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The composition and foraging behaviour of mixed-species flocks of forest-living birds in Madagascar

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Mixed-species flocks of forest living birds were investigated in a rainforest at Perinet/Analamazaotra (Andasibe), Madagascar. Most insectivorous birds in the area participated in mixed-species flocks. Flocks were composed of foliage gleaners, foliage–branch gleaners, trunk gleaners and flycatchers. Species whose foraging techniques and foraging locations in vegetation were similar were different from each other in foraging heights. The nuclear species often occurred in small conspecific flocks in and out of mixed-species flocks.

Mixed-species flocks formed by insectivorous birds in the tropics are prominent in their size and species diversity (e.g. Moynihan 1962, Croxall 1976, Jones 1977, Greig-Smith 1978, Powell 1979, Wiley 1980). Mixed-species flocks comprise two different types of participants, nuclear species and attendant species, according to the regularity of participation and their roles in maintaining flock cohesion (Davis 1946, Moynihan 1962, Morse 1970, Greig-Smith 1978, Hutto 1987). The importance of flocking and its advantages (i.e. predator avoidance and facilitation in food searching) are likely to vary between nuclear and attendant species. In addition, niche separation among members of mixed-species flocks has been recognized (Morse 1970, Austin & Smith 1972, Croxall 1976, Hogstad 1978, Alatalo 1981).

Madagascar has a unique avifauna and many endemic species (Dee 1986). Only a few previous studies have dealt with mixed-species flocking and foraging habits of Malagasy birds (Rand 1936, Thompson 1987). In this paper we present quantitative data on the composition of mixed-species flocks of forest birds in Madagascar and the foraging behaviour of flock members.

STUDY AREA AND METHODS

The study was carried out in a rainforest at the Perinet/Analamazaotra (Andasibe) Reserve, about 150 km east of Tananarive, Madagascar (18°56'S, 48°25'E), at 920–1020 m a.s.l., during the periods 17–24 August and 13–22 October 1989. The forest is a mid-montane tropical moist forest, dominated by *Weinmannia, Tambourissa, Symphonia, Dalbergia, Ravensara* and *Vernonia* in the canopy layer, with the dense understorey dominated by *Cyathea, Dypsis, Plantago, Smilax, Rubus, Alchemilla* and *Sanicula* (Jenkins 1987).

Two observers walked separately in early morning and mid-afternoon along paths cut on the ridge and along the stream in the forest. The study route was 'A'-shaped with a total length of about 2.3 km. Once encountered, a flock was followed for as long as possible until contact was lost, and the foraging behaviour, foraging location and composition of the flock were recorded. Following Hutto (1987), we defined a flock as a group of two or more individuals of single or mixed species, occurring within 20–30 m of one another and moving in concert. On occasion, it was difficult to distinguish between flock participant and non-participant because of the difficulty in determining their direction of movement. We included such birds as flock participants in all cases, though it was possible that they were observed with a flock by chance. Because two observers investigated the same route separately twice a day and the area covered was small, it is likely that the same flocks were encountered two or more times in a day. However, flocks of identical species composition were seldom encountered (i.e. only two of 89 flocks encountered whose species composition was ascertained), which suggests frequent turnover of flock members as observed by Powell (1979). Hence, we treated each flock as an independent unit in analysing species composition. Often, we could not count the number of individuals of each flock species because the birds were not marked and they moved around rapidly.

We recorded the foraging height (relative position of vegetation), height of vegetation, location in vegetation and foraging technique. For abundant species, focal individuals were changed for each record, but because flock members were not marked, several records were collected on the same individuals in a flock. In some cases, recording was made consecutively on the same individuals, but only one record was collected unless the bird moved to a new foraging position.

Five types of foraging technique were recognized; gleaning, hovering (i.e. catching sedentary prey during the hover), probing, snatching (i.e. jumping upon 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. Six categories of the foraging location were recognized; leaf, twig, branch, trunk, air, and undergrowth and ground.

