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Vertical distribution and daily patterns of birds in the dry deciduous forests of central western Madagascar

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Abstract: Data on the vertical distribution and ecological requirements of forest birds in western Madagascar are poorly documented. Strata use of forest-dwelling birds associated with vegetation structure and daily temperature patterns was examined in the dry deciduous forest of Kirindy. Six line transects of 1000 m each were used to survey birds and linear sampling to quantify vegetation structure. Data loggers were employed to record differences in temperature across vertical forest strata. A total of 3468 observations of 37 bird species were recorded. In the early morning, birds called frequently and used the canopy, at mid-day, when temperature in the upper strata increased on average around 7ºC, they tended to descend along a vertical gradient to the denser vegetation of the understory, presumably to avoid heat stress. In the case of larger-bodied canopy birds, they occupied the mid-story during the heat of the day. Regardless of the time of the day, the mid-story was widely used by forest birds for feeding, roosting, and preening. These results demonstrate the sensitivity and vertical movements of birds to varying environmental conditions and provide new information on the ecology of Malagasy dry forest-dwelling birds.

Key words: Birds; vertical strata use; daily pattern; dry deciduous forests; Madagascar.

Introduction

In general, forest-dwelling birds present considerable variation in terms of species composition across the vertical vegetation strata, ranging from the ground to canopy (Dinanti et al. 2018). Indeed, many species of birds show strict stratification, which has been interpreted as adaptations to a particular vertical portion of the forest habitat (Brokaw and Lent 1999). On the other hand, a number of studies have shown that in forest-dwelling birds there is often a daily pattern of shifts to different vertical portions of the forest (Bell 1982; Walther 2002; Chmel et al. 2016). These results have highlighted that shifting patterns in the vertical strata by birds are associated with ecological factors, including vegetation structure,

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temperature, and ambient light. This information is important to understand aspects of the ecological requirement, resilience and response of birds to environmental change. The analysis of vertical distributions of birds provides important insight associated with conservation strategies and forest management (Jayson and Mathew 2003).

Different publications on Malagasy birds report in a general fashion the vertical distribution of forest-dwelling taxa (e.g. Langrand 1990; Morris and Hawkins 1998; Raherilalao and Goodman 2011; Safford and Hawkins 2013), but precise details in a quantitative sense on the forest strata occupied or daily shifts are poorly documented. Some studies have reported on the vertical distribution of Malagasy birds (Yamagishi et al. 1992; Urano et al. 1994; Rajaonarivelo 2016), but most of this work has focused on a species, a genus, or a specific family, and few details are available at the community level. This current study has two goals: 1) to document the vertical stratification of the avian community occupying a dry deciduous forest in central western Madagascar and 2) to document daily shifts in the vertical strata used by birds related to vegetation structure and temperature.

Materials and methods

Study area

The study was conducted in the Kirindy Forest (Centre National de Formation, d'Études et de Recherches en Environnement et Foresterie or CNFEREF, hereafter "Kirindy"), part of Menabe Antimena Protected Harmonious Landscape, and located in central western Madagascar. The site, an area of lowland dry deciduous forest, ranging between 18 to 40 m above sea-level, is situated about 40 km northeast of Morondava off the Route Nationale 8 (RN8) that leads from Mahabo to Belo sur Tsiribihina. The study site located at 20°03'–20°10'S, 44°28'–44°46'E, is a forest concession covering 10,000 ha and includes an ecotourism zone administrated by CNFEREF and a research station managed by the Deutsches Primatezentrum (DPZ).

The vertical structure of the forest concession is classified into three distinct layers: lower, intermediate and upper stratum (canopy) including emergent trees (Rakotonirina 1996). Forest height depends on the soil characteristic and local water regime. In the more humid areas, trees can reach 20 to 25 m, while in the driest areas, canopy height rarely attains 12 to 15 m. Goodman et al. (2018) reported that the forest height at the site is between 12 to 20 m, and the dense understory vegetation between 1 and 5 m is dominated by lianas and shrubs. Generally, in the drier forested parts of the concession, the intermediate and upper strata can be combined at the level of the intermediate layer. However, in the rich humid soils, the upper stratum is well separated from the intermediate layer (Rakotonirina 1996). This variation in vegetation structure is linked to variation in plant species composition, as intraspecific variation depending on soil characteristic. For the current study, sampling areas where laid in an area of the forest with a canopy height between 8 and 20 m.

Daily temperatures average is between 20.0°C to 30.3°C and mean annual precipitation is around 954 mm (Goodman et al. 2018). Two distinct seasons characterize the region with a long dry period from May to October, followed by a rainy season from November to April. In the context of this study, data were collected during the rainy season (25.I. to 17.II.2018) at two different sites, which included the forest parcel CS7 (20°04'26''S, 44°40'17''E) situated to the south of the Piste de Conoco, and at N5 (20°03'24''S, 44°39'32''E) located in the northern portion of the concession. The breeding period of birds in Malagasy dry deciduous forest is generally from November to January (Raherilalao and Wilmé 2008).

