

Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest of western Madagascar

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Hino, T. 1998. Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest of western Madagascar. – J. Avian Biol. 29: 17–24.

I examined the feeding rates and foraging niches of seven species regularly participating in heterospecific avian flocks in a deciduous dry forest of western Madagascar in two different social situations, viz. when the species was foraging alone or with conspecifics, and in heterospecific flocks, respectively. The species responded differently to mixed-flocking. A change in feeding sites and/or techniques was found in six species, five of which increased their feeding rates when foraging in heterospecific flocks. In mixed flocks, they tended to use similar substrates. That such interspecific convergence enhanced feeding rate might be explained by social learning, kleptoparasitism or a beating effect. Benefits gained through these effects were greatest in two species consistently acting as followers, Crested Drongo *Dicrurus forficatus* and Paradise Flycatcher *Tersiphone mutata*. Although as leaders, Newtonia *Newtonia brunneicauda* and Long-billed Greenbul *Phyllastrephus madagascariensis* often attracted other species, they also increased their feeding rates through some mutualistic effects. Another leader, Rufous Vanga *Shetba rufa* was the only species that neither changed foraging niche nor feeding efficiency in different social situations. Its participation in heterospecific associations probably resulted from other species exploiting the vanga's ability to detect predators. Therefore, the organization of multispecies flocks in Madagascar was mainly based on mutualism and commensalism which increased feeding efficiency.

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The formation of mixed-species flocks may benefit birds by increasing foraging efficiency and predator avoidance (reviews in Morse 1977, Barnard and Thompson 1985). Birds in heterospecific flocks may forage more efficiently due to social learning (Krebs 1973), beating (Swynnerton 1915), minimizing re-visitation of sites (Cody 1971) and by allowing more time to feeding (Sullivan 1984a). At the same time, flocking birds may avoid predation due to early detection (Thompson and Barnard 1983) and confusion of predators (Morse 1970). However, there are also costs associated with flocking to part or all of the flock members in the form of increased competition for food (Alatalo et al. 1985), kleptoparasitism (Brockmann and Barnard 1979), aggressive interactions (Metcalfe and Furness 1987) and the effect of dominance hierarchies (Cimprich and Grubb 1994).

Most studies of avian mixed-species flocks have focussed on either interspecific differences in resource use (e.g., Morse 1970, Alerstam et al. 1974, Alatalo et al. 1985, 1987) or on the costs and benefits of flocking (e.g., Krebs 1973, Sullivan 1984a, Sasvári 1992). The former have mainly emphasized the negative interactions among flock members (but see Munn and Terborgh 1979, Mönkkönen et al. 1996).

Multispecies flocks of birds are observed all the year round in the forests of Madagascar, which has a unique avifauna and many endemic species (Langrand 1990). Eguchi et al. (1993) have already investigated how flock-participating species segregate with respect to feeding sites and techniques. In this paper, I examine changes in foraging niche and feeding rates of flock-participating species in two different social situations, viz. when foraging alone or with conspecifics, and in

Table 1. Average number of conspecific individuals associating together and percentage of observations in heterospecific flocks (N1 = no. of encounters) for the seven regular species during the breeding and nonbreeding seasons, and percentage of time each species was the leader in interspecific associations (N2 = no. of observations).

	N1	Number of conspecifics (mean \pm s.d.)	% participation in heterospecific flocks	N2	% leading
Crested Drongo					
breeding	52	1.27 \pm 0.45	48.1	19	10.5
nonbreeding	57	1.61 \pm 0.68**	93.0**	40	7.5
Paradise Flycatcher					
breeding	58	1.33 \pm 0.48	48.3	24	12.5
nonbreeding	90	1.43 \pm 0.50	88.9**	51	5.9
Common Newtonia					
breeding	32	1.94 \pm 0.77	56.3	12	91.7
nonbreeding	105	2.07 \pm 0.96	76.2*	43	93.0
Rofus Vanga					
breeding	45	2.22 \pm 1.13	48.9	22	90.9
nonbreeding	29	1.85 \pm 0.75	51.7	11	90.9
Blue Vanga					
breeding	16	1.56 \pm 0.51	87.5	12	50.0
nonbreeding	31	1.74 \pm 0.58	96.8	19	57.9
Long-billed Greenbul					
breeding	24	1.96 \pm 0.91	75.0	15	26.7
nonbreeding	45	3.38 \pm 2.12**	80.0	24	79.2**
Ashy Cuckoo Shrike					
breeding	29	1.52 \pm 0.74	62.1	12	66.7
nonbreeding	47	1.60 \pm 0.80	87.2*	22	50.0

