Bird communities of the Parc National de Marojejy, Madagascar: With reference to species diversity and elevational distribution changes between 1996 and 2021

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Abstract

Considering ongoing worldwide environmental change associated with a range of different factors, the related dynamics of bird community shifts in tropical forest environments remains poorly understood. Investigations along ecological gradients, such as elevational transects of mountains, where variables to potentially explain the distribution of different biotic elements, including shifts in temperature, humidity, and rainfall, change in a continuous manner. These are excellent natural settings to measure possible change. Herein we present details on such a study of birds and compare their distribution and density on the slopes of the Parc National de Marojejy in northeastern Madagascar and compare data from 1996 and 2021 collected in a comparable manner.

Three complementary standardized methods were used to collect data at five sites between 450 and 1875 m and near the Mandena-summit trail: general observations, mist-netting of understory birds, and point counts. The protocols for these methods followed in close detail those used in 1996 for a parallel ornithological elevational inventory of the same areas of the Marojejy Massif. During the 2021 survey, a total of 80 bird species were recorded at the five sites, a large proportion of these taxa being forest dependent. When the 2021 bird list is combined with those from 1996, 91 species were recorded in the survey zone.

Comparing data from the two inventories, four species were not recorded during the 2021 inventory in the upper elevational zone at 1875 m from montane ericoid thicket, but were present in 1996: *Margaroperdix madagarensis*, *Coturnix coturnix*, *Caprimulgus madagascariensis*, and *Eremopterix hova*. An overview of the point count data indicated that the local bird populations, despite variation in their observed densities between the two surveys, were largely unchanged except for three species of the endemic Malagasy subfamily Vanginae: *Tylas eduardi*, *Euryceros prevostii*, and *Artamella viridis*. The lack of measured changes in the density of the balance of bird taxa might reflect a certain level of resilience with respect to environmental dynamics. Moreover, given that most are forest-dependent and subject to changes in ecological conditions associated with 1) the effects of local anthropogenic pressures, for which we have little evidence in the transect area over the course of the past 25 years, 2) climate, for which there is evidence of change over the past few decades, and 3) natural events, principally the impacts of cyclones, these aspects, at least based on the measured time scale, seem not to have impacted aspects of their distribution and density within the forest transect zone.

Résumé détaillé

L'avifaune du Parc National de Marojejy est bien connue mais la dynamique de la communauté d'oiseaux des milieux forestiers face à celle de l'environnement reste mal connue. Aussi, une étude le long du gradient altitudinal sur la tendance des populations a été menée pour comprendre la résilience des espèces à la variation des conditions écologiques de l'environnement. Cinq sites entre 450 et 1875 m d'altitude en suivant la piste touristique principale Mandena-Sommet ont été inventoriés. Ils ont été installés de manière à couvrir les différents types d'habitats représentatifs du transect allant de la forêt humide sempervirente de basse altitude jusqu'aux fourrés éricoïdes et aux prairies de hautes montagnes. Trois méthodes complémentaires ont été utilisées pour collecter les données ; elles comprennent les observations générales, y compris les observations au-dessus de la canopée, la capture

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aux filets des oiseaux de sous-bois et les points d'écoute. Le protocole de ces méthodes suit autant que possible celui de 1996 puisque la réplication de l'étude et la standardisation des approches adoptées constituent des moyens appropriés pour une analyse comparative des données obtenues entre les différentes années pour mieux comprendre la tendance de la communauté d'oiseaux du parc. Un total de 80 espèces, dont une grande partie est forestière dépendante, a été enregistré dans les cinq sites au cours de l'inventaire dont le Site 3 est le plus diversifié avec 60 espèces et le Site 5 contient la plus faible richesse spécifique avec 30 espèces. Six nouveaux enregistrements de 2021 des espèces qui n'ont pas été inventoriées le long du transect altitudinal en 1996 sont *Accipiter madagascariensis*, *Dryolimnas cuvieri*, *Tyto soumagnei*, *Gactornis enarratus*, *Hartertula flavoviridis* et *Schetba rufa*. Avec ces espèces additives, la richesse spécifique de ce transect atteint 91 espèces. Comme dans la plupart des massifs forestiers malgaches, la distribution d'espèces observées sur le Massif de Marojejy est une distribution assez classique. Elle atteint le nombre maximal d'espèces dans la limite supérieure de la forêt de basse altitude, ensuite ce nombre diminue au fur et à mesure que l'on monte dans la forêt de hautes montagnes.

En se basant sur les données de l'inventaire de 1996 qui constituent des données référentielles, les résultats ont montré l'absence de quatre espèces des habitats ouverts au cours de l'inventaire de 2021, notamment *Margaroperdix madagarensis*, *Coturnix coturnix*, *Caprimulgus madagascariensis* et *Eremopterix hova*, répértoriées dans les prairies altimontaines de Marojejy en 1996. De plus, une vue d'ensemble de la tendance des populations a indiqué que la communauté et la plupart des populations d'oiseaux, qui la composent, malgré la variation de leurs densités observée seraient stables, à l'exception de quelques-unes qui apparaissent être vulnérables. Ces dernières qui sont *Tylas eduardi*, *Euryceros prevostii* et *Artamella viridis* appartenant à la famille des Vangidae, endémique de la région Malagasy, présentent une diminution significative de leurs densités relatives entre 1996 et 2021. Ces informations pourraient refléter le niveau de la résilience des espèces par rapport à la dynamique de l'environnement, mais comme la plupart des espèces sont forestières dépendantes, un changement important des conditions écologiques, dû entre autres aux effets conjugués des pressions anthropiques, du changement climatique et des cataclysmes naturels pourrait avoir des effets néfastes sur la structure de la communauté. La conservation des écosystèmes naturels du parc s'avère ainsi cruciale pour la survie à long terme de la communauté d'oiseaux de cette aire protégée.

Introduction

Climate change has become a major concern on a global scale due to its impacts on different aspects, including those associated with socio-economic, medical, and environmental domains (Bourque, 2000; Sultan *et al.*, 2015). On Madagascar, the Direction Météorologique in Antananarivo noted that the climate has warmed up over the past 30 years with an increase in temperature of 0.9ºC on average, except in the north and southwest with a more abrupt augmentations ranging from 1.5 to 4ºC (Rakotondrafara *et al*., 2018). Jury (2022) predicts that the air temperature on the island will increase from 24 to 28ºC by 2100. However, based on this same author, rainfall will decline from 4.3 mm/day in 1950 to 3.6 mm/day in 2100.

The consequences of such environmental vicissitudes in the recent geological past of Madagascar, based in many areas largely on natural climate change, led to the disappearance of ecosystems and a large number of animal species (Goodman & Jungers, 2014). The study of Wilmé *et al*. (2006) also posits the impacts of Quaternary climate change, leading to the recent patterns of microendemism on the island and its biogeographic complexity. However, few scientific studies have been carried out to address recent evolution of the extant ecosystems and biodiversity of the island, including for forest-dwelling birds. One of the impediments in properly measuring shifts at a local level in different animal groups is the lack of initial reference data, leading to often speculative conclusions, as well as the presence of other factors with major impacts on the environment, such as anthropogenic pressures. Among the rare information available are those from the work of Andriamasimanana and Cameron (2013). These authors projected that many species of forest-dependent birds are vulnerable in the near future to climate change due to a reduction of suitable habitats. Thus, in-depth and comparative studies at the same sites over time are essential to collect needed information to address critical issues of the impact of change through time and its relationship to conservation biology.

The past 35 years or so has seen major strides in knowledge on the birds of Madagascar. This work

has taken multiple forms and include the publication of several guides to the birds of Madagascar and neighboring islands that have facilitated field identification (Langrand, 1990; Hawkins *et al.,* 2015; Morris & Hawkins, 1998; Sinclair & Langrand, 1998; Sinclair *et al*., 2006), detailed site inventories of previously unknown or poorly known forested areas, including along elevational transects and aquatic zones (Hawkins & Goodman, 1999; Goodman *et al*., 2000; Rabarisoa *et al*., 2006, 2020), new insights into bird biogeography (Hawkins, 1999; Raherilalao & Wilmé, 2008; Goodman & Raherilalao, 2013), and large-scale efforts through molecular biology studies to put the living bird fauna into an evolutionary history context and provide new insights on the systematic relationships of a significant portion of the endemic higher taxonomic groups and species (Johansson *et al*., 2008; Jønsson *et al*., 2012; Reddy *et al*., 2012; Fuchs *et al*., 2016; Younger *et al*., 2018, 2019a, 2019b, and for a review see Safford *et al*., 2022). Further, during this period a few endemic bird species have been described as new to science (Goodman *et al*., 1996, 1997, 2011; Younger *et al*., 2018), as well as the publication of field studies that provide insight into the breeding biology of endemics (Urano *et al*., 1994; Nakamura *et al*., 2001a, 2001b, 2009a, 2009b), and the impacts of deforestation, habitat fragmentation, and climate change on the modern avifauna (Langrand & Wilmé, 1997; Andriamasimanana & Cameron, 2013; Gardner, 2022). A major synthesis has been published in book form on the birds of the Malagasy Region, defined as including Madagascar and the neighboring archipelagos of the Comoros, Mascarenes, and Seychelles (Safford & Hawkins, 2013), as well as a recent synthesis of the Malagasy avifauna (Safford *et al*., 2022). Given the number of detailed quantitative field inventories over the last decades and the time interval since some of the earlier modern surveys, it is appropriate to revisit sites to examine possible vicissitudes in the local avifauna through time, and, if found, try to understand the factors behind these changes. Goodman *et al*. (2018a) noted that the maximum temperature in the park increased by 1.1ºC between 1984 and 2014. These values were calculated from a single site within the park and do not take into account presumed variation in climatic shifts along the elevational gradient of the eastern slopes of the massif from lowland moist evergreen forest to the montane grassland above forest line. Further, this shift in temperature also needs to be superimposed on a 1.7% loss in forest cover in the protected area between 1996 and 2016, with some watersheds experience greater human pressures than others (Tahinarivony, 2023a, 2023b, herein).