Bird sampling

To census birds, preexisting trails were used in the form of line transects (Bibby et al. 2000). Three line transects were employed at each of the two study sites (CS7 and N5), each 1000 m in length and with stations at 200 m intervals. Observation was made three times a day, which included from 0600–0830 hours; from 0900–1130 hours, and from 1430–1700 hours. At the two study sites, each line transect line was censused on four occasions and at intervals of 12 days. During each census, species, activity, and vertical height of all birds directly observed up to 25 m distance on either side of the transect trail were estimated; these details were only noted at the first observation of a given individual (Bell 1982). To facilitate data collection, height was classified based on nine categories: 0 m (on the ground), 0–1 m, 1–2 m, 2–4 m, 4–6 m, 6–8 m, 8–10 m, 10–15 m, and 15–20 m. These values were grouped into four strata as defined by Walther (2002): (1) canopy or upper layer equivalent to the space from 8 to 20 m with discontinuous crown (including emergent), (2) mid-story or middle layer from 2 to 8 m, (3) understory or lower layer from the ground and 2 m, and (4) ground layer which included litter, dead wood, and fallen tree trunks. Activities of birds were grouped into five categories: feeding (foraging behavior and food consumption), singing (vocalizing which included contact and alarm calls), moving (short flight or hopping in vegetation or walking on vegetation or ground), roosting (perching on different forms of support, resting, and sun basking), and preening (Urano et al. 1994; Partasasmita et al. 2017).

Habitat characterization

Vegetation structure was characterized along the line transects based on the method of Gautier et al. (1994), that does not take into account floristic composition. Along each linear 1000 m transect at intervals of 20 m and using an 8 m vertical pole, the height of contact points with vegetation (trunk, branch, liana and leaves) was recorded. When over 8 m, the height was visually estimated. Vegetation cover at each stratum is expressed as a percentage and used to calculate the number of contacts at measured points along each transect (Gounot 1969).

Temperature recording

Data loggers "Tinytag View 2 TV-4500" (Gemini Data Logger, Chichester) were used to record temperature every 15 minutes at the central point of each transect and during the period of this study. Following the above defined vertical strata of vegetation structure, these devices were installed in a vertical manner: 1) understory between the ground and 2 m, 2) mid-story from 2 to 8 m, and 3) canopy from 8 to 20 m in height; all were placed in shaded areas to reduce direct solar radiation.

Data analyses

Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances, was used to document bird assemblage patterns as a function of height categories (0–1 m, 1–2 m, 2–4 m, 4–6 m, 6–8 m, 8–10 m, 10–15 m and 15–20 m). Analysis was performed with the "vegan" package in R (Oksanen 2019). The vertical distribution of the most common bird species was analyzed with the non-parametric Kruskal-Wallis test, as measures of bird species abundance violates parametric rules. A Dunn post hoc test was performed when a significant difference was obtained from the Kruskal-Wallis test. The data included in the analysis were focused on the abundance (number of contacts) of the most common birds, recorded at each strata category (ground, understory, mid-story and canopy) during 24 survey days. The same statistical tests were performed to examine variation in the proportion of vegetation cover and temperature across the vertical strata (understory to canopy).

The analysis of the effect of vertical stratification of the forest (four strata categories) and daytime (three time intervals) on the abundance of birds and their associated behavioral activities was assessed with generalized linear model. For this, the abundance for the bird community and for each of the most common species were tested separately, as well as the frequency on different bird behavioral activities. Linear regression was used to analyze the influence of environmental variables on the vertical variation of the abundance and species richness (number of species) of the bird community. The environmental variables refer to the proportion of vegetation cover (data from each transect lines), and mean daily minimum, maximum and mean of temperatures (values from each of the 24 survey days) along the vertical strata ranging from understory to canopy. All these different statistical analyses employed R software v.3.6.1 (R Core Team 2019), and probabilities of < 0.05 were considered significant.

Results

Vertical strata preference of birds

On the basis of vegetation height categories, there is a shift in bird species composition along the first axis from ground (0 m) to canopy at 15–20 m high (Figure 1). NMDS plot shows that the majority of bird species are mainly located and most abundant between 0–1 m to 8–10 m, and the curved line of points form an arch. *Lophotibis cristata* (Boddaert, 1783) and *Mesitornis variegata* Geoffroy Saint-Hilaire, 1838, were mainly found on the ground (Table 1) and showed a clear separation from the other largely ground-dwelling birds, which also frequented vertically superior strata (Figure 1). For example, *Nesoenas picturata* (Temminck, 1813) was significantly abundant on the ground and in the mid-story especially at 4–6 m (Tables 1 and 2). Parrots such as *Coracopsis nigra* (Linnaeus, 1758), and *C. vasa* (Shaw, 1812) were significantly more abundant on the canopy (Table 2). However, these species show different patterns canopy height classes, with *C. nigra* more often recorded at 8–10 m, while *C. vasa* was more frequent at 10–15 m (Table 1). Otherwise, bird species such as *Eurystomus glaucurus* (Müller, 1776) and *Leptopterus chabert* (Müller, 1776) seem more frequent at 10–15 m than at 15–20 m in height (Figure 1; Table 1). Generally, small insectivorous passerines such as *Newtonia brunneicauda* (Newton, 1863), *Ploceus sakalava* Hartlaub, 1861, and *Terpsiphone mutata* (Linnaeus, 1766) were more abundant in the mid-story compared to other strata (Table 2). However, *N. brunneicauda* was found especially at 4–6 m, while *P. sakalava* and *T. mutata* were more frequent at 2–4 m in height (Table 1).

Vertical variation in vegetation cover and temperature

The amount of vegetation cover varied as a function of forest height and the highest percentage (more than 70%) was found in the lower strata (0 to 2 m) (Figure 2). As vegetation height increased, vegetation cover declined, and the upper strata, above 12 m, was characterized by the lowest value (less than 20%). Further, there was significant variation in the percentage of vegetation cover between the different strata (Kruskal-Wallis test: df = 2; $\chi^2 = 29.26$; $p < 0.001$, Dunn post hoc test: $p < 0.001$). With respect to temperature, mean and maximum values decreased along the vertical gradient from the canopy to understory, while minimum temperature increased from the canopy to understory (Table 3).

