ORIGINAL ARTICLE

# Breeding bird community and mixed-species flocking in a deciduous broad-leaved forest in western Madagascar

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**ORNITHOLOGICAL SCIENCE**



**Abstract** The breeding bird population of a deciduous broadleaved forest in western Madagascar was censused by means of territory mapping. Despite the foliage structure being simpler, neither species richness nor density was less than those in mature temperate forests. Species diversity was higher in the western Madagascan forest owing to the higher species evenness. Tree-cavity nesters and bark foragers were few because woodpeckers, nuthatches, and tits have not colonized Madagascar. The scarcity of birds nesting on or near the forest floor may be attributable to abundance of nest-predators such as large lizards and snakes in these areas. The bird community was dominated in abundance by the members of mixed-species flocks, almost all of which forage in the canopy. Mixed-flocking can be beneficial for these birds to avoid predation by raptors, which were frequently observed in the canopy. Since most of the flock members had relatively similar territory sizes resulting in similar densities, the high species evenness in this community may have resulted from mixed-flocking by canopy-foraging species.

**Key words** Forest bird community, Madagascar, Mixed-species flocks, Predators, Species evenness

Bird species diversity is generally higher in tropical forests than in temperate forests. This latitudinal gradient of species diversity has been mainly explained by external factors such as the structural complexity of habitat (MacArthur et al. 1966), climatic stability (Stiles 1978) and predictability or diversity of food resources (Karr 1971; Schoener 1971). In contrast, Powell (1989) explained the high species richness in the neotropical avifauna as arising from the internal structure of the community itself. Multispecies territoriality (i.e., the year-round communal defence of territory) by the core species of mixed-species flocks reduces the densities of small species because they have larger territories than expected from their body size. As a result, a greater number of small species can coexist owing to the under-utilization of food resources in such a community.

Madagascar, which lies within the tropical region, supports various kinds of forests including: rain forest, deciduous broad-leaved forest, and subarid scrub. Although the avifauna is highly unique with >50% of the breeding species endemic (Langrand 1990), there have been no quantitative studies of Madagascan forest bird communities. Multispecies bird flocks are observed all year round in Madagascan forests (Eguchi et al. 1993; Hino 1998, 2000) as well as in other tropical forests (Bell 1983; Powell 1989; Jullien & Thiollay 1998). Hino (1998, 2000) has shown that the core species of mixed flocks in deciduous broadleaved forest in Madagascar gain mutual benefits relating to foraging and/or anti-predation. The deciduous forest is an appropriate habitat to examine the factors, other than foliage structure, that may explain the differences between bird communities in tropical and temperate forests. In this paper, I describe the characteristics of breeding bird communities in a deciduous broad-leaved forest in western Madagascar by comparing them with those of temperate forests in Japan. Then I consider the effect of predators and multispecies flocking to explain the characteristics of the Madagascan bird community.

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## METHODS

This study was conducted in a 450×550-m quadrat (called Jardin A) in a deciduous broadleaved forest in the Ampijoroa Forest Reserve (16°35′S, 46°82′E; ca. 200 m asl), about 110 km southeast of Mahajanga. In this forest, 113 tree species are listed by Razafy (1987). The mean annual precipitation of the area is about 1500 mm, 97% of which is recorded during the wet season (November to April), and the mean annual temperature is 26.8°C (Razafy 1987).

Ten censuses of breeding bird populations were conducted using the territory mapping method, walking steadily around the whole study site from 10–20 October 1994. All birds seen or heard within 50 m of either side of the census trail were recorded on a scale map. The territories overlapping the border of the study area were recorded as half territories (0.5). Raptorial species (e.g. *Otus rutilus*, *Accipiter madagascariensis*, *A. francessi*, *Polyboroides radiatus*) and forest-edge species (e.g. *Falculea palliata*, *Merops superciliosus*, *Caprimulgus madagascariensis*, *Coracopsis vasa*), which were observed during the census, were excluded from the analysis of this study.

