named species but is ascribed to individuals that are morphologically similar.

Discussion

Identity of prey compared with that taken in coastal Queensland and Fiji

While flies were numerically the most common invertebrates (43%) in the 32 boluses collected from Fiji swiftlets (Tarburton 1986a) they fell to being the second most common prey (24%) in the 45 boluses collected from swiftlets at Chillagoe. Planthoppers, which made up 24% of the diet and were the second most common prey in Fiji, were the most common prey (47%) in the samples from Chillagoe. Most other taxa were found in similar proportions except for spiders which composed only 1% of prey in Fiji and mad up 4% of prey at Chillagoe; beetles were 7% of prey in Fiji and were only 2% of prey at Chillagoe. Swiftlets feeding over rainforests in coastal Queensland (Smyth 1980), took prey that was more like that of the Fijian swiftlets than those at Chillagoe. Their prey consisted of more flies (50.5%) than plant lice (26.9%) and fewer spiders (2.7%) than were taken by birds at Chillagoe.

The most common flying insects avilable to swiftlets in Fiji and the second most common available at Chillagoe were flies. Whereas in Fiji, the major portion of the prey was flies, they were not the most common prey in Chillagoe. This could be explained if the planthoppers which the Chillagoe birds concentrated on were to be found in swarms or localised areas not sampled with my sweep-net.

Another factor that can cause large variation in the taxonomy of prey in comparative studies, is the variation in prey composition and density that does occur between seasons at the same site (Tarburton 1986a). The estimate of density of available prey found in this study is far below the average of 95 ± 29 (n = 16), insects caught in the same net in Fiji.

If true then the White-rumped Swiftlet in Fiji would appear to have greater ability than most swifts, including A. s. chillagoensis, to capture that more manoeuvrable prey (Tarburton 1986b). This is possible as A. s. assimilis weighs less and has longer wings than A. s. chillagoensis. Since flies are not as large a majority in the available prey at Chillagoe compared to Fiji, this may also help explain their under-representation in the diet of A. s. chillagoensis.

Non-fly prey may also be easier to obtain at Chillagoe. Evidence for this is that while Fijian birds forage for 15.5 hours a day, swiftlets at Chillagoe forage for only 13 hours. Fijian swiftlets leave their caves just after 0400 hrs and return for the night mostly after dark between 1930 and 2000 hrs. The majority of swiftlets at Chillagoe do not leave the cave until around 0530 hrs and most return before dark around 1830 hrs.

Swiftlets at Chillagoe are only gathering food for one chick, whereas Fijian swiftlets are collecting food for two chicks. Fijian birds also breed in larger colonies than those at Chillagoe, which means that on overage they have to fly further to their feeding areas. However, we need not appeal to either of these explanations for as was shown in Tarburton (1986a), such variation could result from the time of sampling. Examples given there show that the most abundant taxon in the prey of swifts varies with time, both through a season and between seasons.

A. s. chillagoensis did not take its prey in similar taxonomic proportions to those available within the size range that it handled (Table 2). If it did, social insects would predominate, followed by flies, thrips, planthoppers and beetles. The proportion of each taxon in available prey is very close to that available in Fiji (Tarburton 1986a) as well as in Costa Rica and Panama (Hespenheide 1975), except that thrips equal beetles at Chillagoe and flies were less represented than in Fiji. As Hespenheide (1975) predicted, the proportion of flies caught was below that available. The reason he gave was that the manoeuvrability of flies is said to be better than that of social insects and beetles. However, as Tarburton (1986a) has shown, the proportion of flies in a sample varies largely with the time of sampling and these data may not contradict those from Fiji where flies predominated in only one of the two large samples. Alternatively, one can accept Hespenheide's (1975) suggestion that flies are more manoeuvrable than most insects and that this helps explain their infrequent occurrence in the prey of aerial predators in general. The underrepresentation of social insects in the diet of swiftlets from both Chillagoe and Fiji does not support Hespenheides' suggestion that the poor manoeuvrability and tendency to swarm make this prey taxon preferred above flies and beetles.

Size of prey

Because A. s. chillagoensis ($x = 9.3 \pm 0.04$ g) is significantly larger in body mass ($t_{400} = 15.4$, P < 0.001) than A. s. assimilis (x = 8.19 ± 0.06 g), and because prey size has been positively related to the body size of insectivorous birds (Hespenheide 1971, 1975; Dyrcz 1979), we would expect that A. s. chillagoensis would take larger prey than A. s. assimilis. The average size of prey taken by A. s. chillagoensis $(3.64 \pm 0.24 \text{ mm})$ was significantly larger ($t_{-4} = 4.32$, P< 0.001) than the average size of prey taken by A. s. assimilis $(2.48 \pm 0.11 \text{ mm})$. However, the available prey sampled by sweep-net was significantly larger ($t_{32} = 4.37$, P< 0.001) at Chillagoe (2.58 \pm 0.17 mm) than at Fiji (1.74 \pm 0.09 mm). It has been suggested (Hespenheide 1975) that prey smaller than the minimum size taken is not taken due to either perceptual reasons or because the relative ease of capture for the different taxa converges at small sizes to very similar values.

Conclusions

Although flies were the commonest of the insects available they were second most common to planthoppers in the prey of *A. s. chillagoensis*. However, as only one of the 260 insects caught in the sweep-net was a jumping plant louse, which composed 31% of the prey in the good season, it is clear that the sampling technique was not adequate in all respects. Despite this deficiency it was shown that the swiftlets were taking larger prey than that which was available at some of their feeding sites.

A. s. chillagoensis took larger prey in larger boluses which contained fewer individuals than was the case for A. s. assimilis. Each bolus taken by A. s. chillagoensis had an average of 10 species more than those taken by A. s. assimilis. Thirty-two boluses of invertebrates taken by A. s. chillagoensis contained 303 species, whereas the same number of boluses taken by *A. s. assimilis* contained 167 species. That there are no other swifts or swallows resident in the area may help account, as much as the difference in size between Australia and Fiji, for *A. s. chillagoensis* having larger prey of more species available to it than does *A. s. assimilis*.

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Riassunto – Si sono analizzati 45 boli rigurgitati ai pulcini da parte di genitori di *Aerodramus spodiopygius chillagoensis* in sei grotte del Queensland, a Chillagoe. Le prede più numerose sono state: Omotteri, Ditteri, Imenotteri e Isotteri. Il maggior numero di esemplari ritrovati è dato da cicaline (Omotteri) (47%), mosche (Ditteri) (24%). Il numero di prede per bolo varia tra 7 e 587 (media=149). Il peso medio è di 0.33 g (estremi 0.11 - 0.62 g). La lunghezza media delle prede è 3.6 mm, valore superiore alla lunghezza media degli insetti disponibili (2.2 mm). Il numero di specie ritrovate in ciascun bolo varia tra 2 a 83 (media=40). Cumulativamente si sono individuate 317 specie di insetti. *Aerodramus spodiopygius* si riproduce in un periodo considerato secco, quando si pensa che gli insetti siano più abbondanti nell'isola. Nonostante ciò, la densità di prede potenziali in Chillagoe è significativamente inferiore a quella riscontrata nel periodo riproduttivo, nelle isole Fiji.

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