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Comparative foraging ecology of Madagascar vangids (Vangidae)

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The Vangidae, an endemic family in Madagascar, contains 14 species in 11 genera. The foraging behaviour of 13 species of vangids was investigated during the periods August–November 1989 and September–November 1990. These vangids are grouped into six bill types according to their bill shape, using the analogy of gripping tools: (1) forceps, (2) radio pliers, (3) strong pinchers, (4) pliers, (5) standard and (6) flat forceps types. We recognized seven foraging niches: (A) canopy-gleaning, (B) general, (C) ground-snatching, (D) trunk/branch-probing, (E) leaf and twig/branch-gleaning/probing, (F) leaf and twig/branch-gleaning and (G) trunk-gleaning niches. Two or more coexisting species with the same foraging niche differed in their bill types. Those vangids that exploited similar resources segregated in their bill types, geographic ranges and/or foraging niches, presumably to avoid severe competition. Several vangid species partially occupied the ecological niche that would be filled by woodpeckers elsewhere.

Madagascar lies near Africa's southeast coast and is separated by the Mozambique Channel, which at its narrowest is about 400 km wide. Around 70 million years ago (at about the end of the Cretaceous), Madagascar was still joined to Africa. After separating from eastern Africa 65 million years ago, Madagascar became the earth's fourth largest island, an isolated area and an arena for the evolution of animals. The great majority of birds would have arrived subsequently, mainly from Africa. But this island was never colonized by certain families (e.g. Picidae, Sittidae, Laniidae, Paridae) which inhabit forests of most parts of the world. Therefore, we may expect a vast ecological release for these vacant niches in Madagascar.

The endemic family Vangidae (or, more recently, as members of Vangini, Malaconotinae, Corvidae [Sibley & Monroe 1990]) contains 14 species in 11 genera (Langrand 1990) and shows a striking ecological radiation, comparable with that of the Hawaiian drepanids or the finches of the Galapagos (Lack 1947, Amadon 1950, Grant 1986). This family has been considered to be most closely related to the helmet shrikes (Prionopidae) of Africa (Benson 1984, 1985).

Although all species of vangas subsist mainly on insects (Rand 1936, Milon *et al.* 1973, Langrand 1990) little is known of the comparative foraging ecology of this family. The aim of this paper is to report on the foraging behaviour of each vangid species quantitatively and to clarify how they are ecologically segregated on an isolated large island.

STUDY AREA AND METHODS

Field survey

The study was carried out in seven study sites: eastern rain forests (Perinet, Mananara, Masoala and Ranomafana), western dry deciduous forest (Ampijoroa), gallery forest (Berenty) and spiny desert (Beraketa), during the periods August–November 1989 and September–November 1990 (Fig. 1). The vegetation of each site was described by Jenkins (1987).

We walked transects in the forests, mainly along paths; once we encountered a foraging vangid, we recorded the foraging height to the nearest 5 m, foraging station in vegetation and foraging technique. When we encountered a flock of vangids, different focal individuals were used for each record, but because flock members were not marked, it is likely that several records were collected for the same individuals in a flock. In some cases, observations were made consecutively on the same individuals, but only when the bird moved to a new foraging position. We treated each record as an independent unit in analysing foraging behaviour.

Five types of foraging techniques were recognized: gleaning, hovering (i.e. catching sedentary prey during the hover), probing, snatching (i.e. jumping on sedentary prey and snatching it off) and hawking (i.e. flycatching aerial prey). In the case of hawking, the foraging height was determined as the height of the perch from which sallies were made.