Diurnal vertical movement

Daily fluctuation of the abundance of birds across vertical strata

The abundance of birds across the vertical strata varied significantly with the time of day (Generalized linear model: df = 6; $p < 0.001$). In general, both abundance and species richness were positively related to the vertical variation in vegetation cover and temperature (Table 4). However, as shown in Figure 3, the proportion of bird species observed in the

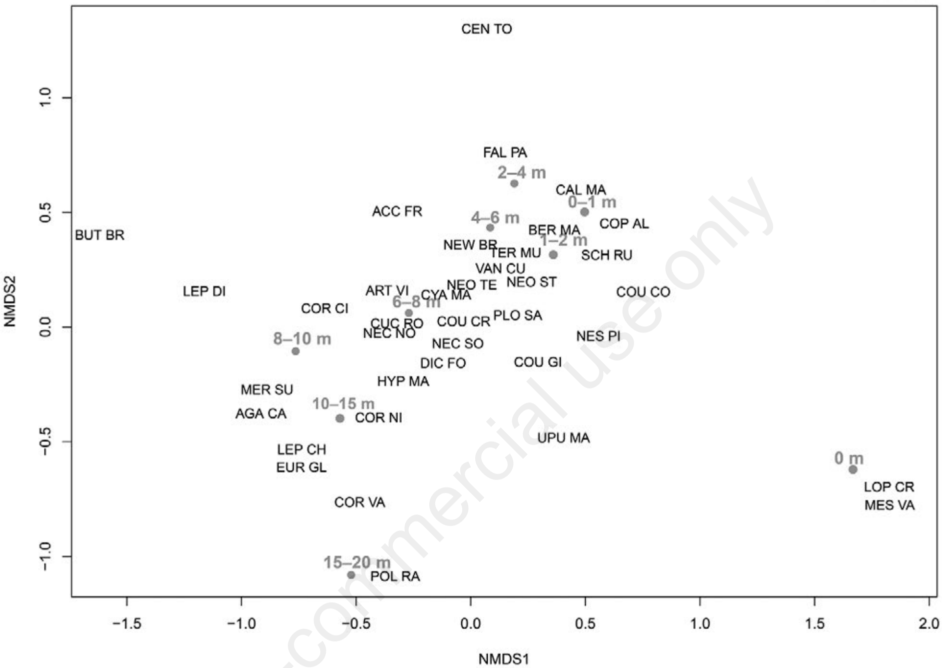

Figure 1. Two-dimensional non-metric multidimensional scaling (NMDS, Bray-Curtis distance metric, stress value = 0.094) plot, showing the assemblage of 37 bird species (marked in black) as a function of height categories (marked in grey). ACC FR: *Accipiter francesii* Smith, 1834, AGA CA: *Agapornis cana* (Gmelin, 1788), ART VI: *Artamella viridis* (Müller, 1776), BER MA: *Bernieria madagascariensis* (Gmelin, 1789), BUT BR: *Buteo brachypterus* Hartlaub, 1860, CAL MA: *Calicalicus madagascariensis* (Linnaeus, 1766), CEN TO: *Centropus toulou* (Müller, 1776), COP AL: *Copsychus albospecularis* (Eydoux & Gervais, 1836), COR CI: *Coracina cinerea* (Müller, 1176), COR NI: *Coracopsis nigra* (Linnaeus, 1758), COR VA: *Coracopsis vasa* (Shaw, 1812), COU CO: *Coua coquereli* Grandidier, 1867, COU CR: *Coua cristata* (Linnaeus, 1766), COU GI: *Coua gigas* Boddaert, 1783, CUC RO: *Cuculus rochii* Hartlaub, 1863, CYA MA: *Cyanolanius madagascarinus* (Linnaeus, 1766), DIC FO: *Dicrurus forficatus* (Linnaeus, 1766), EUR GL: *Eurystomus glaucurus* (Müller, 1776), FAL PA: *Falculea palliata* Geoffroy Saint-Hilaire, 1836, HYP MA: *Hypsipetes madagascariensis* (Müller, 1776), LEP CH: *Leptopterus chabert* (Müller, 1776), LEP DI: *Leptosomus discolor* (Hermann, 1783), LOP CR: *Lophotibis cristata* (Boddaert, 1783), MER SU: *Merops superciliosus* Linnaeus, 1766, MES VA: *Mesitornis variegata* Geoffroy Saint-Hilaire, 1838, NEC NO: *Nectarinia notata* (Müller, 1776), NEC SO: *Nectarinia souimanga* (Gmelin, 1788), NEO ST: *Neomixis striatigula* Sharpe, 1881, NEO TE: *Neomixis tenella* (Hartlaub, 1866), NES PI: *Nesoenas picturata* (Temminck, 1813), NEW BR: *Newtonia brunneicauda* (Newton, 1863), PLO SA: *Ploceus sakalava* Hartlaub, 1861, POL RA: *Polyboroides radiatus* (Scopoli, 1786), SCH RU: *Schetba rufa* (Linnaeus, 1766), TER MU: *Terpsiphone mutata* (Linnaeus, 1766), UPU MA: *Upupa marginata* Cabanis & Heine, 1860 and VAN CU: *Vanga curvirostris* (Linnaeus, 1766).

Table 1. Distribution of bird species recorded during this study based on vertical strata: Gr (ground), Un (understory), Mi (mid-story), and Ca (canopy), and height categories (m). Taxonomy status follows Goodman and Raherilalao (2018) and dietary classification based on Wilmé (1996). Fru (fruit), Ins (insect), Nec (nectar), See (seed), and Ver (vertebrate). N: number of observations.