At each encounter, whether each individual participated in mixed-species flocks (foraging with two or more different species for more than 10 min; Jullien & Thiollay 1998) was recorded from 10 October to 12 November. The mixed-flocking propensity of each species was calculated as the percentage of the number of times the species was found foraging in a mixed flock relative to the total number of times this species was encountered (Jullien & Thiollay 1998). Categorization of foraging and nesting habits followed Langrand (1990), Yamagishi et al. (1997), Morris and Hawkins (1998) and my field observations, and body lengths followed Langrand (1990). Species diversity (D) and evenness (E) were calculated using Simpson's indices: $D=1/\Sigma P_i^2$ and $E=D/S$, where $P_i$ is the proportion of abundance for species i and S is the number of species.

Vegetation structure was surveyed in 120 sample plots (5 m×5 m) at 50 m intervals on 15–17 November 1994. The number of trees or woody plants stems in each of four categories of diameter at breast height (DBH: <5 cm, 5–15 cm, 15–30 cm, 30 cm<) and the height of the tallest tree were recorded for each plot. At eight different height strata (0–1 m, 1–2 m, 2–4 m, 4–6 m, 6-10 m, 10 m<), and four categories of foliage volume (0: none, 1: 1–33%, 2: 34–66%, 3: 67–100%) were recorded by eye in all plots, averaged and multiplied by 25% for each stratum.

For comparison, three studies of the bird communities in deciduous broadleaved forests in Japan were selected. The following points were considered in selecting the studies: (1) the territory mapping technique had been used; (2) the number of censuses was equal to or greater than 10; (3) the census area was larger than 10 ha; (4) the forests were natural and undisturbed (e.g. no grazing); (5) coniferous trees were not a major component of the forests; (6) the forest area, including the census site, was large enough not to be influenced by surrounding habitats.

## RESULTS

The Madagascan study site was characterized by its high density of small trees or woody plants <15 cm in DBH (Table 1). The canopy was lower than 16 m (mean=12.4 m±1.3 SD, N=120). Foliage coverage was most dense at 4–8 m in height (Fig. 1).

**Table 1.** Densities of trees and woody plants in DBH-class.

| DBH (cm) | Number/ha |
|---|---|
| 1–5 | 23,294 |
| 5–15 | 3,455 |
| 15–30 | 336 |
| 30– | 54 |
| Total | 27,139 |

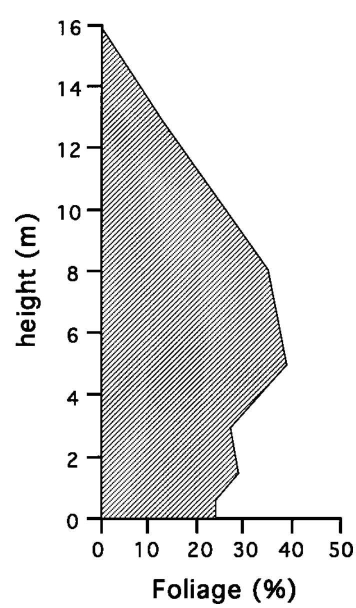


**Fig. 1.** Vertical distribution of foliage coverage.

**Table 2.** The body length, nesting- and foraging-sites, food item, density and mixed-flocking propensity of each species of breeding birds.