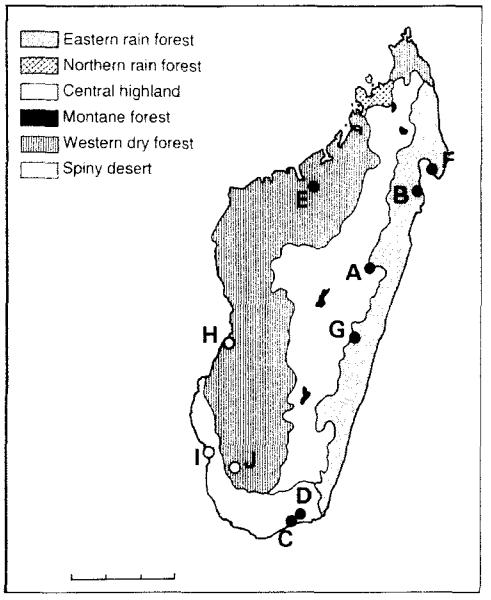


Figure 1. The seven study sites (filled circles) in Madagascar used for this study: A = Perinet, B = Mananara, C = Berenty, D = Beraketa, E = Ampijoroa, F = Masoala, G = Ranomafana. Three open circles indicate the names of sites used in other studies cited in this article: H = Morondava, I = Toliara, J = Beza Mahafaly. The scale line represents 300 km.

Five categories of foraging station were recognized: leaf/twig, branch, trunk, air and undergrowth/ground. Thirteen species were observed in this study; we never encountered Bernier's Vanga *Oriolia bernieri*.

In order to divide the members of this family into guilds based on foraging niche, a cluster analysis, based on combined data of foraging technique and foraging station in vegetation, was carried out by calculating Euclidean distances according to Landres and MacMahon (1980).

Bill measurement

The bill length, depth and width of 70 vangid specimens in the Tsimbazaza Botanical/Zoological Museum were measured to the nearest 0.1 mm using a caliper. The percentages of depth/length and width/length and the ratio of depth/width were calculated. In order to divide the members of this family morphologically into several bill shape groups, a cluster analysis, based on the combined data on these six elements, was carried out.

Scientific and common names follow Langrand (1990) and are listed in the Appendix.

RESULTS

Bill shape

The bill shapes of this family vary so widely that it is difficult to believe these vangids belong to a single family (Fig. 2). The Appendix shows the results using wing and bill measurements for each species, and Figure 3 gives a dendrogram based on the combined data on the six bill elements. At the 70% similarity level, five clusters can be recognized. Using the analogy of gripping tools, these are (1) forceps type (Sickle-billed), (2) radio pliers type (White-headed and Hook-billed), (3) strong pinchers type (Pollen's, Van Dam's and Lafresnaye's), (4) pliers type (Helmet) and noncharacteristic type (Rufous, Blue, Chabert's, Red-tailed, Tylas and Nuthatch Vangas). The last large group is divided into two subgroups. One is (5) standard type (Rufous, Blue, Chabert's and Red-tailed), the other is (6) flat forceps type (Tylas and Nuthatch). Thus, we divided vangids into six groups according to their bill shapes.

Foraging niche

For two species, the Blue and Sickle-billed Vangas, we collected enough data to compare the differences in foraging behaviour between different localities (Table 1). There were significant differences in the foraging technique of Sickle-billed Vangas and in the foraging height of Blue Vangas. The Blue Vanga may have preferred higher parts at Perinet simply due to plentifulness of tall trees (see also Eguchi *et al.* 1993b). The branchless and leafless peculiar form of *Didierea*, a dominant xerophytic tree in Beraketa, may have promoted the Sickle-billed Vanga's probing behaviour on trunks. On the whole, there were no clear tendencies in foraging behaviour at different sites; therefore, we pooled our data from different sites.

Figure 4 compares foraging height, foraging station in vegetation and foraging technique among 13 vangid species, and Figure 5 shows a dendrogram based on the combined data on foraging technique and foraging station. Vangids were classified into two main groups according to their foraging station: (1) branch or trunk (lower half of the dendrogram) and (2) canopy or ground groups (upper half). Then the former was subdivided into three subgroups according to foraging technique: mainly probing (Sickle-billed and Pollen's), mainly gleaning (Nuthatch) and probing/gleaning (Van Dam's, White-headed, Lafresnaye's and Tylas). The latter was subdivided into two subgroups: mainly gleaning (Red-tailed and Blue) and the rest (Chabert's, Hook-billed, Helmet and Rufous).