** p < 0.01; Mann-Whitney's U-test.

* p < 0.05; **p < 0.01; Fisher's probability test.

heterospecific flocks, respectively. I discuss positive effects of multispecies association that vary among species, and compare the flock organization in Madagascar with that in the temperate region.

Study area and methods

The study area was the Botanical Garden A in the Ampijoroa Forest Reserve (16°35'S, 46°82'E), located about 110 km southeast of Mahajanga. This forest belongs to the western deciduous dry forest in Madagascar. The vegetation mainly consists of trees below 10 m in height and 15 cm in DBH. The ground layer is sparse.

Observations were made from 17 October to 12 November 1994 (breeding season) and 23 August to 8 October 1995 (nonbreeding season). I walked around the study area (450 m \times 550 m) in the morning (0600–1100 hours) and in the afternoon (1400–1700 hours). Whenever encountering flocking or solitary birds, I recorded the kind and abundance of each species. I obtained data by 2-min focal sampling, during which I recorded frequency of prey (arthropods) capture, prey type and size, feeding sites and feeding techniques used, and frequency of aggressive interactions with other birds. For feeding sites, five categories of height (0–1 m, 1–3 m, 3–6 m, 6–10 m, > 10 m) and six of location (air, leaf, branch, trunk, bush, ground) were distinguished. I also differentiated between six types of feeding technique (gleaning, probing, hanging, snatching,

hovering, sallying). For flocking birds, I changed to a new focal individual for each record. To avoid bias due to repeated observations of the same individuals, I collected data from individuals in different territories in the study area (no. of territories ranged from five in Blue Vanga to 18 in Common Newtonia during the breeding season; scientific names below). I also recorded which species initiated movements (leader) and which species followed it (follower), respectively, as well as dominance relationships between flock members.

As an index of foraging efficiency, I calculated the mean number of prey captures per two minutes. Samples, in which no active prey searching took place owing to resting, singing, etc. were excluded in these calculations. I used Pianka's index, $[\sum p_{ij} \cdot p_{hj}] / [\sqrt{\sum p_{ij}^2} \sqrt{\sum p_{hj}^2}]$, where p_{ij} and p_{hj} are the proportions of observations in category j for species i and h respectively (Pianka 1973), to calculate interspecific overlaps of feeding habits. I combined data for the two seasons because no significant seasonal differences in foraging niches or feeding rates were found. Body weights of birds were obtained from H. Rakotomanana (pers. comm.).

Results

Flock participation

In all, 17 species were observed in mixed-species flocks in the study area. Of these, seven frequently joined

Table 2. Dominance relationships among the seven regular flock-participating species. 'Other species' includes all the species except the regular species. The figures show the number of attacks by a species in the top row against a species in the column to the left.

Species attacked	RV	DR	PF	Species attacking		LG	CN	OS
				CS	BV			
Rufous Vanga (RV)	*		1					
Crested Drongo (DR)	4	*			1			2
Paradise Flycatcher (PF)	3	4	*				2	
Ashy Cuckoo Shrike (CS)		3		*				1
Blue Vanga (BV)		4	1	1	*			1
Long-billed Greenbul (LG)	4	3				*		
Common Newtonia (CN)	1	1	9	1	2	2	*	2
Other species (OS)	3	1					1	*
Total as attacking	15	17	10	2	3	2	3	
as attacked	1	7	9	4	7	7	18	
% as attacking	93.8	70.8	52.6	33.3	30.0	22.2	14.3	

mixed flocks (45–95% of total encounters) during both the breeding and (more frequently) the non-breeding season (Table 1); these species were, Crested Drongo *Dicrurus forficatus*, Common Newtonia *Newtonia brunneicauda*, Madagascar Paradise Flycatcher *Tersiphone mutata*, Rufous Vanga *Shetba rufa*, Blue Vanga *Cyanolanius madagascariensis*, Long-billed Greenbul *Phyllastrephus madagascariensis* and Ashy Cuckoo Shrike *Coracina cinerea*. The Blue Vanga was the species showing the strongest tendency to join heterospecific flocks in both seasons.