In this context, we surveyed during October and November 2021 the birds occurring on the eastern slopes of the Marojejy Massif at five different sites along an elevational transect from 450 to 1875 m and each site in a different vegetational formation. The bird survey sites, dates, and field techniques followed in fine detail an earlier inventory along the same transect conducted in October and November 1996 (Goodman *et al*., 2000). Herein we present the details of the 2021 fieldwork and make comparisons to the results of 1996, which provide a context to decipher possible changes in the local bird fauna along the elevational transect over a 25-year period.

Review of ornithological exploration of Marojejy and neighboring areas

The Marojejy Massif, which was incorporated in 1958 into one of the earliest protected areas on Madagascar under the status of a Réserve Naturelle Intégrale and was changed in 1998 to the statute of a Parc National (Humbert, 1955; Goodman *et al*., 2018a), is from an ornithological perspective one of the best-known mountains on the island (Goodman *et al*., 2018b). Current details on the birds of the massif are based on numerous field visits by bird biologists over nearly a century and here we provide a review of the ornithological work conducted in the Marojejy region.

To our knowledge, the first ornithological research in the Marojejy area was by members of the Franco-Anglo-Américaine expedition, who surveyed numerous localities across the island between 1929 and 1931. Between 19 August and 7 September 1930, they worked a site “one day west” of Andapa and collected numerous specimens (Rand, 1932, 1936). Their base camp was close to the modern Réserve Spéciale d’Anjanaharibe-Sud, to the west of the Andapa basin.

In 1958, Paul Griveaud visited Marojejy for entomological studies, but also made some observations on the avifauna, as well collecting some bird specimens (Griveaud, 1960; see Goodman *et al*., 2023, herein, for further details on the sites he worked). To our knowledge, the next ornithological team to visit the massif was in September 1972, and they worked the eastern portion of the reserve and added numerous species to the local list (Benson *et al*., 1976, 1977). Based on a visit to Marojejy in 1987 and a review of previous information from the site,

Nicoll and Langrand (1989) reported a total of 103 bird species for the protected area.

Between August and late October 1988, a group of students associated with the University of Cambridge, many of which later in their careers would become prominent members of the ornithological and conservation communities, and in collaboration with Malagasy counterparts, conducted a biological inventory of several sites within the reserve (Safford & Duckworth, 1990). A subsequent publication associated with this fieldwork focused on the birds (Evans *et al*., 1992) and in total 104 bird species were documented at that point in time within and around the reserve. One of the many noteworthy findings of this group was the rediscovery of the endemic Madagascar Serpent Eagle, *Eutriorchis astur*, which had not been properly documented anywhere on the island since the 1930s (Sheldon & Duckworth, 1990), but today is known from a range of sites (Rene de Roland & Thorstrom, 2022).

Between mid-October and early December 1994, a multidisciplinary group of biologists conducted an inventory of the Réserve Spéciale d'Anjanaharibe-Sud, about 40 km to the west of Marojejy. This group visited four sites on the eastern slopes of the Anjanaharibe-Sud Massif, between 875 m and the summital zone at 1950 m (Goodman, 1998). The ornithological results of this survey were published and include detailed information on natural history and density estimates based on systematic point counts and mist-netting (Hawkins *et al*., 1998), and specific information on the local community of raptors (Thiollay, 1998), including additional regional observations of *E*. *astur*. Two years thereafter, an elevational transect of the eastern sector of the Parc National de Marojejy was conducted between 4 October and 20 November 1996 at five sites ranging between 450 and 1875 m (Figure 1, labeled as Camp 1 to Camp 5 and these designations used herein for these specific sites). The general results are presented in Goodman (2000) and the ornithological results in Goodman *et al.* (2000).

In subsequent years, other regional forests were surveyed for birds (Raherilalao & Goodman, 2003) and included: 1) between 7 and 22 October 1999, two sites at 820 and 1200 m in the forested corridor between Marojejy and Anjanaharibe-Sud, which then was referred to as the Betaolana Forest and has subsequently been declared as a protected area known as Paysage Harmonieux Protégé du Corridor Marojejy-Anjanaharibe Sud-Tsaratanàna partie Sud or COMATSA Sud (Goodman *et al.*, 2018a); 2) between 25 October and 10 November 1999, two sites at 1200 and 1600 m along the western slopes of the Anjanaharibe-Sud Massif, which a few years later this portion of forest was added to the Anjanaharibe-Sud protected area (Goodman *et al*., 2018a); and 3) between 13 and 30 October 2001, along the northwestern slopes of Marojejy, which formed a portion of the originally gazetted reserve (Figure 1, labeled as Site 1 and Site 2).

In the context of a World Heritage Site/UNESCO and Madagascar Biodiversity Fund project, between 6 May and 2 June 2016, ecological studies were conducted at three sites on different portions of the Marojejy Massif (Figure 1): Betsiasisa in the southwest (near Antanimbaribe), and Antsahabe and Beamalona in the northeast and close to Mandena (Raherilalao *et al*., 2016). The focus of these studies was the effect on the local vertebrate fauna from illegal extraction of rosewood (*Dalbergia*). The analysis showed that the distribution of *Dalbergia* species did not extend to these portions of the protected area. Some people took advantage of the 2009 socio-political crisis and entered the park for the exploitation of other hardwood species (e.g. *Diospyros*), seriously degrading certain forest habitats. From the perspective of understanding the impact of illegal exploitation of these natural resources on the biota of the park, given the lack of earlier inventory baseline data, it was not possible to measure local changes in the forest bird communities. Using comparisons based on the avifaunal characteristics of forested zones in northern Madagascar, it was concluded in a preliminary manner that the integrity of the Marojejy bird communities appeared to be maintained (Raherilalao *et al*., 2016).

Between mid-November and December 2020, a multidisciplinary biological inventory was carried out at two sites (Camp 3 at 1300 m and Camp 4 at 1625 m), comprising different portions of the medium altitude moist evergreen forest along the main touristic trail of the Parc National de Marojejy. Detailed information on species richness, abundance, levels of endemism, and habitat specifications (forest, aquatic and open areas) were obtained (Raherilalao *et al*., unpublished data).

A synthesis of information on terrestrial protected areas on Madagascar was published in late 2018 (Goodman *et al*., 2018a), and the cumulative list based on ornithological exploration and bird specimens in natural history museums around the world obtained from Marojejy brought the local bird list to 119 species. An analysis of the "state of