At the 70% similarity level, seven clusters were formed. These were (A) canopy-gleaning group (Red-tailed and Blue), (B) general group (Chabert's, Hook-billed and Helmet), (C) ground-snatching group (Rufous), (D) trunk/branch-probing group (Sickle-billed and Pollen's), (E) leaf and twig/branch-gleaning/probing group (Van Dam's and White-headed), (F) leaf and twig/branch-gleaning group (Lafresnaye's and Tylas) and (G) trunk-gleaning group (Nuthatch). These groups represented foraging niches.

The most noteworthy discovery in this study was the foraging behaviour of the Sickle-billed Vanga. It belonged to group D and employed its long, slender and curved upper

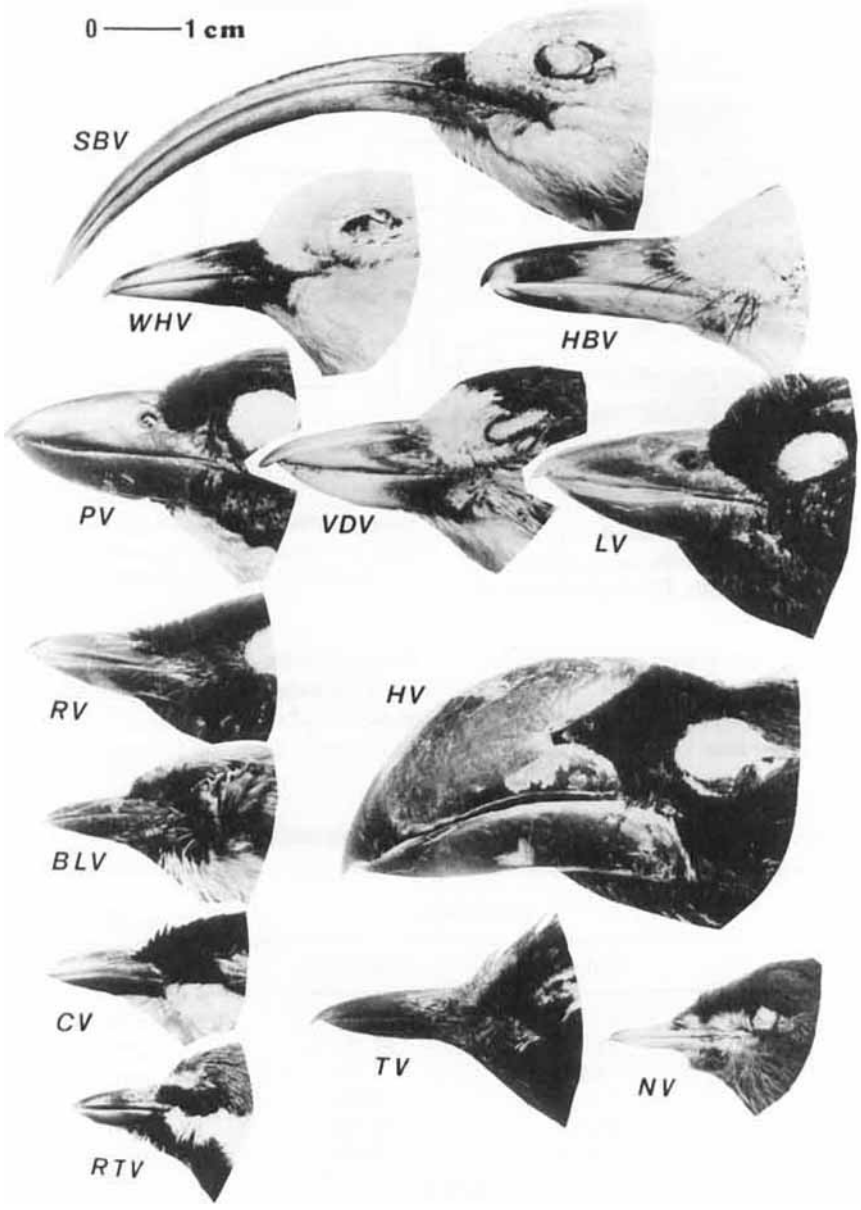


Figure 2. Sizes and shapes of the bills of 13 vangid species (see also Fig. 3). SBV = Sickle-billed Vanga, WHV = White-headed Vanga, HBV = Hook-billed Vanga, PV = Pollen's Vanga, VDV = Van Dam's Vanga, LV = Lafresnaye's Vanga, HV = Helmet Vanga, RV = Rufous Vanga, BLV = Blue Vanga, CV = Chabert's Vanga, RTV = Red-tailed Vanga, TV = Tylas Vanga, NV = Nuthatch Vanga. (Courtesy of Tsimbazaza Botanical and Zoological Garden.)

beak to extract insects from the surfaces of trees and from crevices in the bark.

There were significant negative correlations between the percentage of gleaning and sizes of wing and bill (Table 2). Because bill size was correlated with wing length ($P < 0.05$ for each), small species frequently foraged by gleaning. Probers had a long and deep bill, whilst snatchers had a thick bill (Table 2). The foraging station was not related to wing length, bill size or bill shape, although the foragers on branch and trunk had a slightly slender bill (Table 2).