We collected more data in the morning than in the afternoon because of the greater number of encounters in the former, but there were no diurnal tendencies in the species composition and the mean number of species in the flocks, nor any significant diurnal differences in foraging behaviour of the regular species. We therefore combined data for morning and afternoon. For several species there were significant differences between observers in height of trees in which birds foraged, but the directions of bias were not consistent among species. The height of vegetation also differed from site to site. We could not ascertain whether these differences were due to differences in measuring between observers or to differences of height of vegetation among sites. In the present study, we combined data.

Cole's (1949) coefficient of association (CA) was calculated in order to examine whether the degree of attendance of a given species in a mixed-species flocks was influenced by the presence of other species. Thus,

$$\mathrm{CA} \pm \sigma = \frac{ad - bc}{(a + b)(c + d)} \pm \sqrt{\frac{(a + c)(c + d)}{n(a + b)(b + d)}}$$

The variables are the number of flocks in which both species A and B are present (a), only species A is present (b), only species B is present (c) and neither species is present (d), and n is total number of flocks. If CA is -1 it means perfect avoidance between given two species; if CA is $+1$ it means perfect positive association between them. The formula must be modified if the association is negative ($ad|bc$) (Cole 1949). In order to divide the members of flocks into guilds based on foraging niche, a cluster analysis, based on combined data of foraging technique and foraging location in vegetation, was carried out by calculating Euclidean distances according to Landres & MacMahon (1980).

Scientific and common names follow Langrand (1990).

RESULTS

Species composition of flock

Table 1 shows a list of species joining mixed-species flocks whose composition was ascertained. In August, species composition was ascertained for 47 of 72 flocks encountered and the mean number of species was 4.7 per flock (range 2–12). The Madagascar Paradise Flycatcher *Terpsiphone mutata*, Madagascar White-eye *Zosterops maderaspatana*, Common Newtonia *Newtonia brunneicauda* and Crested Drongo *Dicrurus forficatus* occurred regularly. The former two species participated in more than 50% of 47 mixed-species flocks. In October, species composition was determined for 42 of 44 flocks encountered and the mean number of species was 6.9 per flock (range 2–12). The Common Newtonia, Crested Drongo, Madagascar White-eye, Nelicourvi Weaver *Ploceus nelicourvi* and Madagascar Paradise Flycatcher were ob-

Table 1. *Species joining mixed-species flocks in Perinet/Analamazaotra (Andasibe) Reserve, Madagascar*

Species	No. of flocks joined		
	August	October	Total
Madagascar Lesser Cuckoo *Cuculus rochii*	0	1	1
Velvet Asity *Philepitta castanea*	2	1	3
Sunbird-Asity *Neodrepanis coruscans*	1	1	2
Ashy Cuckoo Shrike *Coracina cinerea*	10	10	20
Long-billed Greenbul *Phyllastrephus madagascariensis*	13	20	33
Spectacled Greenbul *Phyllastrephus zosterops*	12	15	27
Madagascar Bulbul *Hypsipetes madagascariensis*	4	14	18
Red-tailed Vanga *Calicalicus madagascariensis*	14	19	33
Hook-billed Vanga *Vanga curvirostris*	1	0	1
White-headed Vanga *Leptopterus viridis*	1	1	2
Chabert's Vanga *Leptopterus chabert*	6	4	10
Blue Vanga *Cyanolanius madagascariensis*	9	14	23
Nuthatch Vanga *Hypositta corallirostris*	5	8	13
Tylas Vanga *Tylas eduardi*	5	11	16
Madagascar Magpie Robin *Copsychus albospecularis*	2	1	3
Madagascar Paradise Flycatcher *Terpsiphone mutata*	28	23	51
Crossley's Babbler *Mystacornis crossleyi*	2	0	2
Madagascar Brush-Warbler *Nesillas typica*	8	6	14
Common Newtonia *Newtonia brunneicauda*	22	32	54
Common Jery *Neomixis tenella*	11	14	25
Sunbirds[1] *Nectarinia* spp.	11	8	19
Madagascar White-eye *Zosterops maderaspatana*	26	29	55
Nelicourvi Weaver *Ploceus nelicourvi*	11	24	35
Crested Drongo *Dicrurus forficatus*	17	30	47
Total number of flocks	47	42	89

[1] Data are combined for *Nectarinia souimanga* and *N. notata* because of difficulty of identification in field.