Leader-follower relationships

Newtonia and Rufous Vanga were leaders, and Crested Drongo and Paradise Flycatcher were followers regardless of season (Table 1). The greenbul was the only species that changed its role in the associations seasonally, viz. from follower in the breeding season to leader in the nonbreeding season. However, both roles were less pronounced than in the above four species. Blue Vanga and Cuckoo Shrike showed average values for leading when flocks moved, because they lead at some times and followed at others.

These species-specific characteristics in leading or following appeared to be related to the numbers of conspecific individuals (Table 1); leaders had more conspecifics in the flock and followers fewer (% leading vs. conspecific flock size, Kendall's $\tau = 0.425$, $p = 0.034$, $n = 14$; for the two seasons pooled). Newtonia and Rufous Vanga were often found in groups of three to five individuals, and Crested Drongo and Paradise Flycatcher were usually alone or in pairs. This relationship also applied to the Long-billed Greenbul's seasonal change from follower to leader, because its conspecific flock size increased greatly from the breeding to the nonbreeding season.

Dominance relationship

Aggressive interactions between focal birds and individuals of other species occurred at low frequency (0.036 times/min). Interspecific dominance relationships were not linear (Table 2) and were not related to body size (% attacking vs. body weight, Kendall's $\tau = 0.286$, $p = 0.368$, $n = 7$). The drongo attacked all the other regular species but was subordinate to Rufous Vanga, which was the most dominant species. Common Newtonia was the lowest-ranking species, because it was attacked by all the other members. Thus, whether a species was a leader or a follower was not related to its social dominance rank, because the two leader species, Newtonia and Rufous Vanga, were ranked the lowest and highest, respectively.

Feeding sites and techniques

The seven regular mixed-flocking species captured prey at different heights, in different locations and with different techniques. I examined how their feeding sites and techniques changed with social situation (Tables 3–5). Since differences in the species' feeding habits when alone and when in conspecific flocks were small, data from these situations were combined for statistical comparisons with situations when they were in heterospecific flocks.

The species that changed feeding sites and techniques most when joining multispecies flocks was the Crested Drongo. When alone or in conspecific flocks, this species captured most of its prey in the air above 6 m by sallying but increased the frequency of snatching or gleaning the ground or the vegetation below 6 m greatly when in heterospecific flocks. The prey captured also changed from small, flying insects (e.g. Diptera) to large, slow-moving arthropods (e.g. Lepidoptera larvae, Coleoptera, Orthoptera, Arachnida, Diplopoda).

Table 3. Percentage use of height categories for prey-capture by the seven regular flock-participating species when solitary or in conspecific (sol + con) or heterospecific (hetero) flocks.

	N	Feeding height (m) ^a					χ^2 -test		
		1	2	3	4	5	df	χ^2	p
Crested Drongo									
sol + con	50	6.0	16.0	10.0	40.0	28.0			
hetero	82	9.8	23.2	48.8	14.6	3.7	4	37.5	<0.001
Paradise Flycatcher									
sol + con	70	8.6	21.4	44.3	20.0	5.7			
hetero	379	12.1	26.7	47.0	13.7	0.5	3 ^b	6.2	>0.1
Common Newtonia									
sol + con	181	5.5	17.1	39.8	33.7	3.9			
hetero	218	1.4	17.4	49.1	28.0	4.1	4	8.2	<0.1
Rufous Vanga									
sol + con	71	62.0	18.3	14.1	5.6	0.0			
hetero	40	75.0	20.0	5.0	0.0	0.0	2 ^c	4.5	>0.1
Blue vanga									
sol + con	10	0.0	10.0	30.0	60.0	0.0			
hetero	88	1.1	14.8	56.8	26.1	1.1	1 ^{b,d}	4.5	<0.05
Long-billed Greenbul									
sol + con	45	33.3	33.3	31.1	2.2	0.0			
hetero	129	37.2	40.3	17.8	4.7	0.0	3	3.8	>0.1
Ashy Cuckoo Shrike									
sol + con	46	0.0	19.6	52.2	17.4	10.9			
hetero	65	0.0	16.9	40.0	30.8	12.3	3	3.0	>0.1

^a 1, 0–1 m; 2, 1–3 m; 3, 3–6 m; 4, 6–10 m; 5, >10 m.
^b 4 + 5; ^c 3 + 4; ^d 1 + 2 + 3, data combined for the different categories of height to make expected frequencies large enough for tests.