| Species | BL[1] (cm) | Nesting site[2] | Foraging site[3] | Food item[4] | Density (pairs/km$^2$) | Mixed-flocking propensity (%)[5] |
|---|---|---|---|---|---|---|
| *Dicrurus forficatus* | 26 | C | F/A | A | 28.3 | 48.1 (52) |
| *Schetba rufa* | 20 | C | G | A | 34.3 | 50.0 (46) |
| *Cyanolanius madagascariensis* | 16 | C | F | A | 20.2 | 87.5 (16) |
| *Xenopirostris damii* | 23 | C | B | A | 4.0 | 36.4 (11) |
| *Leptopterus viridis* | 20 | C | B | A | 2.0 | 33.3 ( 3) |
| *Nectarinia souimanga* | 10–11 | C | F | A/P | 44.4 | 28.6 (21) |
| *Nectarinia notata* | 14 | C | F | A/P | 12.1 | 25.0 ( 8) |
| *Terpsiphone mutata* | 18 | C | A | A | 38.4 | 48.3 (58) |
| *Neomixis tenella* | 10 | C | F | A | 34.3 | 35.7 (14) |
| *Newtonia brunneicauda* | 12 | C | F | A | 58.6 | 56.3 (32) |
| *Copsychus albospecularis* | 18 | H | G | A | 26.3 | 12.5 (16) |
| *Hypsipetes madagascariensis* | 24 | C | F | A/P | 34.3 | 33.3 (18) |
| *Phyllastrephus madacascariensis* | 18–22 | C | F/B | A | 28.3 | 76.0 (25) |
| *Coracina cinerea* | 24 | C | F | A | 22.2 | 62.1 (29) |
| *Upupa epops* | 32 | H | G | A | 10.1 | 14.3 (14) |
| *Leptosomus discolor* | 50 | H | F | A | 4.0 | 0.0 ( 7) |
| *Eurystomus glaucurus* | 29–32 | H | F | A | 6.1 | 0.0 (11) |
| *Centropus toulou* | 45–50 | C | G | A | 4.0 | 0.0 ( 3) |
| *Coua cristata* | 40–44 | C | F | A | 22.2 | 37.0 (27) |
| *Coua coquereli* | 42 | C | G | A | 16.2 | 0.0 (21) |
| *Coua ruficeps* | 42 | C | G | A | 12.1 | 0.0 (13) |
| *Cuculus rochii* | 28 | P | F | A | 2.0 | 0.0 ( 3) |
| *Coracopsis nigra* | 35 | H | F | P | 2.0 | 0.0 ( 4) |
| *Agapornis cana* | 14–16 | H | F | P | 2.0 | 0.0 ( 3) |
| *Streptopelia picurata* | 28 | C | G | P | 16.2 | 0.0 (17) |
| *Treron australis* | 32 | C | F | P | 2.0 | 0.0 ( 2) |
| *Turnix nigricollis* | 15 | G | G | A/P | 4.0 | 0.0 ( 5) |
| *Mesitornis variegata* | 31 | G | G | A/P | 8.1 | 16.7 ( 6) |
| *Lophotibis cristata* | 50 | C | G | A | 2.0 | 0.0 ( 6) |

[1] Body length followed Langrand (1990).
[2] C=canopy, H=tree-hole, G=ground or bush, D=deposition.
[3] F=foliage, B=bark, G=ground or bush, A=air, F/A or F/B=both sites.
[4] A=animals (arthropods, small reptiles), P=plant materials (seeds, fruits, nectar), A/P=both food.
[5] the percentage of the number of times found foraging in a mixed flock relative to the total number of times encountered (shown in parenthesis).

A total of 29 species and 499 pairs/km$^2$ of birds bred in the study area (Table 2). These values did not differ from those in Japanese forests (Table 3). Nevertheless, the species diversity was high in Madagascar owing to the high species evenness in comparison to Japanese communities (Table 3).

Most Madagascan birds (69% of species and 87% of individuals) nest in canopy foliage including tree forks, very few nest in tree-holes or on the ground (or in bushes) (Table 3). These nesting habits are very different from those of forest birds in Japan. The composition of foraging-site groups also differed between bird communities in Madagascar and Japan although the difference was very small in comparison to that of nesting-site groups. In Madagascar, bark-foraging birds were fewer while foliage-foraging birds were more abundant. The composition of the food items taken by both bird communities was similar.