Table 2. *The number of observations for each category of flocking in the Perinet/Analamazaotra (Andasibe) Reserve, Madagascar. Data for August and October are combined*

Species	Total	Solitary	Single-species flocks	Mixed-species flocks	Percentage of mixed-species flocks
Common Newtonia	85	21	10	54	64
Madagascar White-eye	69	1	13	55	79
Madagascar Paradise Flycatcher	65	12	2	51	78
Crested Drongo	64	13	4	47	73
Long-billed Greenbul	39	1	5	33	85
Nelicourvi Weaver	37	1	1	35	95
Red-tailed Vanga	37	2	2	33	89
Common Jery	36	9	2	25	69
Spectacled Greenbul	32	1	4	27	84
Blue Vanga	23	0	0	23	100
Ashy Cuckoo Shrike	22	1	1	20	91
Tylas Vanga	17	1	0	16	94
Madagascar Brush-Warbler	126	84	28	14	11
Sunbirds[1]	59	34	4	21	35
Madagascar Bulbul	52	4	30	18	35

[1] Data for *Nectarinia souimanga* and *N. notata* are combined.

served in more than 50% of 42 flocks. Except for the Madagascar Lesser Cuckoo *Cuculus rochii*, all participants were passerines, and all passerines observed in the forest except one, the Madagascar Starling *Hartlaubius auratus*, occurred at least once in mixed-species flocks. In total, 25 species were seen participating in mixed-species flocks and 22 of them occurred both in August and October. Because the composition of mixed-species flocks was similar in August and October (Table 1), the data were combined in later analyses.

All species except four (Madagascar Bulbul *Hypsipetes madagascariensis*, Madagascar Brush-Warbler *Nesillas typica* and two species of sunbirds) were observed more often in mixed-species flocks than in single-species flocks or as solitary individuals (Table 2). These are defined as regular species. Although we have no quantitative data, the Madagascar

Table 3. *Interspecific association (Cole's coefficient of association) of species occurring regularly in mixed-species flocks*

	Species[1]										Total no. of observations
	NEW	FLY	DRON	NELI	RVAN	LBGB	SGB	JERY	BVAN	ACS	TVAN	
Madagascar White-eye	0.26*	0.02	0.15	0.10	0.08	0.05	0.01	0.01	−0.16	0.04	−0.09	55
Common Newtonia		0.18	0.14	0.18*	0.18**	0.12	−0.15	0.07	0.03	0.09*	0.07	54
Madagascar Paradise Flycatcher			0.13	0.06	0.03	0.00	−0.10	−0.02	0.05	0.04	−0.02	51
Crested Drongo				0.26**	0.02	0.19*	−0.09	−0.09	0.14*	0.07	0.04	47
Nelicourvi Weaver					0.00	0.41***	0.14	0.01	0.04	0.04	0.06	35
Red-tailed Vanga						0.09	0.09	0.31	−0.06	0.02	0.11	33
Long-billed Greenbul							−0.20	0.07	0.02	0.10	0.04	33
Spectacled Greenbul								−0.34	0.00	0.05	−0.18	27
Common Jery									0.08	−0.29	0.07	25
Blue Vanga										0.05	0.26**	23
Ashy Cuckoo Shrike											0.03	20
Tylas Vanga												16

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[1] Species abbreviations as in Figure 1.