DISCUSSION

We can recognize seven foraging niches from the dendrogram which combined data of foraging techniques and foraging stations (Fig. 5). Except for ground-snatching and trunk-gleaning niches, each occupied by a single species, foraging niches were occupied by two or more species each. In those niches with two or more species, bill types differed from one another, except for the combination of the Red-tailed Vanga and Blue Vanga (Table 3). In general, bill size is related to

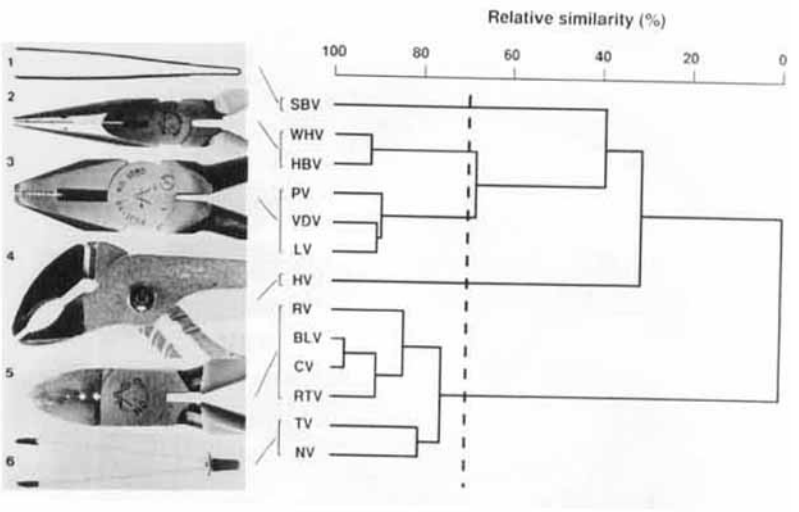


Figure 3. A dendrogram showing bill shape affinities among 13 species of vangids with respect to length, depth, width, 100•depth/length, depth/width and 100•width/length. The dashed line indicates the 70% similarity level. 1 = forceps type, 2 = radio pliers type, 3 = strong pinchers type, 4 = pliers type, 5 = standard type, 6 = flat forceps type (see Fig. 2 for abbreviations of species names).

the prey size preferred (Cody 1974, Wiens 1989); therefore, it is likely that the species with similar foraging habits (foraging station and foraging technique) preferred different prey types. The Red-tailed Vanga and Blue Vanga, with the same foraging niche and the same bill type, were separated by foraging heights (Fig. 4c). Another explanation for the coexistence of these species is that the Blue Vanga invaded Madagascar from the Comoros in the recent past and has

Table 1. *Comparison of foraging behaviour of Sickle-billed and Blue Vangas at two study sites*