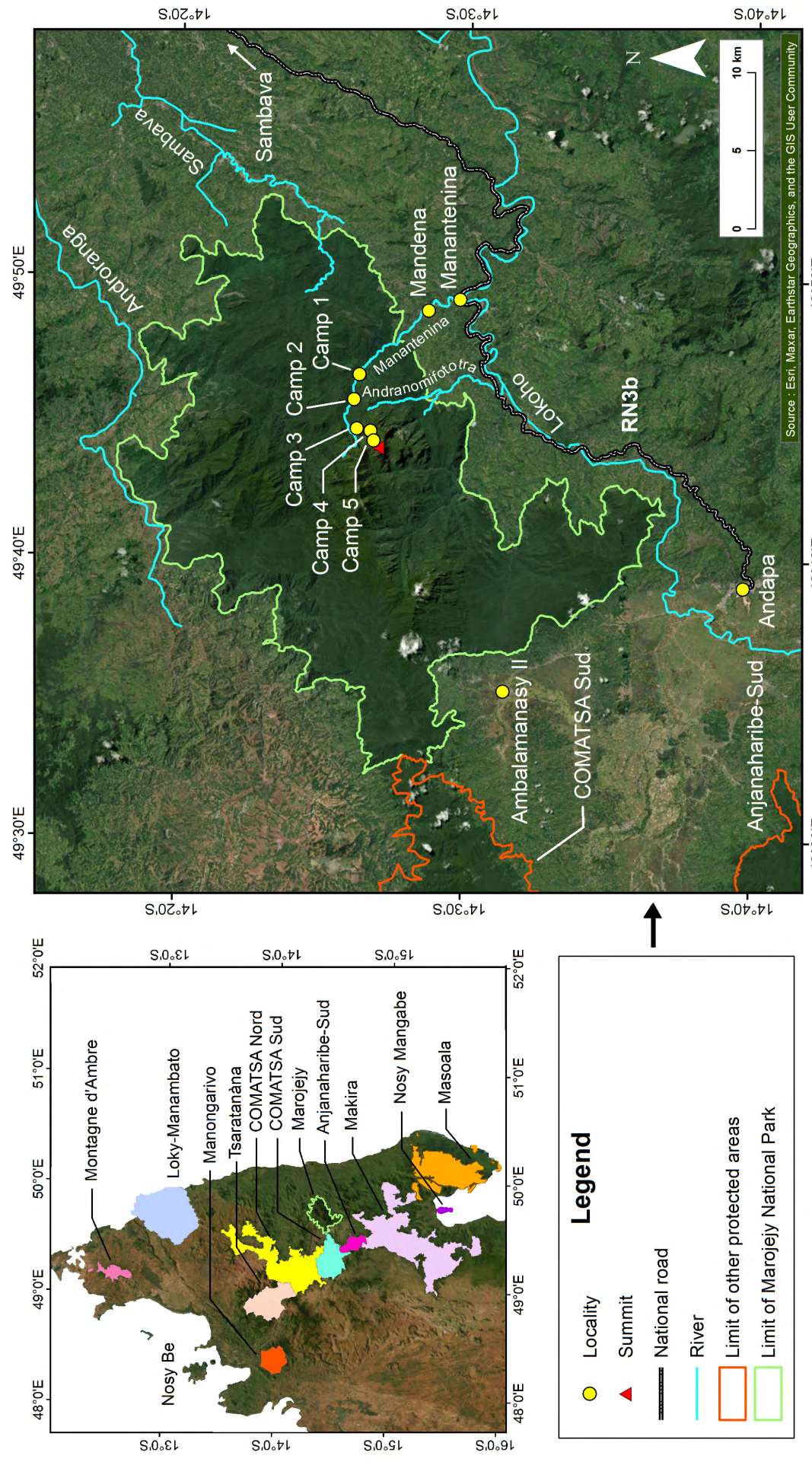

Figure 1. Map showing the position of the Parc National de Marojejy with reference to a network of neighboring protected areas (upper left), excluding a few sites to the west of Tsaratanàna, and a detailed map of Marojejy and the different sites on and around the massif that have been investigated for birds since 1996. The legend concerns the detailed map of Marojejy to the right.

knowledge" concluded that the birds of Marojejy National Park were "reasonably well known" with a score of 4 on a scale of 0 (unknown) to 5 (completely known) (Goodman *et al*., 2018b).

Goals of the current study

Recent studies indicate that climatic change is impacting Madagascar, and these vicissitudes including increasing temperatures, more variable precipitation, more intense cyclones, rising sea levels, and predicted shifts in the distribution of the principal native forest types (Tadross *et al*., 2008; Hending *et al*., 2021; Weiskopf *et al*., 2021). Taking into consideration the levels of deforestation in the moist evergreen forests of Madagascar (Vieilledent *et al*., 2018), superimposed on documented and inferred climatic change across the world and with special reference to the island, it is important to understand the impacts of these variables on the distribution of Malagasy birds, particularly endemic forest-dwelling species. The primary goals of this current study are to document the bird fauna found in late 2021 along an elevational transect between 450 and 1875 m on the eastern slopes of Marojejy using several different techniques: general observations, point counts, and standardized bird netting. We then compared these results to a parallel transect censused in 1996 at the same five sites along the gradient, following in close detail calendar dates and field techniques to understand if measurable changes have taken place and, if so, the possible driving factors. Other ornithological surveys at Marojejy listed above used less formalized census techniques, and so quantitative comparisons made here are limited to those between the 1996 and 2021 surveys

Study site and methods

Study site

Our field study of the Parc National de Marojejy was conducted from 2 October to 15 November 2021 and as part of a multidisciplinary inventory of the local flora and fauna of the massif and presented in this monograph. The survey was associated with the BIOCOM project financed by the Korea International Cooperation Agency (KOICA) and in collaboration with UNESCO Madagascar and Madagascar National Parks. (For an overview of the project and more details on the different sites see Goodman *et al*., 2023, herein). Ornithological data were collected within an altitudinal interval of about 75 m elevation above and below each camp site at 450 m (Site 1), 775 m (Site 2), 1300 m (Site 3), 1625 m (Site 4), and 1875 m (Site 5) that were surveyed in increasing elevational order. The five sites, which are labeled as Camp 1 to Camp 5 on Figure 1, were the same as those surveyed in 1996, and in subsequent years some touristic infrastructure, including cooking shelters, eating areas, and bungalows, were installed at sites 1, 2, and 3. We use the vegetation classification of Gautier *et al*. (2018) to refer to different habitat types and also see Tahinarivony (2023a, herein) for further details on the flora and vegetation at each site along the transect.

Most of the camp sites were situated near running water in closed-canopy forest. The lowest site (450 m, now referred to as Camp Mantella) was next to Manantenina River and several tributaries feeding into the river. The vegetation type at this site was largely dominated by native lowland moist evergreen forest, although extensive areas of secondary forest were present, including several invasive plant species. At the 775 m site, now called Camp Marojejya and associated with a large rock outcrop known as Andampimbazaha, was along the Ambavaomby River, which feeds into the Manantenina River. The forest at this site showed few signs of human disturbance and contained some floristic elements of more upland forest. A marked change in the vegetational structure occurred between the 775 and 1300 m zones -- the tourist site in the latter zone is known as Camp Simpona. Clear montane elements were present in this zone and the vegetation was medium altitude moist evergreen forest, with a lower canopy height than at the two lower camps, and distinctly more epiphytes, ground bryophytes, and lichens. By 1625 m, the forest was dominated by montane floristic elements, including some sclerophyllous plants, and the tree stature was reduced. In this zone, tree roots often formed hollow cavities under a superficial cover of mosses and lichens, especially along ridges and slopes. The 1875 m site was at the ecotone between the upper limit of medium altitude moist evergreen forest with a good proportion of the trees having sclerophyllous aspects and a relatively narrow band of montane ericoid thicket. Slightly higher up and within the transect was montane grassland. The 1875 m camp site was on a ridge and above tree line and adjacent to a small water source. In the largely open area above the camp, exposed rock outcrops often partially covered by geophytes dominated the landscape.

Methods

To inventory the avifauna of each site, three complementary methods were employed, namely: general observations, mist net captures, and point counts. These techniques have been used for the inventory of birds in the forest environments of Madagascar for more than 25 years (Hawkins & Goodman, 1999; Goodman *et al*., 2000; Raherilalao *et al*., 2002). The protocols of these methods follow those used in 1996 for the ornithological inventory along the altitudinal gradient of the Marojejy Massif (Goodman *et al*., 1996), and the data provide the means for a spatio-temporal comparative analysis of the bird community of this protected area over the course of 25 years. With a few modifications, the classification of the forest habitat types used by a given species of bird follows Wilmé (1996).

Survey methods

General observations

General observations were conducted by MJR, TL, and SMG and consisted of walking along preexisting trails in the forest, on non-standard routes, or stationary observations - for example from camps, allowing both visual and acoustic determinations of locally occurring birds. Since most diurnal birds are active in the morning, searches are generally conducted daily between 5:30 a.m. (during the survey period, this time corresponds to sunrise) and 10:30 a.m., but information from any time of the day or night were also employed. Discussions with regional guides were also used to gather information on the local avifauna and human pressures. More than 10 hours per site were spent conducting observations of the forest canopy. This qualitative method provided additional information to supplement data coming from mist-netting and point counts.

Mist-netting

TL and a local assistant employed mist nets to capture understory birds and to determine the species present in each elevational zone and relative density measures; these data were used to supplement information coming from point counts. Mist-netting was especially relevant for species occurring in the lower portion of the forest strata, which include those often difficult to observe.

The first full day at a site was spent identifying and opening narrow lanes in the forest for the installation of nets. Ten nets (36 mm mesh size, 2.6 m high, and 12 m long) were installed at each of the five elevational zones – in most cases evenly distributed between positions on ridges, valleys, and slopes. These devices were run continuously for five days. The bottom pocket of each net was positioned about 20 cm above the forest floor. They were checked about every hour from sunrise to sunset, and once after sunset. Nets were checked more frequently during inclement weather such as heavy rain. Nets were left open during the night, generally to capture nocturnal birds and bats, and rarely mouse lemurs (*Microcebus*). The mist net capture results are expressed by the number of individuals per net and per day, under the term individuals/net-day. The capture rate also provides a relative abundance index that can be used for spatio-temporal comparisons of understory populations.