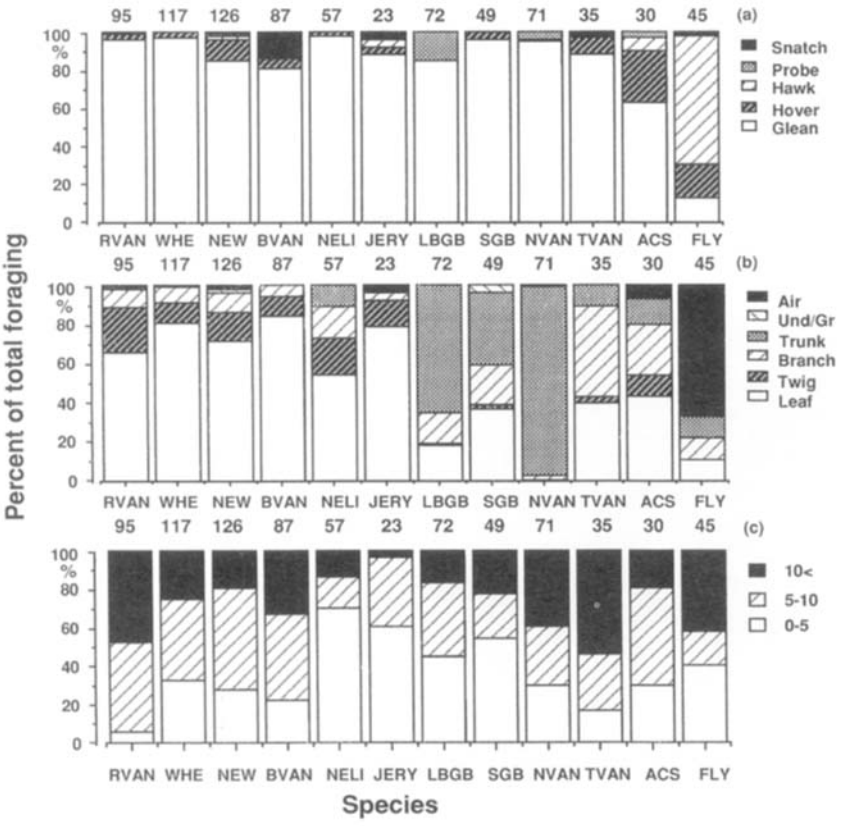

Figure 1. Percentage utilization of foraging categories by regular species in mixed-species flocks in Madagascar. (a) Foraging technique; (b) Foraging location; (c) Foraging height. Figures above graphs are the number of observations. RVAN = Red-tailed Vanga; MWHE = Madagascar White-eye; NEW = Common Newtonia; BVAN = Blue Vanga; NELI = Nelicourvi Weaver; JERY = Common Jery; LBGB = Long-billed Greenbul; SGB = Spectacled Greenbul; NVAN = Nuthatch Vanga; TVAN = Tylas Vanga; ACS = Ashy Cuckoo Shrike; FLY = Madagascar Paradise Flycatcher.

White-eye and the Common Newtonia were often observed with three or more conspecific individuals in mixed-species flocks. Other participants were often observed in twos or singly.

Coefficients of association were calculated for all 12 regular species. Of 66 combinations, nine showed significant association (Table 3). No case of mutual avoidance was significant, nor was prominent hostile behaviour observed between any species. The Common Newtonia showed a significant association with four of the other species, and both Nelicourvi Weaver and Crested Drongo were significantly associated with three others.