	Blue Vanga		Sickle-billed Vanga	
Foraging behaviour	Perinet	Ampijoroa	Ampijoroa	Beraketa
Technique	$n = 92$	$n = 107$	$n = 50$	$n = 85$
Gleaning	78.3%	67.3%	30.0%	12.9%
Hovering	4.3%	9.3%	—	—
Probing	—	2.8%	68.0%	87.1%
Snatching	16.3%	18.7%	2.0%	—
Hawking	0.1%	1.9%	—	—
Statistical test	$\chi^2_2 = 2.54$, n.s.		$\chi^2_1 = 7.15$, $P < 0.01$	
Station	$n = 92$	$n = 107$	$n = 50$	$n = 85$
Leaf/twig	93.5%	95.3%	2.0%	4.7%
Branch	5.4%	1.9%	62.0%	51.8%
Trunk	—	—	36.0%	43.5%
Air	1.1%	1.9%	—	—
Undergrowth/ground	—	0.9%	—	—
Statistical test[a]	n.s.		n.s.	
Height	$n = 92$	$n = 105$	$n = 50$	$n = 85$
>20	1.1%	1.0%	4.0%	1.2%
15–20	4.3%	1.9%	6.0%	8.2%
10–15	27.2%	2.9%	16.0%	8.2%
5–10	45.7%	15.2%	44.0%	44.7%
0–5	21.7%	79.0%	30.0%	37.6%
Statistical test	$\chi^2_2 = 65.6$, $P < 0.001$		$\chi^2_2 = 1.59$, n.s.	

[a] Fisher's exact test.

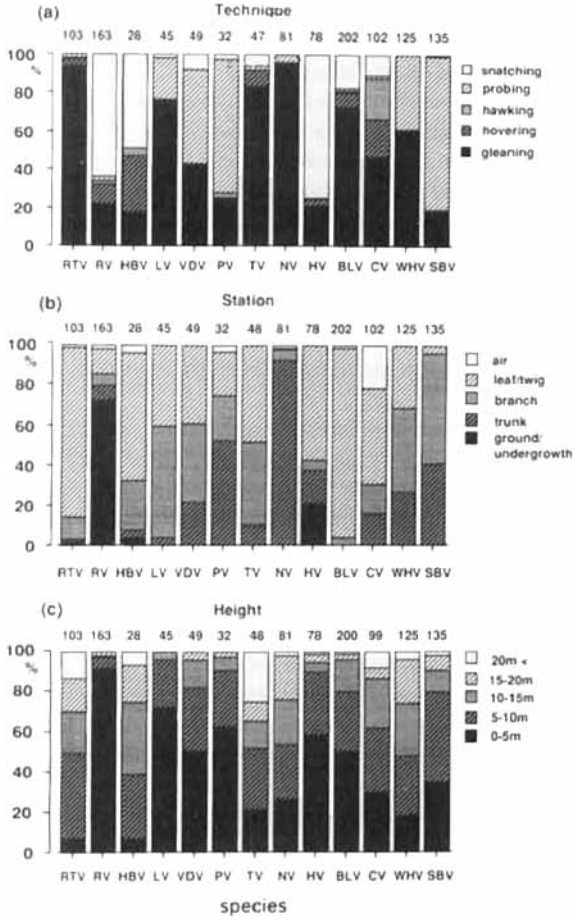
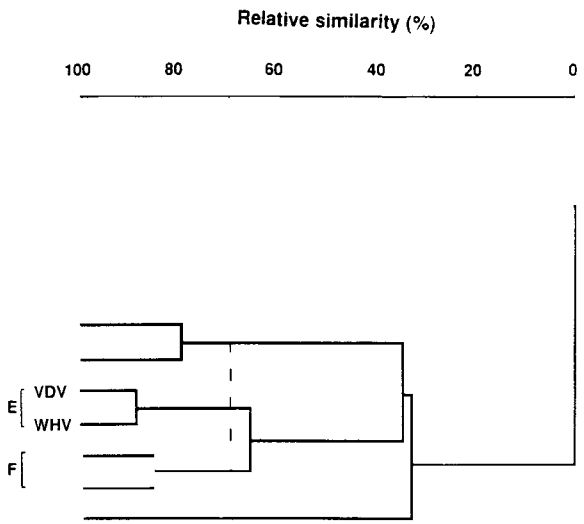