Systematics			N	Strata (%)									Diet
Order	Family	Species		Gr	Un		Mi			Ca			
				0	0–1	1–2	2–4	4–6	6–8	8–10	10–15	15–20	
Ciconiiformes	Threskiornithidae	*Lophotibis cristata*	9	100									Ins, Ver
Falconiformes	Accipitridae	*Accipiter francesii*	11				18	18	55		9		Ver
		Buteo brachypterus	1							100			Ver
		Polyboroides radiatus	3						33	33		34	Ver
Gruiformes	Mesitornithidae	*Mesitornis variegata*	12	100									Ins
Columbiformes	Columbidae	*Nesoenas picturata*	139	57		3	10	16	9	5			Ins, See, Fru
Psittaciformes	Psittacidae	*Agapornis cana*	29						7	55	38		See
		Coracopsis nigra	167				3	11	15	39	30	2	Fru
		Coracopsis vasa	102					3	5	26	54	12	Fru
Cuculiformes	Cuculidae	*Centropus toulou*	4				75	25					Ins
		Coua coquereli	124	49	8	7	23	10	2	1			Ins, Fru
		Coua cristata	89			4	27	27	16	21	4	1	Ins, Ver, Fru
		Coua gigas	16	25		6	6	13	25	25			Ins, Ver
		Cuculus rochii	19				10	22	26	26	16		Ins
Coraciiformes	Meropidae	*Merops superciliosus*	12						25	50	25		Ins
	Coraciidae	*Eurystomus glaucurus*	74						4	30	61	5	Ins
	Leptosomidae	*Leptosomus discolor*	5						40	60			Ins, Ver
	Upupidae	*Upupa marginata*	24	50		4		8	4	34			Ins
Passeriformes	Campephagidae	*Coracina cinerea*	30					16	26	55	3		Ins
	Pycnonotidae	*Hypsipetes madagascariensis*	24			4	4	8	8	29	47		Ins, Fru
	Turdidae	*Copsychus albospecularis*	254	5	29	27	23	11	2	2	1		Ins
	Monarchidae	*Terpsiphone mutata*	256	1	4	10	34	29	15	5	2		Ins
	Cisticolidae	*Neomixis striatigula*	47		12	6	22	28	24	6	2		Ins
		Neomixis tenella	281		2	5	15	39	21	14	4		Ins

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Table 1. Continued from previous page.

Systematics			N	Strata (%)									Diet
Order	Family	Species		Gr	Un			Mi			Ca		
				0	0–1	1–2	2–4	4–6	6–8	8–10	10–15	15–20	
Passeriformes	Bernieridae	*Bernieria madagascariensis*	183	2	22	10	26	29	3	4	4		Ins
	Nectariniidae	*Nectarinia notata*	18				6	34	16	33	11		Ins, Nec
		Nectarinia souimanga	372		2	6	16	19	18	20	18	1	Ins, Nec
	Vangidae	*Artamella viridis*	20				5	30	30	30	5		Ins, Ver
		Calicalicus madagascariensis	7	14	14		14	44	14				Ins
		Cyanolanius madagascarinus	114			3	11	38	18	25	5		Ins, Fru
		Falculea palliata	11			9	9	73	9				Ins, Ver
		Leptopterus chabert	48						4	44	46	6	Ins, Fru
		Newtonia brunneicauda	313		2	3	20	39	25	10	1		Ins
		Schetba rufa	114	3	12	17	32	21	10	5			Ins, Ver
		Vanga curvirostris	14		7	7	22	14	36	14			Ins, Ver
	Dicruridae	*Dicrurus forficatus*	377		1	2	10	17	21	33	13	3	Ins
	Ploceidae	*Ploceus sakalava*	145		3	10	26	25	17	13	4	2	Ins, See

Table 2. Results of Kruskal-Wallis and Dunn post hoc tests on the vertical stratification of the most common bird species. For the codes to the vertical strata see Table 1.

Species	Kruskal-Wallis test			Dunn post hoc test					
	df	χ2	p	Gr–Un	Gr–Mi	Gr–Ca	Un–Mi	Un–Ca	Mi–Ca
Bernieria madagascariensis	3	58.46	***	***	***	ns	ns	**	***
Copsychus albospecularis	3	68.02	***	***	***	ns	ns	***	***
Coracopsis nigra	1	3.88	*						
Coracopsis vasa	1	24.47	***						
Coua coquereli	3	43.91	***	**	***	***	ns	*	***
Cyanolanius madagascarinus	2	37.33	***				***	***	***
Dicrurus forficatus	3	74.48	***	ns	***	***	***	***	ns
Nectarinia souimanga	2	44.22	***				***	***	ns
Neomixis tenella	2	29.37	***				***	*	**
Nesoenas picturata	3	21.10	***	***	ns	***	**	ns	*
Newtonia brunneicauda	3	71.04	***	ns	***	***	***	ns	***
Ploceus sakalava	2	24.93	***				***	ns	***
Schetba rufa	3	26.54	***	**	***	ns	ns	ns	***
Terpsiphone mutata	3	68.58	***	**	***	ns	***	ns	***

*P value = *** < 0.001, ** < 0.01, * < 0.05, ns: not significant.*

Table 3. Temperature values from the data-loggers placed in three different vertical strata. The results of the Kruskal-Wallis and Dunn post hoc tests on vertical variation for each variable are presented. For the codes to the vertical strata see Table 1.