Seventeen species were observed in mixed-species flocks during the breeding season. Of these, seven species were regular members of mixed flocks (flocking propensity=48–88%) and another seven species were occasional members (flocking propensity=25–

**Table 3.** A comparison of species numbers and densities of each group for nesting- and foraging sites and food items, species-diversity and evenness of the bird community between Madagascan and Japanese forest bird communities.

| | Madagascar | | Japan[5] | |
|---|---|---|---|---|
| | No. of species[4] | No. of pairs/km$^2$ | No. of species[4] | No. of pairs/km$^2$ |
| Nesting site[1] | | | | |
| C | 20.0 | 436.4 | 7–11 | 61–83 |
| T | 6.0 | 50.5 | 10–12 | 195–279 |
| U | 2.0 | 12.1 | 7– 9 | 111–209 |
| D | 1.0 | 2.0 | 1 | 2–9 |
| Foraging site[2] | | | | |
| F | 15.0 | 294.9 | 10–12 | 185–229 |
| B | 2.5 | 20.2 | 5– 6 | 53–61 |
| G | 10.0 | 133.3 | 9–11 | 109–180 |
| A | 1.5 | 52.1 | 2– 4 | 39–100 |
| Food item[3] | | | | |
| A | 22.5 | 427.3 | 20–21 | 317–404 |
| P | 6.5 | 73.7 | 7– 9 | 74–152 |
| O | 0.0 | 0.0 | 1– 2 | 2–6 |
| Total | 29.0 | 499.0 | 29–31 | 422–491 |
| Species diversity | | 16.9 | | 13.3–15.0 |
| Species evenness | | 0.58 | | 0.46–0.52 |

1 C=canopy, H=tree-hole, G=ground or bush, D=deposition
2 F=foliage, B=bark, G=ground or bush, A=air
3 A=animals (arthropods, small reptiles), P=plant materials (seeds, fruits, nectar), O=ominifarious food
4 0.5 was given to each group for the birds categolized to two groups (e.g., F/B in Table 2)
5 Fujimaki (1986, 1988) and Hino & Nakano (1992).

37%). Almost all of these species were small- or medium sized birds (<30 cm in BL) eating arthropods or small reptiles in the canopy, although the substrates preferred (foliage, bark, air) varied among species. In contrast, the bird species that did not, or rarely participated in mixed flocks (flocking propensity=0–17%) were large birds (>30 cm) that typically forage on the ground and those that eat plant material.

Almost all of the most abundant species were regular or occasional members of mixed-species flocks (Fig. 2). A significant positive correlation was found between abundance and flocking propensity (Kendall's $\tau$=0.506, $P<0.0001$).

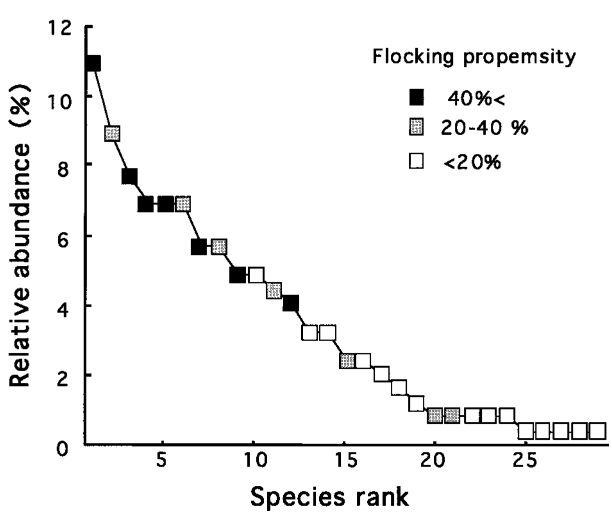


**Fig. 2.** Mixed-flocking propensity and the relative abundance of species arranged in decreasing order of abundance.

## DISCUSSION

Although the deciduous broad-leaved forest studied in western Madagascar was mature, the characteristics of its vegetation structure (i.e. abundant small trees and low foliage height) corresponded to those of a young forest in a temperate region (Aber 1979). In general, bird species diversities are lower in young forests than in mature forests owing to their simpler structure (Bongiorno 1982; Helle 1985).