The Paradise Flycatcher’s feeding patterns also differed between social situations, with an increase in hovering when in heterospecific flocks, whereas prey type remained unchanged. However, the variation in feeding locations increased. Although there was no change in mean feeding height, if Rufous Vangas were present in the mixed flocks, the flycatchers foraged more in vegetation below 3 m where the vangas frequently foraged ($\chi^2 = 20.50$, $df = 1$, $p < 0.001$).

Height and location of Blue Vanga and Ashy Cuckoo Shrike changed significantly when they foraged in mixed flocks. Blue Vanga, which specialized in taking prey from leaves by hanging upside down on branches, did so at lower heights in mixed flocks. The Ashy Cuckoo Shrike not only foraged with a variety of techniques in the canopy, but also used more diverse substrates when in multispecies flocks. Although not statistically significant ($0.05 < p < 0.1$), Common Newtonia and Long-billed Greenbul in mixed flocks tended to forage in different sites from when alone or in conspecific flocks. The Newtonia, which forages among leaves and branches with an even use of gleaning, hovering and sallying, increased the use of the middle canopy, and the greenbul, a gleaner (also the only prober) in the layer below 6 m, captured prey in a greater diversity of locations.

Rufous Vanga was the only species that did not show any change in foraging sites or techniques in different social situations. It most often captured prey from the ground by snatching.

When in mixed flocks, interspecific overlaps in feeding height increased significantly in Crested Drongo and Blue Vanga and those in feeding location increased in Crested Drongo, Paradise Flycatcher, Blue Vanga and Long-billed Greenbul (Table 6). Greenbul also increased the overlap in feeding technique. On the whole, feeding locations became more similar among species in multispecies flocks (Wilcoxon’s signed-ranks test, $p = 0.0005$, $n = 21$).

Feeding rate

Mean feeding rates were related to the species’ body size, with larger species feeding more slowly (Kendall’s $\tau = -0.714$, $p = 0.0243$, $n = 7$). For each species, feeding rates were compared between different social situations (Table 7).

None of the species differed in mean feeding rate between when foraging alone and in conspecific flocks. Five species, however, Crested Drongo, Paradise Flycatcher, Newtonia, Long-billed Greenbul and Ashy Cuckoo Shrike captured prey significantly more often when participating in mixed flocks. If the drongo’s change in diet (see above) is also considered, its energy intake per time unit was much greater in mixed flocks. On the other hand, the two vanga species’ feeding rates remained constant regardless of social situation.

Table 4. Percentage use of location categories for prey-capture by the seven regular flock-participating species when solitary or in conspecific (sol + con) or heterospecific (hetero) flocks.

	N	Feeding location ^a						χ^2 -test		
		AR	LF	BR	TR	BS	GR	df	χ^2	p
Crested Drongo										
sol + con	50	62.0	24.0	4.0	0.0	0.0	10.0			
hetero	82	22.0	45.1	13.4	2.4	0.0	17.1	3 ^b	22.9	<0.001
Paradise Flycatcher										
sol + con	70	42.9	40.0	15.7	0.0	0.0	1.4			
hetero	379	35.6	49.3	5.5	2.1	1.3	6.1	4 ^c	14.3	<0.01
Common Newtonia										
sol + con	181	8.8	64.6	22.1	2.8	1.7	0.0			
hetero	218	9.2	71.6	17.9	0.9	0.0	0.5	3 ^d	3.0	>0.1
Rufous Vanga										
sol + con	71	2.8	23.9	8.5	2.8	1.4	60.6			
hetero	40	2.5	25.0	2.5	2.5	5.0	62.5	2 ^{b,e}	0.3	>0.1
Blue Vanga										
sol + con	10	0.0	90.0	10.0	0.0	0.0	0.0			
hetero	88	0.0	90.9	9.1	0.0	0.0	0.0	1	— ^f	>0.1
Long-billed Greenbul										
sol + con	45	0.0	37.8	42.2	15.6	4.4	0.0			
hetero	129	0.8	42.6	25.6	14.0	10.1	7.0	4 ^e	8.2	<0.1
Ashy Cuckoo Shrike										
sol + con	46	0.0	78.3	21.7	0.0	0.0	0.0			
hetero	65	6.2	66.2	9.2	9.2	9.2	0.0	2 ^{c,e}	11.8	<0.01