Most captured birds were released, and these were checked for the presence of a brood patch and cloacal protuberance, and some were weighed. Before releasing a given individual near the site of capture, they were marked with an indelible marker on a primary feather. Within each elevational zone, the first primary feather was marked for birds captured on the first day of netting, the second primary feather on the second day, and so on, until the fifth and final day of netting. This marking technique provided a means to recognize recaptured individuals and indicated the chronology of the recaptures.

Point counts

Point count sites were installed in different microhabitats (valley, slope, and ridge) within each elevational zone to estimate the relative density of birds (Bibby *et al*., 2000). Fifteen points, each separated by 150 m and along previously established trails, were used at Sites 1 to 4, with only 11 points used at Site 5 because of its very rugged topography. All birds seen or heard by MJR within 25 m of the point count site and during a 10-minute period were noted, as well as the approximate distance to the observer. During a session, upon arrival at a new point count site, a pause of two to three minutes was allowed to lapse before commencing the survey. As most birds are active in the first portion of the morning, counts are made between 5:30 a.m. (early dawn and still largely dark) and 9:00 a.m. Each point was visited at least twice during the sampling period of each transect site. This method provides both qualitative and quantitative data on measures of bird density.

Comparative analysis of population abundance between 1996 and 2021

As net capture was limited to understory birds and sampling was only conducted at sites within a few hundred meters of each camp site, we use herein data from the point counts to examine bird population trends on the eastern side of the Parc National de Marojejy.

In order to assess possible differences between the point count surveys conducted in 1996 and 2021, the density representing the ratio of the total number of individuals of each species and the area of all point counts sampled at each site, expressed in number of individuals per hectare, was calculated according to the following formula:

$$\text{Relative density} = \frac{\text{Number of individuals per species}}{\text{Surface of a PC x niPC}}$$

with ni = total number of point counts, and PC = number of point counts.

The number of point counts sampled at each site in 1996 was greater than in 2021, but this does not impact the method of calculating the density (number of individuals) of a given per unit area. The calculated densities were compared by species and elevational zone using the Student's t-test. The analyses were performed using R Studio software (version 3.5.1). The value $\alpha = 0.05$ was taken as a threshold for significant statistical differences between the densities of 1996 and 2021. The comparative analyses were conducted in two stages. The first examined the entire bird community of the eastern slopes and the second by species with all sites combined.

Systematic order and nomenclature

The higher-level systematic arrangement and species taxonomy used herein follow Safford *et al*. (2022). Several changes have taken place in the systematics of Malagasy birds since Langrand (1995), which was mainly used in the results from the 1996 bird study of Marojejy (Goodman *et al*., 2000). The genus Mentocrex is now recognized (for the Malagasy species *M*. *kioloides*) as distinct from *Canirallus* (García-R *et al*., 2014); Malagasy former members of the genus *Phyllastrephus* are now placed within two different endemic genera (*Bernieria* and *Xanthomixis*) and these species, as well as others, belong a previously unrecognized endemic radiation, the family Bernieridae (Cibois *et al*., 2001; Younger *et al*., 2019b). There are numerous changes in the family designation of different Passeriformes, comprising, for example, the species composition of the Vangidae, including the genus *Newtonia* (formerly a Sylviidae), *Mystacornis crossleyi* (formerly a Timaliidae), and *Pseudobias wardi* (formerly a Monarchidae) and *Ispidina madagascariensis* is now placed in the Malagasy endemic genus *Corythornis* (Marks & Willard, 2005). Other generic changes include *Ninox superciliaris* being transferred to *Athene* (Wink, 2008), *Brachypteracias squamiger* being placed in the monospecific genus *Geobiastes* (Kirchman *et al*., 2001), *Mirafra hova* in *Eremopterix* (Alström *et al.*, 2013), *Dromaeocercus brunneus* in *Bradypterus* (Alström *et al.*, 2011), the two Malagasy *Ploceus* species in *Nelicurvius* (De Silva *et al*., 2017), and the Malagasy *Lonchura* in *Lepidopygia* (Payne & Sorenson, 2003).

Results

Specific richness and composition

A total of 80 bird species were inventoried in 2021 at the five sites between 450 and 1875 m in the Parc National de Marojejy. The bird local community is largely composed of forest-dependent species (88.8%), followed by species adapted to open areas (10.0%). Aquatic forms are represented only by a single species (1.2%).

The highest species richness was found at Site 2, being in the upper limit of lowland moist evergreen forest, with 60 species, and the lowest at Site 5, being in the upper reaches of the massif with only 30 species. In general, the local avifauna is more diversified at lower elevations and specific richness decreases with increasing elevation. Tables 1 and 2 present the distribution of the species inventoried at the five different sites.

Comparing the avifauna of the vegetation formations along the elevational gradient (Table 1), the following observations can be presented: 12 species were found only in in lowland moist evergreen forest (occurring at Site 1 and Site 2), and distributed as follows: three in Site 1 (*Geobiates squamiger*, *Athene superciliaris*, and *Hartlaubius auratus*); four in Site 2 (*Aviceda madagascariensis*, *Mentocrex kioloides*, *Tyto soumagnei*, and *Schetba rufa*); and five shared between the two sites (*Accipiter francesiae*, *Treron australis*, *Coua serriana*, *Asio madagascariensis*, and *Zoonavena grandidieri*). Five species characterize the upper medium altitude moist evergreen forest zone (at Site 3 and Site 4), three of which were only found during the 2021 survey at Site 3 (*Mesitornis unicolor*, *Gactornis enarratus*, and *Hartertula flavoviridis*); one at Site 4 (*Neodrepanis*

Table 1. Distribution of birds recorded along the elevational transect of the eastern slopes of the Parc National de Marojejy during the 1996 and 2021 surveys, with information on their regional endemism, distributional status, and habitat use.

Key to presence/absence status: + = species recorded in zone in 1996 (Goodman *et al.*, 2000), * = species recorded in zone in 2021 (herein), and - = species not recorded in zone in either 1996 or 2021.

Key to endemism: taxonomic endemism is indicated at family, genus, species, and subspecies level, or not endemic. Most species endemic at the subspecies level are Malagasy Region endemics.

Habitat: largely based on Wilmé (1996) with some modifications.

Species	Name used in Goodman *et al.* (2000)	Endemism to Madagascar	Habitat	Site 1	Site 2	Site 3	Site 4	Site 5
Margaroperdix madagarensis	*Margaroperdix madagascariensis*	Genus	Open areas	-	-	-	-	+
Coturnix coturnix		Not endemic	Open areas	-	-	-	-	+
Nesoenas picturatus	*Streptopelia picturata*	Subspecies	Forest/open areas	+*	+*	*	-	-
Treron australis		Subspecies	Forest	+*	*	-	-	-
Alectroenas madagascariensis		Species	Forest	+*	+*	+*	*	-
Mesitornis unicolor		Family	Forest	-	+	*	-	-
Coua caerulea		Subfamily	Forest	+*	+*	+*	+*	+*
Coua reynaudii		Subfamily	Forest	+*	+*	+*	*	+*
Coua serriana		Subfamily	Forest	+*	+*	+	-	-
Centropus toulou		Subspecies	Forest/open areas	+*	+*	+	-	*
Cuculus rochii		Species	Forest	+*	+*	+*	+*	+*
Gactornis enarratus		Genus	Forest	-	-	*	-	-
Caprimulgus madagascariensis		Subspecies	Open areas	-	-	-	-	+
Zoonavena grandidieri		Subspecies	Forest	+*	+*	+	-	+
Apus balstoni	*Apus barbatus*	Subspecies	Open areas	+*	*	+*	+*	+*
Apus melba		Subspecies	Open areas	+*	+	+	+	+*
Cypsiurus gracilis	*Cypsiurus parvus*	Subspecies	Open areas	-	-	-	-	+
Mentocrex kioloides	*Canirallus kioloides*	Genus	Forest	+	+*	+	+	-
Sarothrura insularis		Species	Open areas	-	*	-	-	+*
Dryolimnas cuvieri		Subspecies	Aquatic	*	*	-	-	*
Lophotibis cristata		Genus	Forest	+*	+*	*	-	-
Polyboroides radiatus		Species	Forest/open areas	+*	-	-	*	-
Aviceda madagascariensis		Species	Forest	-	*	+	+	+
Accipiter francesiae	*Accipiter francesii*	Subspecies	Forest/open areas	+*	*	-	-	-
Accipiter henstii		Species	Forest	+	-	-	+	-
Accipiter madagascariensis		Species	Forest	*	-	*	-	-
Buteo brachypterus		Species	Forest/open areas	+*	+*	+*	+*	+*
Tyto soumagnei		Species	Forest	-	*	-	-	-
Otus rutilus		Subspecies	Forest	+*	+*	+*	+*	-
Athene superciliaris	*Ninox superciliaris*	Species	Forest/open areas	+*	-	+	-	-
Asio madagascariensis		Species	Forest	+*	*	+	-	-
Leptosomus discolor		Species	Forest/open areas	+*	+*	+*	-	-
Corythornis madagascariensis	*Ispidina madagascariensis*	Species	Forest	+*	+*	*	*	-
Corythornis vintsioides	*Alcedo vintsioides*	Subspecies	Aquatic	+	-	-	-	-
Eurystomus glaucurus		Subspecies	Forest/open areas	-	-	+	-	-
Brachypteracias leptosomus		Family	Forest	+*	+*	+*	+	-
Geobiastes squamiger	*Brachypteracias squamiger*	Family	Forest	+*	+	-	-	-
Atelornis crossleyi		Family	Forest	-	-	+*	+*	+
Atelornis pittoides		Family	Forest	-	*	+*	+	-
Falco eleonorae		Not endemic	Open areas	-	-	-	-	+*
Falco peregrinus		Subspecies	Open areas	+	*	-	-	*