Neither the species richness nor the density of breeding birds (except raptorial or forest-edge species) in the study area differed from those of mature temperate forests in Europe and Japan (about 30 species and 500–700 pairs/km$^2$; Hino 1990, 1993). Moreover, species diversity was high owing to the high species evenness. That is, the Madagascan study area had a more diverse bird community than would be predicted from an examination of its vegetation structure. Razafy (1987) listed 113 species of trees in the forest reserve including the study area. This number of tree species is much higher than that seen in temperate forests (<40 species at most, Hino 1990). One of the factors explaining the high bird diversity of the study area may be the high tree species diversity of the forest. Many studies have shown that more diverse bird communities are found in forests with more diverse tree composition (e.g. Rice et al. 1984; Verner & Larson 1989).

The composition of nesting-site groups differed considerably between Madagascan and Japanese bird communities. Tree-hole nesters were few in Madagascar because ancestral woodpecker, nuthatch, and tit species failed to colonize the island. In particular, the absence of woodpeckers (which excavate their own nesting cavities annually thereby creating a valuable cavity resource in trees), must have had a considerable negative influence on the nesting habits of other species. The scarcity of species nesting on or near the forest floor may be attributable to the abundance of terrestrial nest-predators such as large lizards *Oplurus cuvieri* and snakes *Leioheterodon madagascariensis*. These reptiles are considered to be major predators on the eggs and/or fledgling of *Schetba rufa* (Eguchi et al. 2001), *Terpsiphone mutata* (T. Mizuta pers. com.) and *Coua coquereli* (T. Masuda pers. com.) although they build their nests in the low (1–5 m high) canopy.

The composition of foraging–site groups also differed in abundance between Madagascan and Japanese bird communities. The reason why the bark-foraging birds were few will be the same one why the cavity nesters are few, that is, the failure in colonization of ancestral woodpecker, nuthatch, and tit species. Although some of the Vangidae species observed during this study, such as *Xenopirostris damii* and *Leptopterus viridis*, have evolved as bark foragers thorough adaptive radiation (Yamagishi & Eguchi 1996), this niche seems not to have been full occupied by birds in Madagascar.

The present bird community was dominated, in terms of abundance, by the members of mixed-species flocks. Flocking propensities were more than 48% among regularly flocking species and more than 25% among occasionally flocking species despite observations being made during the breeding season. In the non-breeding season, flocking propensities were almost double (Hino 1998). Almost all flocking species forage in the canopy, where raptors (e.g. *O. rutilus*, *A. madagascariensis*, *A. francessi*, *P. radiatus*) were frequently observed. Mixed-species flocking may be an effective strategy for avoiding predation as well as of achieving increased foraging efficiency (reviews in Morse 1977, Barnard and Thompson 1985). In fact, mobbing of raptors by flock members was often observed in the study area.

The anti-predatory value of mixed-flocking may be enhanced if the flock members move consistently together within a communal territory, that is, multi-species territoriality in neotropical rain forests (Munn & Terborgh 1979; Powell 1989; Jullien & Thiollay 1998). Powell (1989) demonstrated that multispecies territoriality should increase species richness. Species evenness should also increase through this system since the community is composed of species with the same density. Although the mixed-flock members in the study area did not hold communal territories rigorously, similar sized territories appear to be maintained by regular flock-members (except the most dominant species *Newtonia brunneicauda*) resulting in similar densities (20–38 pairs/km$^2$). *N. brunneicauda* may have adjusted its home range size to that of the other flock members by forming conspecific flocks consisting of two pairs with neighboring territories (Hino 2000). In the present avian community, therefore, the high species evenness may have resulted from mixed-flocking among canopy-foraging species.

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