Variables	Daily mean of temperature (ºC)			Kruskal-Wallis test			Dunn post hoc test		
	Understory	Mid-story	Canopy	df	χ2	p	Un–Mi	Un–Ca	Mi–Ca
Minimum temperature	22.1	21.9	21.6	2	1.45	ns			
Mean temperature	28.2	29.6	30.9	2	32.89	***	***	***	***
Maximum temperature	33.1	37.5	38.2	2	26.79	***	**	***	ns

*P value = *** < 0.001, ** < 0.01, ns: not significant.*

Table 4. Results of linear regression model on the influence of environmental factors (independent variables) on the daily variation of the abundance and species richness of birds (dependent variables) in the different vertical strata.

Dependent variables	Independent variables	F	rho	p
Bird abundance	Vegetation cover	65.06	0.73	***
	Minimum temperature	59.62	0.71	***
	Mean temperature	56.86	0.70	***
	Maximum temperature	82.95	0.77	***
Bird species richness	Vegetation cover	50.31	0.67	***
	Minimum temperature	51.46	0.68	***
	Mean temperature	44.02	0.64	***
	Maximum temperature	46.55	0.65	***

*P value = *** < 0.001.*

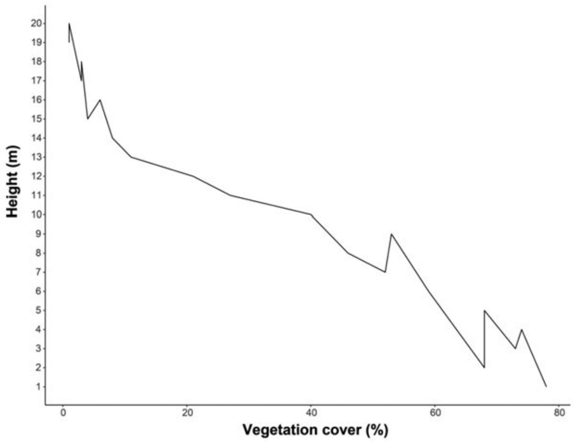

Figure 2. Vertical vegetation cover profile as a function of vertical height based on data from six surveyed line transects.

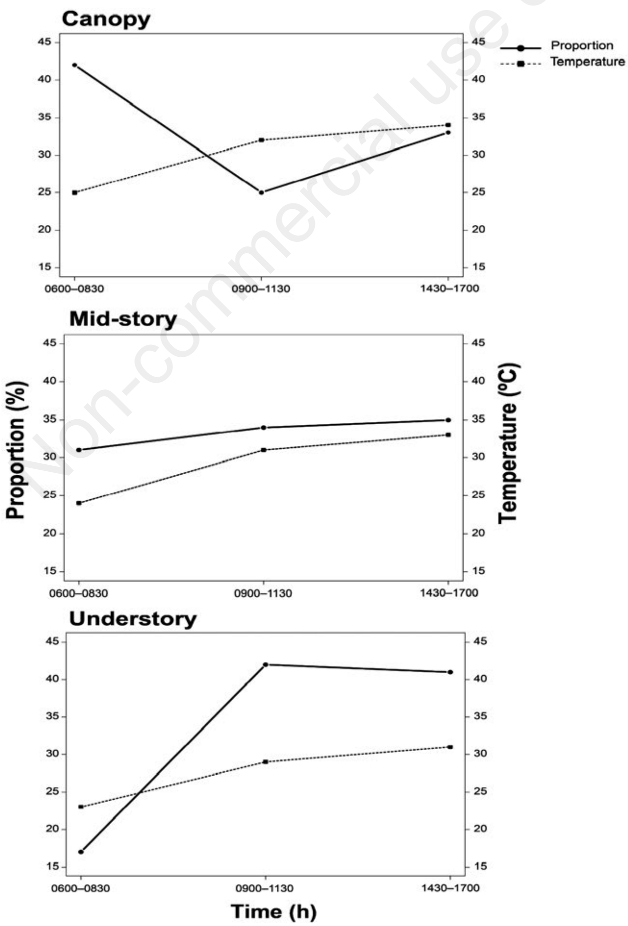

Figure 3. Proportion of birds observed in the three vertical strata as a function of daily variation in temperature.

canopy was not positively correlated with temperature. In fact, early in the morning between 0600–0830 hours, the proportion of bird observation in the understory was low (17%) and the highest proportion was found in the canopy (42%) and when the average ambient temperature (25.1ºC) was around 2ºC higher than in the understory (23.5ºC) (Figure 3). Towards the mid portion and the end of the morning, between 0900–1130 hours, temperature increased by about 7ºC in the canopy level (32.6ºC), while in the understory the temperature increased less (28ºC) (Figure 3). Hence, during this period, the proportion of bird observation in the canopy decreased by 17%, while in the understory the percentage increased by 25%. Unlike the case for canopy and understory, the proportion of observations at the mid-story level showed little variation during day hours, despite shifts in temperature (Figure 3).