Figure 4. Percentage of utilization of foraging categories by 13 species of vangids (see Fig. 2 for abbreviations of species names). (a) Foraging technique; (b) Foraging station; (c) Foraging height. Figures above graphs are the number of observations.



not had sufficient time to differentiate into different niches. This possibility is suggested by the fact that the Blue Vanga is the only species living outside Madagascar (Milon *et al.* 1973, Langrand 1990).

Langrand (1990) has given approximate range distributions of the 13 vangid species included in this study. We assembled available data on the number of species coexisting at ten localities (Table 3). Six patterns of distribution were recognized: (a) wide-ranging, (b) rain and dry forests, (c) rain forest, (d) dry forest and spiny desert, (e) spiny desert and (f) restricted patterns.

Hutchinson (1959) found an average character ratio (larger/smaller) of approximately 1.3 in the bill size or body length among coexisting but ecologically similar species and concluded that this value was a limit to permit coexistence. Several cases have contradicted this conclusion, and other criticism has emerged (see Wiens 1989). However, some level of limiting similarity (MacArthur & Levins 1967) may be expected between coexisting species. Table 4 shows the average character ratio in wing length and bill length among vangids coexisting in the same habitat. The wing length ratios were near 1.1. The maximum ratio in this family was 2.3, the largest being the Sickle-billed Vanga and the smallest being the Red-tailed Vanga. The average ratios of bill length were larger than those for wing length (Table 4). The maximum ratio was also much larger for bill length (7.5), the largest being the Sickle-billed Vanga and the smallest being the Nuthatch Vanga (Appendix). Thus, the variation was greater in bill length than in wing length. The average ratios of bill length exceeded 1.3 in both dry forests and spiny deserts but not in rain forests (Table 4). There were some cases of coexistence with a very small difference in the bill length. For example, the White-headed Vanga and Van Dam's Vanga coexisted in the dry forest in Ampijoroa (Table 3), although the character ratio between them was almost unity (Appendix). Thus, in spite of similar body and bill sizes, many species of vangids coexisted in the same localities. They may have attained this by separating into different microhabitats and by adopting different foraging techniques.

It is obvious that two or more species with the same foraging niche differed in their distribution or, conversely, differed in their foraging niches when their distribution patterns were the same. The only exception is the combination of Chabert's Vanga and Hook-billed Vanga, both being generalists. Generalists may be able to coexist by virtue of the variety of foraging techniques and foraging stations. Thus, of the 13 species of Vangidae which exploited similar resources, all were insectivorous (Rand 1936, Milon *et al.* 1973) but were segregated by bill type, foraging height, foraging

Table 2. *Correlations between foraging ecology and morphology of vangids. Figures are correlation coefficients at P < 0.05 level*

	Foraging technique[a] (%)			Foraging station[b] (%)	
	GL	PR	SN	L/TW	BR/TR
Wing length	−0.67	n.s.	n.s.	n.s.	n.s.
Bill length	−0.65	n.s.	n.s.	n.s.	n.s.
Bill depth	−0.55	n.s.	0.63	n.s.	n.s.
Bill width	−0.57	n.s.	0.79	n.s.	n.s.
D/L ratio[c]	n.s.	n.s.	n.s.	n.s.	n.s.
D/W ratio[c]	n.s.	n.s.	n.s.	n.s.	n.s.
W/L ratio[c]	n.s.	n.s.	n.s.	n.s.	n.s.