Species	Name used in Goodman *et al.* (2000)	Endemism to Madagascar	Habitat	Site 1	Site 2	Site 3	Site 4	Site 5
Coracopsis nigra		Subspecies	Forest	+*	*	*	*	+
Coracopsis vasa		Subspecies	Forest	-	+	+	+	-
Philepitta castanea		Subfamily	Forest	+*	+*	+*	+*	-
Neodrepanis coruscans		Subfamily	Forest	+*	+*	+*	*	-
Neodrepanis hypoxantha		Subfamily	Forest	-	-	+	+*	-
Coracina cinerea		Subspecies	Forest	+*	+*	+*	+*	-
Newtonia amphichroa		Genus	Forest	+*	+*	+*	+*	+*
Newtonia brunneicauda		Genus	Forest	+*	+*	+*	+*	+
Tylas eduardi		Genus	Forest	+*	+*	+*	+*	+
Calicalicus madagascariensis		Genus	Forest	+*	+*	+*	+*	+*
Leptopterus chabert		Genus	Forest	+	+*	*	*	+
Mystacornis crossleyi		Genus	Forest	+*	+*	+*	+	-
Cyanolanius madagascarinus		Subspecies	Forest	+*	*	+*	*	-
Vanga curvirostris		Genus	Forest	+*	+*	+*	*	*
Pseudobias wardi		Genus	Forest	+*	+	*	+*	*
Schetba rufa		Genus	Forest	-	*	-	-	-
Euryceros prevostii		Genus	Forest	+*	+*	+*	+	-
Oriolia bernieri		Genus	Forest	+	*	*	-	-
Artamella viridis	*Leptopterus viridis*	Genus	Forest	+*	+*	+*	+*	-
Dicrurus forficatus		Subspecies	Forest/open areas	+*	+*	+*	*	-
Terpsiphone mutata		Subspecies	Forest	+*	+*	+*	+*	-
Eremopterix hova	*Mirafra hova*	Species	Open areas	-	-	-	-	+
Neomixis striatigula		Genus	Forest	+*	+*	+*	+*	-
Neomixis tenella		Genus	Forest/open areas	+*	+	+	-	-
Neomixis viridis		Genus	Forest	+*	+*	+*	+*	-
Nesillas typica		Subspecies	Forest/open areas	+*	+*	+*	+*	+*
Bradypterus brunneus	*Dromaeocercus brunneus*	Genus	Forest	-	-	+	+*	+*
Oxylabes madagascariensis		Family	Forest	+*	+*	+*	+*	-
Bernieria madagascariensis		Family	Forest	+*	+*	+*	*	-
Cryptosylvicola randrianasoloi		Family	Forest	-	-	+*	+*	+*
Hartertula flavoviridis		Family	Forest	-	-	*	-	-
Xanthomixis cinereiceps	*Bernieria cinereiceps*	Family	Forest	-	-	+*	+*	*
Xanthomixis zosterops	*Bernieria zosterops*	Family	Forest	+*	+*	+*	*	-
Crossleyia tenebrosa	*Bernieria tenebrosa*	Family	Forest	-	+	-	-	-
Crossleyia xanthophrys	*Bernieria xanthophrys*	Family	Forest	-	-	+*	+*	*
Randia pseudozosterops		Family	Forest	+*	+*	+*	+*	-
Phedina borbonica		Subspecies	Open areas	+	+	*	*	+*
Hypsipetes madagascariensis		Subspecies	Forest/open areas	+*	+*	+*	+*	+*
Zosterops maderaspatanus		Subspecies	Forest/open areas	+*	+*	+*	+*	+*
Hartlaubius auratus		Species	Forest/open areas	+*	-	-	-	-
Copsychus albospecularis		Species	Forest/open areas	+*	+*	+*	*	-
Monticola sharpei		Species	Forest	-	*	+*	+*	+*
Saxicola torquatus	*Saxicola torquata*	Subspecies	Open areas	-	-	-	+*	+*
Cinnyris notatus	*Nectarinia notata*	Subspecies	Forest	+*	+*	+*	*	*
Cinnyris sovimanga	*Nectarinia souimanga*	Subspecies	Forest/open areas	+*	+*	+*	+*	+*
Nelicurvius nelicourvi	*Ploceus nelicourvi*	Species	Forest	+*	+*	+*	-	-
Foudia madagascariensis		Species	Open areas	+	+*	+	-	+*
Foudia omissa		Species	Forest	+*	+*	+*	*	*
Lepidopygia nana	*Lonchura nana*	Genus	Open areas	+	-	-	-	-
Motacilla flaviventris		Species	Open areas	+*	+*	-	+*	-

Table 2. Details of ornithological surveys in each elevational zone within the Parc National de Marojejy during the inventories of 1996 and 2021.

Elevational zone	Duration of visit (days)	Point counts	Species recorded	Forest species recorded (percentage)	Species restricted to the zone
Site 1 | 1996	10	19	64	59 (92.2)	7
Site 1 | 2021	5	15	57	53 (93.0)	3
Site 2 | 1996	10	22	53	51 (96.2)	2
Site 2 | 2021	5	15	60	55 (91.7)	4
Site 3 | 1996	10	22	57	55 (96.5)	1
Site 3 | 2021	5	15	55	53 (96.4)	3
Site 4 | 1996	9	16	40	37 (92.5)	0
Site 4 | 2021	5	15	47	43 (91.5)	1
Site 5 | 1996	7	11	32	22 (68.8)	6
Site 5 | 2021	5	15	29	22 (73.3)	1

hypoxantha), and the remaining species at both sites (*Atelornis crossleyi*). At Site 5, *Falco eleonorae*, a migratory species that forages in open air space, was the only taxon during the 2021 inventory restricted to the upper portion of the massif.

Number of contacts and calculation of relative densities

Out of the 80 species found on massif during the 2021 inventory, 56 (70% of the total number of species) were identified during point counts, which encompassed 833 different bird contacts across the elevational transect. (The more detailed data for each site are presented in Appendix 1.) The four most abundant species were *Cinnyris sovimanga*, *Hypsipetes madagascariensis*, *Nesillas typica*, and *Zosterops maderaspatanus*. Across all sites, the number of contacts for these species varied from 46 to 221. For *C. sovimanga* more than 20 contacts were accrued at each site, whereas *H. madagascariensis*, the second most abundant species, had up to 20 and 22 contacts, at 450 m and 775 m, respectively. For *N. typica* and *Z. maderaspatanus*, the highest values were noted at Site 5 and Site 3, respectively. In contrast, more than 48% of recorded species were noted at most five times across the five sites, including eight species (14.3%) with a single contact (*Accipiter madagascariensis*, *A. francesiae*, *Buteo brachypterus*, *Neodrepanis hypoxantha*, *Leptopterus chabert*, *Cyanolanius madagascarinus*, *Euryceros prevostii*, and *Hartlaubius auratus*).

Table 3 shows density calculations based on the point count data. The average densities of bird species in the different elevational zones suggest that certain populations were not stable between the 1996 and 2021 point counts. The analyses indicate decreased densities for a considerable number of local populations, such as *Cryptosylvicola randrianasoloi* and *Monticola sharpei*, while others increased densities, including *Coua caerulea* and *Cinnyris sovimanga* (Table 3). However, the overall statistical analyses indicate that the community as a whole (t = 0.40848, df = 110.83, P = 0.6837), and most species appear to be stable between these two inventory periods. The estimated population size of three species, *Tylas eduardi* (t = 3.0149, df = 6.29, P = 0.0222), *Euryceros prevostii* (t = 2.4697, df = 5.71, P = 0.050), and *Artamella viridis* (t = 4.3638, df = 7.53, P = 0.003) were significantly reduced.

Mist-netting captures of understory birds

Mist-netting during the 2021 transect resulted in the capture of 205 individuals belonging to 32 species: fewer individuals but four additional species than in 1996 (Table 4). Ten species captured in 2021 were not captured in 1996. Of those 10 species, only *Hartertula flavoviridis* was not recorded by any census method during the 1996 transect, and the species was only identified in 2021 based on mist-netting. This technique also allowed the detection of *Crossleyia xanthophrys* at Site 3 and *Xanthomixis cinereiceps* at Site 5, both species not detected by other census methods at these sites in 2021.