The most common species recorded in the dry deciduous forest of Kirindy, showed significant daily variation in their vertical pattern (Table 5). Between 0600–0830 hours in the morning, the proportion of observations of *Bernieria madagascariensis* (Gmelin, 1789), *Neomixis tenella* (Hartlaub, 1866), *Schetba rufa* (Linnaeus, 1766), and *Terpsiphone mutata* were higher in the canopy compared to the other times of the day, when these species tended to descend vertically to the mid-story and understory (Figure 4). In the early morning (0600–0830 hours), *Copsychus albospecularis* (Eydoux & Gervais, 1836) was more frequent in the mid-story than in the canopy and during this period the ground-frequenting species *Nesoenas picturata*, shifted upward to the mid-story (Figure 4). By the end of the

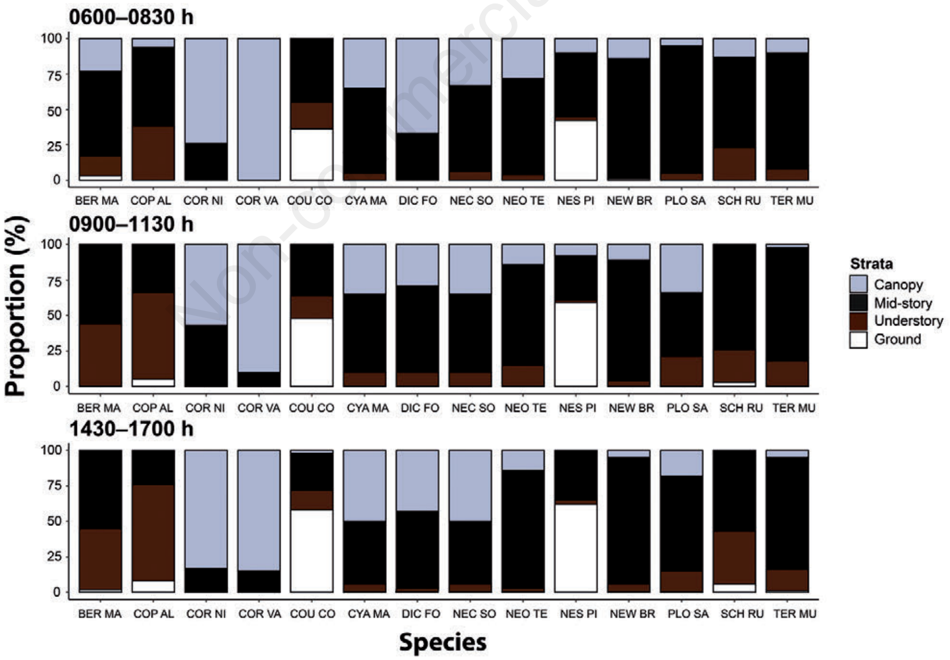

Figure 4. Proportion of observations for the most common bird species as a function of vertical strata and the time of day. BER MA: *Bernieria madagascariensis*, COP AL: *Copsychus albospecularis*, COR NI: *Coracopsis nigra*, COR VA: *Coracopsis vasa*, COU CO: *Coua coquereli*, CYA MA: *Cyanolanius madagascarinus*, DIC FO: *Dicrurus forficatus*, NEC SO: *Nectarinia souimanga*, NEO TE: *Neomixis tenella*, NES PI: *Nesoenas picturata*, NEW BR: *Newtonia brunneicauda*, PLO SA: *Ploceus sakalava*, SCH RU: *Schetba rufa*, and TER MU: *Terpsiphone mutata*.

Table 5. Results of the generalized linear model on the influence of vertical stratification, time of day and their interaction on the abundance of the most common bird species.

Species	Explanatory variables	Generalized linear model				
		df	Deviance	df residual	Deviance residual	p
Bernieria madagascariensis	Stratum	3	154.50	284	271.02	***
	Time of day	2	2.72	282	268.30	ns
	Stratum * Time of day	6	46.31	276	221.99	***
Copsychus albospecularis	Stratum	3	247.50	286	388.78	***
	Time of day	2	10.84	284	377.93	**
	Stratum * Time of day	6	36.16	278	341.76	***
Coracopsis nigra	Stratum	1	33.01	142	314.97	***
	Time of day	2	2.44	140	312.53	ns
	Stratum * Time of day	2	8.57	138	303.95	*
Coracopsis vasa	Stratum	1	85.31	142	254.06	***
	Time of day	2	8.21	140	245.84	*
	Stratum * Time of day	2	9.38	138	236.45	**
Coua coquereli	Stratum	3	86.43	287	235.92	***
	Time of day	2	9.66	285	226.25	**
	Stratum * Time of day	6	6.47	279	219.78	ns
Cyanolanius madagascarinus	Stratum	2	84.36	213	247.80	***
	Time of day	2	2.59	211	245.21	ns
	Stratum * Time of day	4	13.37	207	231.83	***
Dicrurus forficatus	Stratum	2	204.75	213	400.39	***
	Time of day	2	14.08	211	386.31	***
	Stratum * Time of day	4	45.97	207	340.34	***
Nectarinia souimanga	Stratum	2	149.68	213	299.50	***
	Time of day	2	1.95	211	297.55	ns
	Stratum * Time of day	4	10.27	207	287.28	*
Neomixis tenella	Stratum	2	218.05	213	391.57	***
	Time of day	2	3.92	211	387.65	ns
	Stratum * Time of day	4	18.54	207	369.11	***
Nesoenas picturata	Stratum	3	102.48	265	354.10	***
	Time of day	2	8.38	263	345.72	*
	Stratum * Time of day	6	12.91	257	332.81	*
Newtonia brunneicauda	Stratum	2	391.78	214	266.38	***
	Time of day	2	7.70	212	257.68	*
	Stratum * Time of day	4	9.57	208	249.11	*
Ploceus sakalava	Stratum	2	69.83	214	316.77	***
	Time of day	2	5.12	212	311.65	ns
	Stratum * Time of day	4	21.15	208	290.50	***
Schetba rufa	Stratum	3	112.32	284	330.05	***
	Time of day	2	3.59	282	326.46	ns
	Stratum * Time of day	6	16.38	276	310.08	*
Terpsiphone mutata	Stratum	3	386.74	285	253.58	***
	Time of day	2	7.68	283	245.89	*
	Stratum * Time of day	6	9.59	277	236.30	ns

*P value = *** < 0.001, ** < 0.01, * < 0.05, ns: not significant.*

morning (0900–1130 hours), *N. picturata* returned to the ground, *C. albospecularis* moved into the understory, and canopy birds such as *Coracopsis nigra* and *C. vasa* moved to the mid-story (Figure 4).