[a] GL = gleaning; PR = probing; SN = snatching.
[b] L/TW = leaf and twig, BR/TR = branch and trunk.
[c] D/L ratio = 100•bill depth/bill length, D/W ratio = bill depth/bill width, W/L ratio = 100•bill width/bill length.

station, foraging technique or geographic range. As a result, they presumably avoided severe competition.

Foraging niches of vangids, of course, may be influenced by interactions with birds other than vangids or with other animals. The Aye-aye *Daubentonia madagascariensis* is a primate with several unusual morphological characteristics. In particular, the combined function of the Aye-aye's continuously growing chisel-like incisors and its narrowed third finger has drawn the attention of many workers (von Linnee & Gmelin 1788). These two peculiar morphological traits are commonly thought to represent an adaptation for the extraction of wood-boring insect larvae. It has been suggested that the Aye-aye fills an ecological niche normally filled by true woodpeckers, which are absent from Madagascar (Cartmil 1974, Petter 1977). However, Iwano and Iwakawa (1988) recently claimed that the Aye-aye's specialized incisors and third finger are an adaptation for feeding on hard nuts, especially nuts of the Ramy *Canarium madagascariensis*. This would mean that the Aye-aye is not a substitute for woodpeckers. Moreover, because the Aye-aye is a nocturnal animal, it could not be a diurnal substitute for woodpeckers. This niche seems to remain unfilled in the ecosystem of this island.

In Madagascar, the forest-living passerines other than vangids mainly occupy the "canopy-gleaning niche" (Eguchi *et al.* 1993a, 1993b). On the other hand, seven species of vangids utilize trunks or branches or both (Fig. 4b and niches D, E, F and G in Fig. 5). The discovery of the foraging habit of the Sickle-billed Vanga in this study, namely that they use their long, slender and curved upper beak to extract insect larvae from holes or crevices in trees, suggests that this species is a true substitute for woodpeckers. Even with this species, however, the niche of woodpeckers, with special adaptations for boring through the concealing wood and for probing the exposed tunnel to catch the retreating insect, is not completely occupied. Thus, we may conclude that several vangid species each partially fill the role of woodpeckers on this island.

We are grateful to Professor J. Kikkawa for his helpful comments

Table 3. *Comparison of foraging niche and bill type among 13 species of Vangidae in relation to their distribution ranges. See Figures 2, 3 and 5 for abbreviations of species names, bill types and foraging niches, respectively. See the text for distribution patterns (distribution after Jenkins [1987] and Langrand [1990]. Parentheses indicate new records from our observation*

	RTV	BLV[a]	CV	HBV	HV	RV	SBV	PV	VDV	WHV	LV	TV	NV
Foraging niche	A	A	B	B	B	C	D	D	E	E	F	F	G
Bill type	5	5	5	2	4	5	1	3	3	2	3	6	6
Distribution pattern	a	b	a	a	c	b	d	c	f	a	e	c	c
Locality													
Rain forest													
Ranomafana	+	+	+	+		+		+		+		+	
Perinet	+	+	+	+	+	+		+		+		+	+
Mananara	+	+	(+)	+	+	+		+				+	+
Masoala	+	+	+	+	+	+		+		+		+	+
Dry forest													
Ampijoroa	+	+	+	+		+	+		+	+			
Morondava	+	+	+	+		+	+			+			
Spiny desert													
Toliara	+		+	+			+			+	+		
Beza Mahafaly			+	+			+			+	+		
Berenty	+		+	+			+			+	+		
Beraketa			(+)	(+)			(+)			(+)	(+)		

[a] Blue Vanga (BLV) also occurs in the Comoros.