^a AR, air; LF, leaves; BR, branches; TR, trunks; BS, bushes, GR, ground.

^b BR + TR + BS; ^c TR + BS; ^d TR + BS + GR; ^e AR + LF, data combined for the different categories of location to make expected frequencies large enough for tests.

^f Fisher's probability test.

Discussion

The present study has demonstrated changes in the use of foraging heights, foraging locations, feeding techniques, and in feeding rates, of seven regular flock-participating species when foraging alone or with conspecifics versus in mixed-species flocks. To the species studied, some advantageous effects of mixed-species flocking can be proposed: (1) social learning; (2) kleptoparasitism (to some, negative to others); (3) beating; (4) more time to feed; and (5) predation avoidance (reviews in Morse 1977, Barnard and Thompson 1985). The first four effects should increase feeding efficiency.

Changes in the use of feeding sites and/or techniques were found in six species when in mixed-species flocks versus either alone or with conspecifics. Five of these species increased their feeding rates and used more similar substrates in mixed flocks than when foraging alone or with conspecifics, as also found by Ogasawara (1970) and Buskirk (1976). This result is contrary to that expected from competition resulting in increased interspecific segregation in resource use, as suggested by MacArthur (1972) and often demonstrated in studies of multispecies flocks (e.g., Alatalo et al. 1985, 1987, Cimprich and Grubb 1994).

If convergence enhances feeding rates of flocking

species, this may be partly explained by social learning or social facilitation (Krebs 1973, Waite and Grubb 1988). The social-learning effect appeared to be greatest in Crested Drongo, because not only did it change its feeding habits most but also its diet changed when foraging with other species.

In the drongo, another effect also appeared to contribute to increased foraging efficiency in mixed flocks, namely kleptoparasitism (Brockmann and Barnard 1979), a feeding method frequently adopted by the drongo. This species often observed other flock members carefully without searching for prey by itself, and then usurped the prey from the target.

The other consistent follower, the Paradise Flycatcher, also benefitted much from foraging in heterospecific flocks, as evident from the fact that it had the largest increase in feeding rate among the species. The flycatcher's rapid food intake in mixed flocks was probably a beating effect (Swynnerton 1915), by which salliers and hoverers can capture flying insects flushed as the flock moves. Beating was a species-specific effect for Paradise Flycatcher in the flocks studied, like kleptoparasitism was for Crested Drongo.

More time to feed, by reducing the time scanning for predators when in mixed flocks (Caraco 1979, Sullivan 1984a), would apply to any species that increased its feeding rate, but no time-budgeting was done in the present study.

Table 5. Percentage use of techniques for prey-capture by the seven regular flock-participating species when solitary or in conspecific (sol + con) or heterospecific (hetero) flocks.

	N	Feeding technique ^a						χ^2 -test		
		GL	PB	HG	SN	HV	SL	df	χ^2	p
Crested Drongo										
sol + con	50	6.0	0.0	4.0	6.0	10.0	74.0			
hetero	82	12.2	0.0	6.1	25.6	17.1	39.0	4	17.4	<0.01
Paradise Flycatcher										
sol + con	70	1.4	0.0	0.0	2.9	35.7	60.0			
hetero	379	5.3	0.0	1.3	4.0	49.3	40.1	2 ^b	10.2	<0.01
Common Newtonia										
sol + con	181	29.3	0.0	3.3	3.3	30.4	33.7			
hetero	218	34.9	0.0	0.9	3.2	27.5	33.5	4	4.1	>0.1
Rufous Vanga										
sol + con	71	14.1	0.0	2.8	54.9	1.4	26.8			
hetero	40	17.5	0.0	2.5	52.5	2.5	25.0	2 ^{c,d}	0.2	>0.1
Blue Vanga										
sol + con	10	20.0	0.0	70.0	0.0	0.0	10.0			
hetero	88	23.9	0.0	69.3	1.1	4.6	1.1	1 ^{b,d}	— ^e	>0.1
Long-billed Greenbul										
sol + con	45	68.9	11.1	6.7	6.7	0.0	6.7			
hetero	129	68.2	13.2	1.6	0.8	6.2	10.1	2 ^{b,d}	3.0	>0.1
Ashy Cuckoo Shrike										
sol + con	46	23.1	0.0	7.7	12.8	7.7	48.7			
hetero	65	41.5	0.0	3.1	12.3	13.9	29.2	4	7.3	>0.1