Daily behavior activity patterns and vertical strata

The proportion of bird behavioral activities varied during the course of day, with singing (37%) and preening (45%) mainly conducted between 0600–0830 hours, while activities such as moving (46%) and roosting (42%) were more frequent from 1430–1700 hours. Otherwise, feeding activities (37%) were mainly performed between 0900–1130 hours.

Regardless of time of the day, activities such as feeding, roosting, and preening were commonly conducted in the mid-story; moving activities were more frequent on the ground (Figure 5). However, significant variation was observed in the use of strata categories related to the time of day (Table 6). Song activities were generally carried out in the canopy (59%) between 0600–0830 hours, and the proportion decreased by 15% between 0900–1130 hours. During this latter period, the proportion of singing birds in the mid-story increased (43%), and between 1430–1700 hours the highest proportion (58%) was recorded in the canopy (Figure 5).

Discussion

Vertical strata preference of birds

During this study, bird species recorded in the dry deciduous forest of Kirindy used different vertical strata, ranging from the ground to canopy, and certain species showed a

Table 6. Results of the generalized linear model on the influence of vertical stratification, time of day and their interaction on different bird behavioral activities.

Activity	Explanatory variables	Generalized linear model				
		df	Deviance	df residual	Deviance residual	p
Feeding	Stratum	3	1273.50	282	636.14	***
	Time of day	2	11.20	280	624.94	**
	Stratum * Time of day	6	34.79	274	590.15	***
Singing	Stratum	3	861.69	284	390.77	***
	Time of day	2	8.37	282	382.40	*
	Stratum * Time of day	6	31.89	276	350.51	***
Moving	Stratum	3	234.92	284	341.82	***
	Time of day	2	25.21	282	356.21	***
	Stratum * Time of day	6	13.73	276	342.47	*
Roosting	Stratum	3	710.32	284	600.21	***
	Time of day	2	37.11	282	563.10	***
	Stratum * Time of day	6	41.32	276	521.78	***
Preening	Stratum	3	60.52	284	270.32	***
	Time of day	2	9.82	282	260.50	**
	Stratum * Time of day	6	27.17	276	233.32	***

*P value = *** < 0.001, ** < 0.01, * < 0.05.*

preference for a particular vertical stratum. For example, *Copsychus albospecularis* was more frequent in the understory and *Newtonia brunneicauda* in the mid-story. Some species used only one or two strata, such as *Coracopsis nigra* and *C. vasa* in the upper portion of the forest, and *Lophotibis cristata* and *Mesitornis variegata* were restricted to the ground.

Generally, vegetation cover plays an important role in fine level habitat selection of birds (e.g. refuge to avoid hyperthermia, and nesting sites), and variation along a vertical gradient is important in this regard (Block and Brennan 1993). The vertical vegetation cover profile from the two study sites (CS7 and N5) in the Kirindy forest, indicates that the canopy stratum is characterized by the lowest vegetation cover. Excluding this stratum, statistical results showed that the abundance and species richness of bird community were positively related to vertical patterns of vegetation cover. The period of study coincided with the breeding season of forest birds in Malagasy western dry deciduous forests. Fledglings of different species (e.g. *Bernieria madagascariensis*, *Copsychus albospecularis*, *Coua cristata* (Linnaeus, 1766), *Schetba rufa*, *Terpsiphone mutata*) with a high demand of provisioning by the parents were observed in the understory and mid-story. Compared to the canopy, the denser vegetation cover in the understory and the mid-story offers shelter for nests and juveniles birds against predators. There is some risk of predation on birds in the canopy, where aerial raptors, such as *Accipiter henstii* (Schlegel, 1873), and *Buteo brachypterus* Hartlaub, 1860 often hunt or perch. Downward mobility of birds of large body size (average body mass in parentheses and extracted from Ravokatra et al. 2003) and with different life-history traits such as *Buteo brachypterus* (342 g), *Coracopsis nigra* (246 g), *C. vasa* (525 g),