Table 4. *The average character ratio[a] among vangids in each locality*

	No. of species	Wing length Mean	Wing length s.d.	Bill length Mean	Bill length s.d.
Rain forest					
Ranomafana	8	1.09	0.12	1.14	0.08
Perinet	10	1.10	0.09	1.23	0.21
Mananara	9	1.11	0.09	1.26	0.21
Masoala	10	1.10	0.09	1.23	0.21
Dry forest					
Ampijoroa	8	1.13	0.14	1.31	0.40
Morondava	7	1.16	0.14	1.36	0.41
Spiny desert					
Toliara	6	1.19	0.17	1.44	0.43
Beza Mahafaly	5	1.14	0.15	1.48	0.49
Berenty	6	1.19	0.17	1.44	0.43
Beraketa	5	1.14	0.15	1.48	0.49

[a] Hutchinson (1959).

on the manuscript. We also thank Dr. V. Randrianasolo and Messrs N. Rakotoarison and H. Randriamahazo, Botanical and Zoological Garden Tsimbazaza, for their cooperation in the whole of our project in Madagascar. Many thanks are offered to Drs M. Nakamura and H. Nagata for their help in collecting data. This study was supported by a grant under the Monbusho International Scientific Research Program (Field Research, No. 01041079).

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APPENDIX

Measurements of wing and bill sizes (mm) of 70 specimens of Vangidae stored in Tsimbazaza Botanical/Zoological Museum

Species	Wing length	Bill elements Length	Depth	Width	100·D/L	D/W	100·W/L
Blue Vanga *Cyanolanius madagascarinus* (n = 6)							
Mean	87.84	13.40	6.22	5.02	46.83	1.24	38.01
s.d.	4.46	1.35	0.26	0.39	5.49	0.08	6.93
Nuthatch Vanga *Hypositta corallirostris* (n = 1)	78.20	8.10	2.70	3.40	33.33	0.79	41.98
Hook-billed Vanga *Vanga curvirostris* (n = 2)							
Mean	109.60	27.95	10.75	6.80	38.46	1.58	24.33
s.d.	0.64	0.35	0.35	0	0.78	0.05	0.31

APPENDIX

Continued

Helmet Vanga *Euryceros prevostii* (*n* = 1)	145.30	47.60	27.70	15.80	58.19	1.75	33.19
Tylas Vanga *Tylas eduardi* (*n* = 4)							
Mean	115.90	19.65	6.03	6.13	30.77	0.98	31.33
s.d.	4.60	1.84	0.69	0.26	3.76	0.12	2.43
Rufous Vanga *Schetba rufa* (*n* = 6)							
Mean	104.50	18.15	8.22	7.38	45.17	1.13	41.04
s.d.	2.63	1.23	0.88	0.84	2.32	0.21	7.31
Sickle-billed Vanga *Falculea palliata* (*n* = 6)							
Mean	151.00	60.90	8.80	5.95	14.45	1.50	9.77
s.d.	8.21	2.44	0.57	0.71	0.61	0.22	1.11
White-headed Vanga *Leptopterus viridis* (*n* = 14)							
Mean	114.10	21.17	8.14	5.36	38.57	1.53	25.40
s.d.	4.26	1.18	0.34	0.35	2.60	0.11	2.43
Red-tailed Vanga *Calicalicus madagascariensis* (*n* = 10)							
Mean	65.30	11.43	4.91	3.72	43.04	1.32	32.54
s.d.	2.00	0.63	0.22	0.26	2.54	0.07	1.09
Chabert's Vanga *Leptopterus chabert* (*n* = 10)							
Mean	90.53	14.55	6.36	5.29	43.82	1.21	36.43
s.d.	2.34	0.68	0.27	0.38	3.12	0.10	3.04
Van Dam's Vanga *Xenopirostris damii* (*n* = 3)							
Mean	109.10	21.10	12.33	5.83	58.44	2.12	27.61
s.d.	1.27	0.66	0.74	0.58	2.72	0.21	1.94
Pollen's Vanga *Xenopirostris polleni* (*n* = 2)							
Mean	113.80	22.55	11.20	6.10	49.84	1.84	27.13
s.d.	8.20	1.48	0.42	0.14	5.16	0.03	2.41
Lafresnaye's Vanga *Xenopirostris xenopirostris* (*n* = 5)							
Mean	111.30	23.78	12.10	5.38	50.90	2.25	22.64
s.d.	2.94	0.83	0.60	0.16	2.22	0.12	0.69