^a GL, glean; PB, probe; HG, hang; SN, snatch; HV, hover; SL, sally.

^b GL + HG + SN; ^c GL + HG; ^d HV + SL, the data combined for the different categories of technique to make expected frequencies large enough for tests.

^e Fisher's probability test.

Table 6. Interspecific overlaps of height, location and technique categories used for prey-capture by seven regular flock-participating species when in heterospecific flocks (above) and solitary or in conspecific flocks (below diagonals). DR = Crested Drongo, PF = Paradise Flycatcher, CN = Common Newtonia, RV = Rufous Vanga, BV = Blue Vanga, LG = Long-billed Greenbul, CS = Ashy Cuckoo Shrike. Change in overlap tested with Wilcoxon's signed-ranks test (two-tailed, n = 6); *p < 0.1, ** < 0.05.

	Interspecific overlaps of foraging							Average change in overlap ¹
	DR	PF	CN	RV	BV	LG	CS	
Height								
DR	—	0.99	0.96	0.33	0.96	0.68	0.91	+0.23**
PF	0.63	—	0.94	0.38	0.94	0.74	0.89	+0.05
CN	0.74	0.96	—	0.15	0.99	0.51	0.98	—0.01
RV	0.30	0.46	0.38	—	0.13	0.82	0.13	—0.09
BV	0.80	0.75	0.90	0.21	—	0.48	0.95	+0.12**
LG	0.40	0.79	0.67	0.84	0.38	—	0.49	—0.01
CS	0.60	0.98	0.93	0.31	0.71	0.69	—	+0.02
Location								
DR	—	0.95	0.90	0.62	0.85	0.84	0.87	+0.39**
PF	0.90	—	0.87	0.42	0.82	0.72	0.85	+0.10**
CN	0.47	0.79	—	0.38	0.98	0.90	0.98	+0.09
RV	0.31	0.33	0.39	—	0.37	0.46	0.38	+0.08
BV	0.36	0.68	0.97	0.37	—	0.85	0.98	+0.13*
LG	0.27	0.61	0.84	0.34	0.72	—	0.91	+0.18**
CS	0.36	0.70	0.99	0.39	0.99	0.81	—	+0.12
Technique								
DR	—	0.78	0.80	0.83	0.23	0.37	0.80	+0.05
PF	0.92	—	0.81	0.37	0.11	0.24	0.61	—0.05
CN	0.74	0.83	—	0.50	0.26	0.74	0.95	+0.05
RV	0.51	0.42	0.46	—	0.15	0.35	0.65	+0.05
BV	0.21	0.12	0.29	0.16	—	0.34	0.33	—0.01
LG	0.18	0.10	0.60	0.34	0.37	—	0.85	+0.13*
CS	0.92	0.83	0.86	0.67	0.36	0.51	—	+0.01

¹ Comparisons of mean overlaps when species foraged solitarily or in a conspecific flock and when it foraged with heterospecifics.

Table 7. Average feeding rates (mean number of prey captured per two minutes) by the seven regular flock-participating species when solitary (sol), when in conspecific (con) and heterospecific (hetero) flocks.