Foraging niche

Figure 1 compares foraging height, foraging location in vegetation and foraging technique among 12 species for which there were sufficient data, and a dendrogram based on the combined data on foraging technique and foraging location is shown in Figure 2. At the 70% similarity level, five clusters can be recognized. All were gleaners except the Madagascar Paradise Flycatcher, which was separated on its own (Fig. 1a). Among gleaners, six species (Red-tailed Vanga *Calicalicus madagascariensis*, Madagascar White-eye, Common Newtonia, Blue Vanga *Cyanolanius madagascariensis*, Common Jery *Neomixis tenella* and Nelicourvi Weaver), which concentrated their foraging activities in foliage (Fig. 1b), were combined as a foliage gleaning group. The Tylas Vanga *Tylas eduardi* and Spectacled Greenbul *Phyllastrephus zosterops* were combined as a branch–foliage gleaning group. In spite of a tendency to forage in similar locations as these two species, the Ashy Cuckoo Shrike *Coracina cinerea* was separated into another cluster because of a difference in foraging technique (Figs. 1a and b). The Long-billed Greenbul *Phyllastrephus madagascariensis* and Nuthatch Vanga *Hypositta corallirostris* were combined as a trunk gleaning group (Fig. 1b). Although foraging data were few, the Crested Drongo was often seen hawking in the same manner as the Madagascar Paradise Flycatcher.

All regular members of mixed-species flocks could be divided into three groups according to their foraging height (Fig. 1c). The Red-tailed Vanga and Tylas Vanga often foraged above 10 m. The Nelicourvi Weaver, Long-billed and Spectacled Greenbuls and the Common Jery often foraged below 5 m. The Madagascar White-eye, Common Newtonia, Blue Vanga, Ashy Cuckoo Shrike, Nuthatch Vanga and Madagascar Paradise Flycatcher used all layers, particularly often between 5 m and 10 m.

DISCUSSION

Of the 46 passerines recorded in the Perinet/Analamazaotra (Andasibe) Reserve (Jenkins 1987), 25 species (54%) were

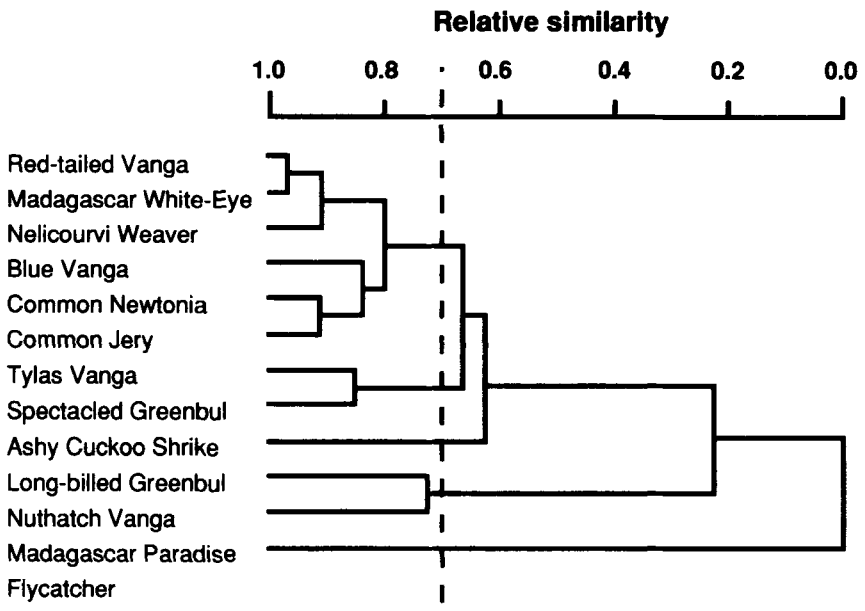

Figure 2. Dendrogram showing interspecific affinities among Malagasy birds in foraging technique and foraging location in vegetation. The dashed line indicates the 70% similarity level.

observed participating in mixed-species flocks at least once, and 17 species (37%) participated more than 10 times. The number of species participating in mixed-species flocks in Madagascar is rather smaller than in tropical forests elsewhere, cf. 55 species in Brazil (Davis 1946), 42 species in Costa Rica (Powell 1979) and 40 species in Sarawak (Croxall 1976), but the proportion of species participating is higher, cf. 24.6% in Mexico (Hutto 1987). The low species diversity in this area may be responsible for these differences. The proportion of migratory species in mixed-species flocks was very small (only the Madagascar Lesser Cuckoo) in the present study, as in other tropical rainforests (cf. Davis 1946, Moynihan 1962, Croxall 1976, Jones 1977, Powell 1979). Because migratory species are very few among Malagasy birds, particularly in land birds (Rand 1936), mixed-species flocks were composed entirely of resident species and, consequently, the composition of the flocks hardly changed seasonally.