Among the 32 species netted in 2021, seven were notably abundant with 13 to 32 individuals captured per species. The four most frequent species include *Nesillas typica* with 32 individuals, *Cinnyris sovimanga* with 25 individuals, and *Philepitta castanea* and *Xanthomixis cinereiceps* with 16 individuals each. However, 10 species were only captured in 2021 on a single occasion at a given elevational zone (*Nesoenas picturatus, Centropus toulou, Athene superciliaris, Neodrepanis hypoxantha*, *Mystacornis crossleyi, Oriolia bernieri,*

Table 3. Density per hectare of bird species detected on point counts in the five inventoried sites in the Parc National de Marojejy beween 1996 and 2021. *P* is the value of probability from t-test analysis, and this value when written in **bold** designates a statistically significant difference.

	Density (ha)										
	1996					2021					
Species	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	***P***
Nesoenas picturatus	0.27					0.34	0.69				0.3497
Alectroenas madagascariensis		0.23				0.69					0.5555
Coua caerulea	2.43	1.16	1.40	1.61	0.45	1.72	1.38	2.07	3.45	2.73	0.1181
Coua reynaudii	0.54	1.63	0.70	1.29	1.82		1.03	0.34	1.03	0.91	0.1422
Coua serriana	2.16	1.16	1.63				0.69				0.1227
Centropus toulou	3.24	0.70	0.23			0.69	0.34			1.36	0.6143
Cuculus rochii	1.89	4.42	4.42	0.97	0.45	0.69	0.69	0.34	0.69		0.0818
Mentocrex kioloides	0.54	0.23					0.69				0.9292
Sarothrura insularis					3.18		0.34			0.91	0.5862
Lophotibis cristata						0.34	0.34				0.1778
Accipiter francesiae							0.34				0.3739
Accipiter henstii				0.32							0.3739
Accipiter madagascariensis								0.34			0.3739
Buteo brachypterus								0.34			0.3739
Otus rutilus		0.47									0.3739
Leptosomus discolor		0.47				0.69					0.7997
Corythornis madagascariensis						1.38	0.34		0.34		0.1797
Eurystomus glaucurus				0.32							0.3739
Brachypteracias leptosomus	0.81	0.47	0.23	0.32			0.34	0.34			0.1916
Atelornis crossleyi			0.47	0.65	0.45						0.0773
Atelornis pittoides			0.23	0.32			0.34	0.34			0.8161
Coracopsis nigra	0.27	2.09	3.02			1.38	1.03	1.72	0.34		0.8038
Philepitta castanea	0.27	0.70	1.63			0.69	0.69	0.69			0.7714
Neodrepanis coruscans	1.35	1.63	1.40					0.69			0.1126
Neodrepanis hypoxantha			4.88	0.97					0.34		0.3094
Coracina cinerea	1.89	0.23	0.47			0.34	1.38				0.7058
Newtonia amphichroa	0.54	0.47	2.79	3.23	3.64	0.69	2.41	2.41	4.48	0.91	0.9630
Newtonia brunneicauda	0.27	3.72	3.26	5.48	0.91	1.72	2.41	1.72	1.38		0.2664
Tylas eduardi	0.81	2.09	3.95	2.26	2.27	0.34		1.03	1.38		**0.0222**
Calicalicus madagascariensis	5.95	3.02	3.26	1.29	0.45	1.72	1.72	2.07			0.1609
Leptopterus chabert	0.27								0.34		0.8761
Mystacornis crossleyi		0.70	2.09	0.97		0.34	0.34				0.1873
Cyanolanius madagascarinus		0.47	1.40	0.65			0.34				0.1691
Vanga curvirostris		0.70	0.23	1.61	0.91	0.34	0.69	1.38	1.38		0.8674
Pseudobias wardi						0.34				0.45	0.1833
Euryceros prevostii	0.81	0.47	0.70	0.32				0.34			**0.0505**
Artamella viridis	1.35	1.40	1.63	0.65	0.91	0.34	0.69				**0.0028**
Dicrurus forficatus	2.16	0.47	0.23	0.00		2.07	0.69	0.34	0.34		0.8367
Terpsiphone mutata	4.05	1.86	1.86	0.32		0.69	1.72	1.72			0.3685
Neomixis striatigula	3.51	2.56	0.70	4.52		3.10	2.76	2.76	2.07		0.9092
Neomixis tenella	4.59	2.33	2.09	0.00		0.69					0.1236
Neomixis viridis	3.51	1.86	1.40	0.65		1.72	0.34				0.1664
Nesillas typica			7.67	5.81	13.64	0.69		2.76	4.48	17.27	0.9272
Bradypterus brunneus				0.00	0.45				1.38	1.36	0.2496
Oxylabes madagascariensis	0.27	1.40	0.70	1.29		2.76	2.76	0.34			0.5590
Bernieria madagascariensis	1.89	1.40	1.40			1.03	4.48	2.07			0.5552
Cryptosylvicola randrianasoloi			2.79	5.81	6.36			0.34	0.34	3.64	0.2147
Xanthomixis cinereiceps									1.03		0.3739
Xanthomixis zosterops	1.89	1.16		1.94		3.45	4.14	0.69			0.5309
Crossleyia xanthophrys			0.47								0.3739
Randia pseudozosterops	2.16	1.40	0.47	2.26		1.72	1.72	1.38	2.41		0.7624
Hypsipetes madagascariensis	5.14	3.26	5.35	6.77	2.73	6.90	7.59	4.14	4.83	7.27	0.1780
Zosterops maderaspatanus	0.54	4.19	2.79	3.87	1.36	2.76	8.62	2.76	1.38	0.45	0.6999
Hartlaubius auratus						0.34					0.3739
Copsychus albospecularis	2.97	1.40	0.23			2.07	3.10	1.03			0.7108

Table 3. (suite)

	Density (ha)										
	1996					2021					
Species	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	***P***
Monticola sharpei			0.93	3.87	2.27			0.34	0.34		0.1602
Saxicola torquatus					4.09					1.36	0.5550
Cinnyris notatus	2.43	1.16	0.70			1.38	3.10	0.34	1.03		0.8148
Cinnyris sovimanga	1.08	7.67	13.95	12.26	13.18	22.76	15.17	13.10	13.45	15.45	0.0680
Nelicurvius nelicourvi	0.27	1.16	0.70			1.03	1.03	0.34			0.8714
Foudia madagascariensis			0.23	0.97							0.2705
Foudia omissa	0.54	0.93			0.45			0.34		0.45	0.3040
Lepidopygia nana	0.27										0.3739

Table 4. Results of understory bird netting in 1996 and 2021 by site along an elevational transect of the Parc National de Marojejy and based on 50 cumulative net-days at each site. Figures do not incorporate recaptures but includes an *Atelornis crossleyi* captured in a bat net.

Species	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**		**Total**	
	1996	**2021**	**1996**	**2021**	**1996**	**2021**	**1996**	**2021**	**1996**	**2021**	**1996**	**2021**
Nesoenas picturatus				1								**1**
Centropus toulou										1		**1**
Accipiter francesiae	1										**1**	
Otus rutilus			2	2	1	1					**3**	**3**
Athene superciliaris		1										**1**
Corythornis madagascariensis	2	1	4	1				1			**6**	**3**
Corythornis vintsioides	1										**1**	
Brachypteracias leptosomus					1						**1**	
Atelornis crossleyi								1				
Philepitta castanea	3	1	16	3	11	7	2	5			**32**	**16**
Neodrepanis coruscans	4		9	1		6					**13**	**7**
Neodrepanis hypoxantha					1		1	1			**11**	**1**
Newtonia amphichroa			2		7	8	5	4		1	**14**	**13**
Newtonia brunneicauda			2								**2**	
Tylas eduardi				1				1				**2**
Mystacornis crossleyi						1						**1**
Vanga curvirostris			3								**3**	
Euryceros prevostii	1	2		2							**1**	**4**
Oriolia bernieri				1								**1**
Artamella viridis						1						**1**
Terpsiphone mutata	3		4	2	5	6					**12**	**8**
Nesillas typica				1	9	4	4	8	8	19	**21**	**32**
Oxylabes madagascariensis		1			7	2					**7**	**3**
Bernieria madagascariensis			4	8		1					**4**	**9**
Cryptosylvicola randrianasoloi									2	1	**2**	**1**
Hartertula flavoviridis						1						**1**
Xanthomixis cinereiceps					7	5	7	1		1	**14**	**16**
Xanthomixis zosterops	2	1	2	3		4					**4**	**8**
Crossleyia xanthophrys					2	2	1	1			**3**	**3**
Hypsipetes madagascariensis			2		1	6				8	**3**	**14**
Zosterops maderaspatanus	6		2		2		1		2		**13**	
Copsychus albospecularis	1	4	1	5		4		1			**11**	**14**
Monticola sharpei					3		2	2			**5**	**2**
Saxicola torquatus									5	4	**5**	**4**
Cinnyris notatus								1				**1**
Cinnyris sovimanga	5	3	5	7	4	7	3	4	5	4	**22**	**25**
Nelicurvius nelicourvi	1	1	1	1	1						**3**	**2**
Foudia madagascariensis									7		**7**	
Foudia omissa	4		3		1	1		2		4	**8**	**7**
Total number of individuals	**34**	**15**	**71**	**38**	**72**	**68**	**26**	**41**	**26**	**43**	**232**	**205**
Total number of species	**13**	**9**	**16**	**15**	**16**	**18**	**9**	**14***	**6**	**9**	**28**	**32**
Average number of birds/net-day	**0.7**	**0.3**	**1.4**	**0.8**	**1.4**	**1.4**	**0.5**	**0.8**	**0.6**	**0.9**	**0.9**	**0.8**

Table 5. Distribution by site of species recorded in 2021 in the Parc National de Marojejy and considered by the IUCN as Near Threatened or threatened (comprising Critically Endangered, Endangered, and Vulnerable).