	Feeding rate			U-test (one-tailed)	
	N	mean	s.d.	sol vs.con	sol + con vs. hetero
Crested Drongo					
sol	22	0.46	0.67		
con	6	0.83	1.21	>0.1	<0.05
hetero	58	0.83	0.84		
Paradise Flycatcher					
sol	28	1.09	1.17		
con	12	1.23	0.88	>0.1	<0.001
hetero	153	2.37	1.44		
Common Newtonia					
sol	27	2.09	1.48		
con	55	2.12	1.31	>0.1	<0.05
hetero	80	2.60	1.38		
Rufous Vanga					
sol	13	0.69	0.72		
con	27	0.59	0.62	>0.1	>0.1
hetero	39	0.69	0.79		
Blue Vanga					
con	4	1.50	0.50		
hetero	47	1.75	1.01	>0.1	>0.1
Long-billed Greenbul					
sol	12	0.92	0.95		
con	10	1.03	0.96	>0.1	<0.01
hetero	69	1.73	1.21		
Ashy Cuckoo Shrike					
sol	14	0.81	0.98		
con	10	0.80	1.54	>0.1	<0.01
hetero	68	1.49	1.39		

The two vanga species did not show any feeding benefits from foraging in mixed flocks. Despite this, Blue Vanga almost always joined mixed flocks, often followed other species, and foraged in the height zone where other members were feeding. Thus, no doubt this species participated in mixed flocks because it gained something by doing so. The Blue Vanga's preference for heterospecific flocking may be explained by more efficient predator avoidance (Thompson and Barnard 1983, Sullivan 1984b, Székely et al. 1989). Although this benefit of flocking may apply to most participants (Herrera 1979), the Blue Vanga's species-specific feeding technique of hanging upside down may make it especially vulnerable to aerial predators.

Rufous Vanga was the only species that changed neither foraging sites nor feeding rate in the different social situations. All the year round, most individuals of this species foraged in cohesive conspecific groups, known as breeding groups (Yamagishi et al. 1995). The group members constantly kept contact with one another by calls, frequently gave alarm calls and even directed attacks at predators. In contrast to the other species, they captured most of the prey on the ground. These characteristics of Rufous Vanga sug-

gest that its conspecific groups moved independently of other species and that its association with heterospecifics probably resulted from other species following it to exploit its ability to detect predators (cf. Sullivan 1984b).

To conclude, the organization of multispecies flocks in Madagascar was mainly based on mutualism and commensalism which increased feeding efficiency. Although negative interactions such as kleptoparasitism by Crested Drongo and interspecific aggressions sometimes occurred, they were less common than in mixed flocks in temperate regions. In winter flocks in boreal forests, socially dominant species frequently follow and supplant subordinate species to obtain food (Sasvári 1992, Hino 1993), and subordinate species almost always shift to less preferred feeding sites to avoid interference from dominant species (Morse 1970, Alatalo et al. 1985, Hino 1993). Therefore, subordinate species often have low intake rates (Sasvári 1992, Cimprich and Grubb 1994) and high predation risk (Suhonen et al. 1993), costs that may be offset by enhanced predator protection (Herrera 1979). This latitudinal difference in flock organization may be attributable to resource abundance (although vegetation structure of the forests studied is similar to that of boreal forests) and phylogenetic relatedness (i.e. different genera in Madagascar vs. mainly the same genus (*Parus*) in temperate regions). Owing to the lack of quantitative studies on the advantages of heterospecific flocking (Buskirk 1976, Bell 1983, Powell 1989, Hutto 1994), we do not know if flocks in the tropics generally are organized on the basis of mutual benefits. Munn and Terborgh (1979) demonstrated mutualistic multispecies territoriality in foraging flocks in Amazonian forests. In boreal forests during the breeding season when resources are renewable and not limiting, however, mixed flocks may be organized by positive associations like those in Madagascar (Mönkkönen et al. 1996)

Acknowledgements – I am grateful to A. Randrianjafy, J. R. Ramanampamonjy and F. Rakotondraparany, Botanical and Zoological Park Tsimbazaza, for their kind cooperation in our project in Madagascar; to UNESCO/PNUD and Conservation International for good facilities in Ampijoroa. I thank S. Yamagishi and K. Eguchi for useful advice on the research. I am also grateful to M. Mönkkönen and A. Dorby for valuable comments on the manuscript. This study was supported by the Grant-in-Aid for Overseas Scientific Survey from the Ministry of Education, Science and Culture of Japan (06041093).

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(Received 30 January 1997, revised 26 May 1997, accepted 16 June 1997.)