Of the 89 mixed-species flocks observed, 70 (79%) included one or both of the Madagascar White-eye and Common Newtonia, which often occurred with several conspecifics. In both single-species and mixed-species flocks, white-eyes and newtonias incessantly uttered noisy calls which may have attracted other species. It is likely that these two were nuclear species *sensu* Moynihan (1962). Moynihan (1962) suggested that integrated mixed-species flocks include certain species showing a high degree of conspecific aggregation and playing a nuclear role. In the course of foraging or moving through vegetation, the single-species flocks of white-eyes and newtonias may have been joined by pairs or individuals of other species, forming a mixed-species flock.

Rand (1936) did not use the term 'nuclear species' but, based on its numerical dominance in mixed-species flocks, suggested such a role for the White-headed Vanga *Leptopterus viridis* in the Malagasy rainforests he investigated (also see Moynihan 1962). However, in the present study and even in other areas (pers. obs.), this species seldom showed conspecific aggregation and appeared in the minority compared with the Madagascar White-eye and Common Newtonia. The latter two species may be better suited to the role of nuclear species in mixed-species flocks in Malagasy rainforests.

The patterns in foraging niche partition in the present study agree, in general, with the results obtained by Rand (1936) and Thompson (1987). Mixed-species flocks were composed entirely of species foraging above the middle layers (Rand 1936, present study). Those foraging near ground cover, such as the Madagascar Brush-Warbler, Madagascar Magpie Robin *Copsychus albospecularis* and Crossley's Babbler *Mystacornis crossleyi*, occurred infrequently in mixed-species flocks. Because they are cryptic and spatially separated from those foraging in upper layers, they may gain few advantages, either food-mediated or predator-mediated, from mixed-species flocking. Differences in travelling speed compared with flock members may also impose a cost on these species in keeping pace with flocks (Hutto 1988).

Separation in foraging niche among the members of mixed-species flocks has been observed in several studies (e.g. Morse 1970, Austin & Smith 1972, Hogstad 1978). Croxall (1976) found little overlap in foraging behaviour among regular species. There was some separation in foraging niche: most species were gleaners but, among members of the same flock foraging on a similar substrate by a similar technique, there was separation by foraging height. For example, among five foliage-gleaners, the Red-tailed Vanga foraged in the highest strata, the Madagascar White-eye, Common Newtonia and Blue Vanga at medium levels and the Common

Jery in the lowest stratum. However, there was also considerable overlap between the two nuclear species, the Madagascar White-eye and the Common Newtonia, and these two species associated frequently with each other in the same flocks.

Overlapping in foraging niche might be important in mixed-species flocks; most flock members were gleaners, which may enhance their foraging efficiency by overlapping foraging heights with one another (copying) (Morse 1970, Waite & Grubb 1988). Similarly, other attendant species in mixed-species flocks may gain advantages from flocking; e.g. flycatching species such as the Madagascar Paradise Flycatcher and the Crested Drongo are likely to catch insects flushed from substrates by the gleaners (Rand 1936, Croxall 1976).

The functional significance of mixed-species flocking has been clarified among temperate species by experiments in the field or laboratory (e.g. Krebs 1973, Sullivan 1984, Waite & Grubb 1988). However, the numbers of species and individuals of flock members are much greater in the tropics, making it difficult to understand the factors influencing flocking without further studies on the roles of individual flock members and foraging shifts in and out of flocks.

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