Key to IUCN categories: NT = Near Threatened, V = Vulnerable, and EN = Endangered. Other definitions: * = present at a given site; End Mad = endemic to Madagascar.

Species	IUCN Status	Endemism	Habitat	Site 1	Site 2	Site 3	Site 4	Site 5
Lophotibis cristata	NT	End Mad	Forest	*	*	*		
Accipiter madagascariensis	NT	End Mad	Forest	*		*		
Mesitornis unicolor	VU	End Mad	Forest			*		
Tyto soumagnei	VU	End Mad	Forest		*			
Brachypteracias leptosomus	VU	End Mad	Forest	*	*	*		
Geobiastes squamiger	VU	End Mad	Forest	*				
Atelornis crossleyi	NT	End Mad	Forest			*	*	
Neodrepanis hypoxantha	VU	End Mad	Forest				*	
Xanthomixis cinereiceps	NT	End Mad	Forest			*	*	*
Hartertula flavoviridis	NT	End Mad	Forest			*		
Oriolia bernieri	EN	End Mad	Forest		*	*		
Euryceros prevostii	EN	End Mad	Forest	*	*	*		
Number of species				**5**	**5**	**9**	**3**	**1**

Artamella viridis, Cryptosylvicola randrianasoloi, Hartertula flavoviridis, and *Cinnyris notatus*).

The highest catch rate averaged over five consecutive days of mist-netting was at Site 3 with 1.4 individuals/net-day and the lowest being in Site 1 with 0.3 individuals/net-day; the rates at the other sites ranged between 0.8 and 0.9 individuals/net-day. Table 4 shows the capture results at the different sites in 1996 and 2021.

The results from comparative mist netting from 1996 and 2021 showed reduced capture rates in 2021 of eight species out of the 40 captured, including *Philepitta castanea*, *Neodrepanis coruscans*, *N. hypoxantha*, *Terpsiphone mutata*, *Oxylabes madagascariensis*, *Zosterops maderaspatanus*, *Monticola sharpei*, and *Foudia madagascariensis*. However, five species showed slight increases in 2021: *Euryceros prevostii*, *Nesillas typica*, *Bernieria madagascariensis*, *Xanthomixis zosterops*, *Hypsipetes madagascariensis*, and *Cinnyris sovimanga*. Based on these results, it appears that outside of the randomness of captures, the population size of a large portion of bird communities was fairly stable between the two inventories.

Endemism

Of the 80 inventoried species in 2021 in the Parc National de Marojejy, 57 or 71.3% are endemic to Madagascar and another 18 or 22.5% are found only in the Malagasy Region. Of the 71 forest-dependent species encountered during the survey, 76.1% are endemic to the island. All five endemic families are present on the Marojejy Massif: Mesitornithidae, Brachypteraciidae, Leptosomidae, Philepittidae and Bernieridae, as well as the two endemic subfamilies, Couinae and Vanginae.

Species conservation status

In total, 85% of the species recorded in 2021, are classified as Least Concern (LC) based on a recent IUCN Red List (IUCN, 2023). The remaining 15% include five species listed as Near Threatened, five as Vulnerable (VU), and two as Endangered (EN); all of these species are forest dependent and endemic to Madagascar, and of the two EN species, it is concerning that one, *Euryceros prevostii*, showed significantly reduced population density. The distribution of these 12 threatened species by site are summarized in Table 5.

Discussion

Methodological considerations

On the basis of the three survey methods (general observation, capture of understory bird species with mist nets, and point counts) used during the 2021 inventory, the cumulative number of species recorded in each of the five elevational zones continued to increase slightly until the end of the sampling period (Figure 2); the exception being Site 4, where the sampling curve reached a plateau after the fourth day. Inference based on these results indicated that at Sites 1, 2, 3, and 5, a few species may have been missed. However, except at Site 5 in 1996, where the maximum species richness was attained after the third day, the cumulative number of registered species per site based on the three survey techniques

are similar to those presented by Goodman *et al*. (2000) for the 1996 survey.

Composition and species diversity

By comparing the list of bird species recorded during the 1996 elevational survey of Marojejy (Goodman *et al*., 2000) to that from 2021, six previously unrecorded species were added to those not known from the five surveyed sites (*Accipiter madagascariensis*, *Dryolimnas cuvieri*, *Tyto soumagnei*, *Gactornis enarratus*, *Hartertula flavoviridis*, and *Schetba rufa*). With these taxa, the species richness found in these two surveys along the eastern altitudinal gradient of the Marojejy Massif reaches 91 species.

Conversely, 12 species were previously observed on the Marojejy Massif in 1996 (Goodman *et al*., 2000), but were not found in 2021 (Table 1). These include three forest species (*Accipiter henstii*, *Coracopsis vasa*, and *Crossleyia tenebrosa*), one of aquatic (*Corythornis vintsioides*) and eight of open habitats (*Margaroperdix madagarensis*, *Coturnix coturnix*, *Caprimulgus madagascariensis*, *Cypsiurus gracilis*, *Eurystomus glaucurus*, *Eremopterix hova*, *Neomixis tenella* [as well as forest], and *Lepidopygia nana*). Several different explanations can be suggested to explain their absence during the 2021 inventory. First, the population size of some species would be small, making the chance of their detection reduced. Secondly, the daily weather conditions, which greatly influence the rate of activity of the birds, may have been different between the survey periods. Thirdly, the gradual regeneration of degraded forest habitats, specifically at Site 1, over the intervening 25 years may have resulted in less favorable habitat for open area species as compared to the situation in 1996. Fourthly, the differences could be associated with general patterns of climate change that have resulted in changes in local meteorological conditions that presumably vary across the altitudinal gradient of the eastern slopes of the massif, including shifts in rainfall patterns and the length of the dry season that would presumably impact major food resources, leading to their absence in the inventoried areas.

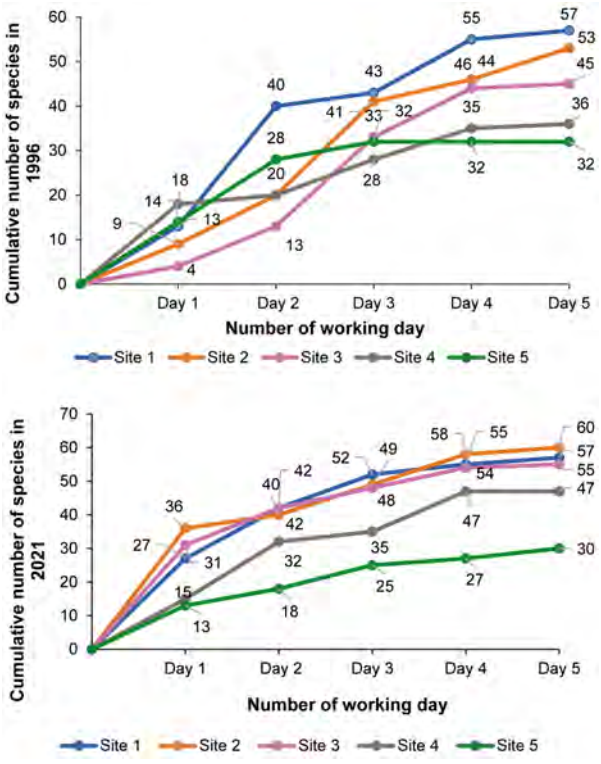

Figure 2. Cumulative curves of bird species recorded within each elevational zone in the Parc National de Marojejy during the 1996 and 2021 surveys as a function of number working days and the combined data from the three survey techniques. Data from 1996 extracted from Goodman *et al.* (2000).

A review of birds known from Marojejy, other than those mentioned in Goodman *et al*. (2000), indicates that 13 additional species have been recorded from the protected area. However, due to the lack of precision as to the localities that many of these different species were observed, several may have been recorded in areas of the park outside the Mandena-summit trail or occurred in particular habitats that are now rare or not present along this trail; these species are not included in the list of birds along the elevational transect based on the 1996 and 2021 field surveys.