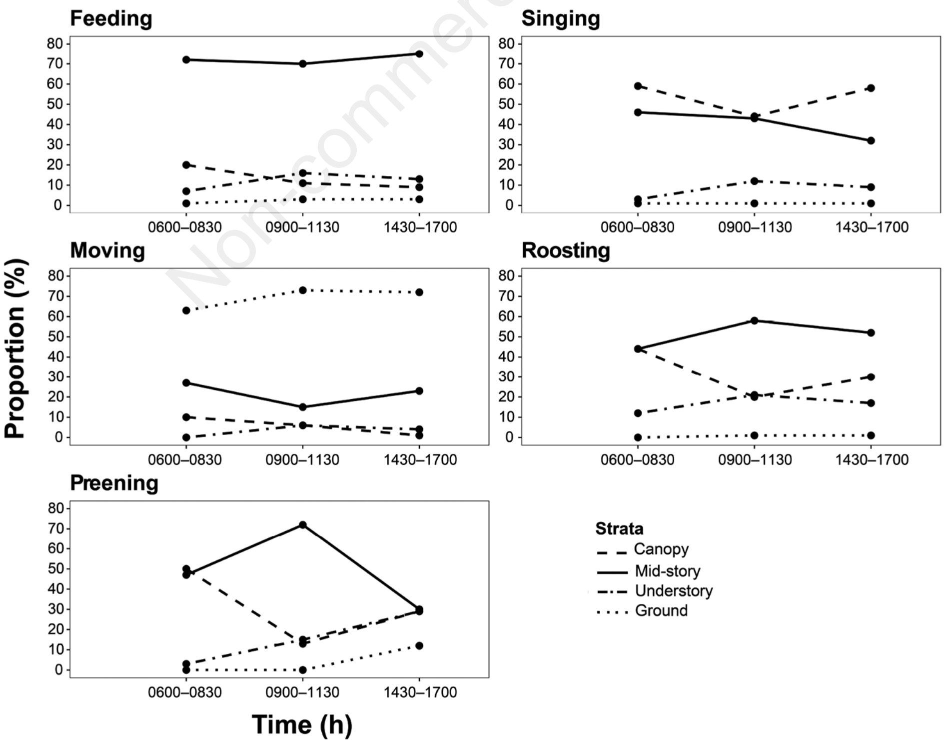

Figure 5. Proportion of bird behavioral activities in the different vertical strata and during different times the day.

Eurystomus glaucurus (148 g), and *Leptosomus discolor* (Hermann, 1783) (255 g) is constrained by the denser vegetation cover. Similarly, large size birds with different body proportions than those occurring in the canopy can be found on the ground, and these include, for example, *Coua gigas* (Boddaert, 1783) (423 g) and *Lophotibis cristata* (over 800 g).

The vertical distribution of arthropods strongly affects the stratification of insectivorous birds, most of which in the context of this study were located in the mid-story and canopy. Different types of insects, such as Coleoptera (e.g. Buprestidae, Curculionidae, and Chrysomelidae), Hemiptera, Hymenoptera, and Diptera (e.g. Empididae and Stratiomyidae), are consumed by forest passerines (Goodman and Parrillo 1997; Safford and Hawkins 2013), and are more abundant in the Kirindy forest in the mid-story and canopy (Rajaonarivelo et al. 2019). However, foraging success of birds is closely associated with different aspects of their morphology and density of vegetation cover in a vertical sense (Brokaw and Lent 1999). Generally, small size birds that glean insects from leaves such as *Newtonia brunneicauda* (12 g), *Neomixis striatigula* Sharpe, 1881 (8 g), and *N. tenella* (7 g) (body masses from Ravokatra et al. 2003), showed a preference for the mid-story as compared to the canopy. Indeed, small birds move frequently by short flights in search of food which requires a notable density of foliage and branches in the mid-story to optimize their movements (Telleria and Carrascal 1994). For frugivorous species, the canopy is characterized by a diversity of fruits and in Malagasy dry deciduous forests, fruit production may be found all the year (Sorg and Rohner 1996). This would explain the abundance of frugivorous birds such as *Coracopsis nigra*, *C. vasa*, and *Hypsipetes madagascariensis* (Müller, 1776) in the canopy.

Daily vertical movement

In the early morning, some forest passerines such as *Bernieria madagascariensis*, *Neomixis tenella*, and *Terpsiphone mutata* can be found singing in the upper portion of the forest. It has been proposed that during this period, song activities are more frequent because of the stability of atmospheric conditions and the low ambient noise at dawn, permitting better transmission of sound (Brown and Handford 2003). In addition, the use of the upper vertical portion of the forest would enhance sound propagation as compared to the understory, with dense vegetation cover obstructing transmission (van Dongen and Mulder 2006). Otherwise, compared to the canopy, understory microclimate in the morning is cooler and moister (Parker 1995). As a result, birds move vertically to help regulate their body temperature and to reduce heat loss, including sunbathing. Early in the morning, species as *Nesoenas picturata*, which is largely ground-dwelling but with scansorial capacity, is more abundant in the mid-story than in the canopy. Similarly, early in the morning, understory birds as *Copsychus albospecularis*, moved generally in the mid-story, in which ambient temperature is significantly higher compared to the understory.

In the middle of the day, due to the intense solar radiation, temperature increases dramatically in the canopy, while humidity decreases (Parker 1995). Thus, bird species such as *Bernieria madagascariensis* and *Schetba rufa*, using, respectively, the canopy for singing and sunbathing during the morning, shifted downward at mid-day to the denser vegetation cover of the lower strata in order to avoid heat and hydric stress. However, from mid-day towards the afternoon when the ambient temperature is the highest, the abundance of some bird species increases in the canopy. Canopy birds as *Coracopsis vasa* was frequently seen in the afternoon compared to the morning, and roosted often in groups of 5 to 20 individuals at the upper portion of the forest. In general, birds inhabiting the canopy experience different environmental conditions and are more tolerant to pronounced diurnal changes in temperature

(Winkler and Preleuthner 2001). Apart from the thermoregulation of birds, variation of microclimate along a vertical axis has a direct effect on the distribution and abundance of arthropods (Basset et al. 2003), and is associated with the daily pattern in the vertical stratification of insectivorous birds. Therefore, if arthropods shift downward during the hot period, the vertical stratification of some bird species is expected to follow the same pattern.

Conclusions

The current study represents the first detailed attempt to define the vertical stratification of a bird community in a tropical dry deciduous forests of Madagascar. In general, several bird species use specific vertical sections of the forest. Further, the results indicate vertical daily movements for certain species associated with varying environmental conditions, specifically density of vegetation and temperature.

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Conflict of interest

No potential conflict of interest was declared by the authors.

Authors' contributions

JAR, SMG and MJR designed the study, and defined the sampling techniques; JAR performed the data collection in the field; JAR and AA analyzed the data; JAR and SMG wrote the manuscript; all authors corrected diverse drafts of the manuscript and approved the final version.

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