The bird community occurring on the Marojejy Massif is largely made up of forest-dependent species. This is to be expected, as the Malagasy terrestrial avifauna is characterized by a large proportion of forest species (Wilmé, 1996; Safford & Hawkins, 2013) and the 1996 and 2021 ornithological inventories took place mainly within the forest. The presence of a certain open area species in the forest environment would normally be an indicator of the state of degradation of a forest environment (Safford & Hawkins, 2013). However, in certain cases the occurrence of such species at Marojejy has to do with particular microhabitats, such as *Motacilla flaviventris* along river margins and other taxa occurring in naturally open habitats such as in the summital area in montane grasslands (see below).

The avifauna of the Marojejy Massif is also characterized by the presence of specialist species outside their typical altitudinal limits. These are the cases of *Neodrepanis coruscans*, normally restricted to the middle and upper portions of medium altitude

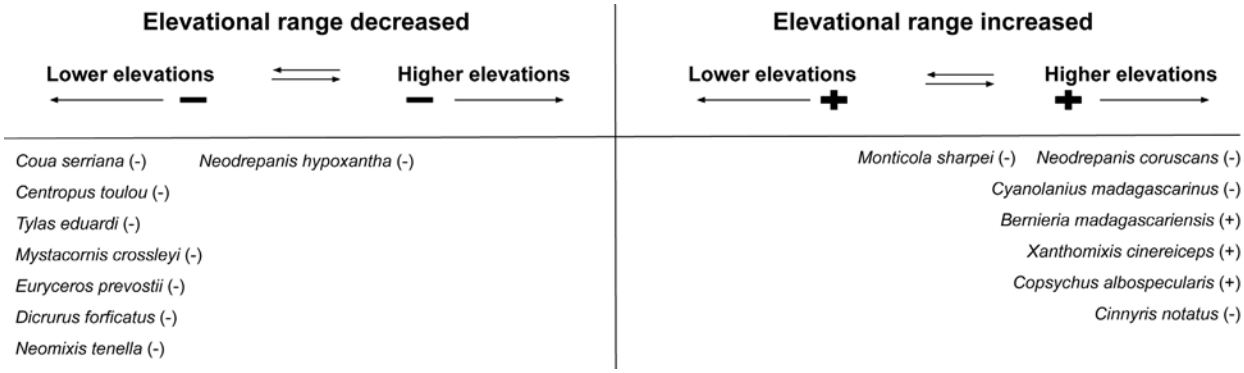

Figure 3. Based on point count and mist-netting data (minimum N > 10 per species), several bird species showed shifts between 1996 and 2021 in their elevational distributions in the Parc National de Marojejy and these are presented in the figure. Elevational range increase refers to the widening of the interval between the minimal and maximal altitudinal distribution of a given species, while decrease refers to the reduction of the interval of a given species. This widening or shrinking is further categorized based on whether the shift occurred in an uphill or downhill direction and tendencies in these different parameters.

moist evergreen forest (Site 4) and *Bradypterus brunneus* in a variety of vegetation types. The highly rugged terrain, with very steep slopes and a significant altitudinal difference with a very short geographical distance, probably allows the movement of species between the different types of forests.

Dynamics of the Parc National de Marojejy bird community: comparisons between 1996 and 2021

Change of species composition

Several factors conspire to make comparisons of the bird community between the 1996 and 2021 studies difficult. These include the complex structure of the moist evergreen forests of Marojejy, varying meteorological patterns, and chance contact with species during a rapid inventory, particularly those that are not locally common, and the presence or absence of a given taxon, some of which were only inventoried in 1996 and others only in 2021. However, the absence of species in 2021 that were only recorded in 1996 above forest line at Site 5, including *Margaroperdix madagarensis*, *Coturnix coturnix*, *Caprimulgus madagascariensis*, and *Eremopterix hova*, are difficult to explain, but might be aligned with changes in climatic conditions and associated habitat modification, resulting in the reduction of local populations of these species and not being observed or their local extirpation.

Change in abundance

Comparison of densities based on point count surveys conducted in parallel manners and during the same calendar period in 1996 and 2015 on the eastern slopes of the Parc National de Marojejy, indicate that in general, the population levels making up the local bird community appear to be stable over the past 25 years. Species-level analyses noted variation in bird species densities in each elevational zone, but no statistically significant change occurred except for the few cases discussed below. As most of the species concerned are forest dependent (Safford & Hawkins, 2013; Safford *et al*., 2022) and the surveys were conducted along the main tourist trail, local human pressures are low in the Manantenina River watershed (Tahinarivony, 2023b, herein). Bird community stability was generally maintained in the surveyed area. This stability may possibly be explained by the resilience of most species in the face of changing ecological conditions associated with the effects of natural cataclysms, climate change, and broader human pressures within the park. Cyclones of varying intensity have passed through the northern region of Madagascar (the most violent being cyclone Hudah in 2000 and cyclone Gafilo in 2004), which presumably impacted the local ecosystem. Also, between 1984 and 2014 the maximum temperature in the park increased by 1.1ºC and there has been some forest loss in the park (Goodman *et al*., 2018a). Although based on the analysis there is apparent stability, the decrease in the density of many species over the course of 25 years, even relatively small, in a portion of the park with low human pressures, might signal a decline in populations for certain species (e.g. *Neodrepanis hypoxantha*, *Mystacornis crossleyi*, *Cryptosylvicola randrianasoloi*, and *Monticola sharpei*). Strengthening conservation actions, especially in areas subject to anthropogenic pressures, is therefore crucial for maintaining the ecological integrity of the protected area.

Species that showed changes in their density between 1996 and 2021 include *Tylas eduardi*, *Euryceros prevostii*, and *Artamella viridis* (Table 3) and these taxa, all belonging to the endemic Malagasy subfamily Vanginae, showed a significant decrease. As these taxa are easily detectable, either by observations or vocalizations, the differences between the estimated densities between the 1996 and the 2021 surveys, both conducted during the same portion of the calendar year, would not be due to sampling errors. We assume that during the interim 25 years between the inventories some environmental change took place at the study sites and resulted in the reduced densities of these three Vangidae. For the cases of *T*. *eduardi* and *A*. *viridis*, the situation may not be too serious as these two species are well represented in the moist evergreen and dry forests, as well as spiny tickets of the island (Goodman & Raherilalao, 2013). In contrast, the conservation status of *Euryceros prevostii* is considered Vulnerable (IUCN, 2023), and according to Andrimasimanana and Cameron (2023), it is considered to be among the most vulnerable species to climate change superimposed on other threats that negatively influences some forest-dependent species, including *E*. *prevostii*, drastically in the future. Among the future impacts of these threats is the progressive reduction of the distributional range of this species, largely restricted in the northern part of the island due to the loss of ecologically favorable forest habitat.

Change in elevational distribution

Several species that in 2021 showed a reduced elevational distribution than in 1996, also shifted to lower portions of the massif. In contrast, species that had a broader elevational range in 2021, as compared to 1996, mostly shifted towards higher elevations (Table 1 and Figure 3). This phenomenon may be affected by changes in climate, especially for insectivores with specialized feeding or species with low tolerance to abrupt environmental changes such as for Vangidae species.

Among the species which had a decrease in elevational range, all were detected via point counts, general observation, and mist-netting captures on fewer occasions in 2021 than in 1996 (*Coua serriana*, *Neodrepanis hypoxantha*, *Tylas eduardi*, *Mystacornis crossleyi*, *Euryceros prevostii*, *Dicrurus forficatus*, and *Neomixis tenella*). All species that were detected via the same techniques more often in 2021 than in 1996 also shifted in elevational range to higher portions of the massif (*Cyanolanius madagascarinus*, *Oriolia bernieri*, *Bernieria madagascariensis*, *Xanthomixis cinereiceps*, and *Copsychus albospecularis*) (Table 1).

In summary, based on the results presented herein, changes due to several factors, such as climate change and anthropogenic pressures, have been observed for a considerable number of bird species; in some cases, the differences are minor and for some others more significant. However, it is difficult to precisely measure the level of importance of these changes over the course of 25 years, in part associated with differences in parameters such as observer abilities, number of point counts, and perhaps some stochastic aspects. As this study is among the first on Madagascar to examine population tendencies of a large and notably mobile bird community in a complex forest ecosystem, other exercises on the massif, as well as other sites, are needed.

Species accounts

Birds of prey (*Accipiter madagascariensis*, *A. henstii*, *Athene superciliaris*, and *Asio madagascariensis*)

Accipiter madagascariensis was not detected on the 1996 transect but was recorded twice in 2021 (Sites 1 and 3). *Accipiter henstii* was recorded in 1996 at Site 1 and Site 4 but was not detected during the 2021 transect. *Athene superciliaris* was found at Sites 1 and 3 in 1996 and only detected at Site 1 in 2021. *Asio madagascariensis* was detected at Sites 1 and 3 in 1996 and at Sites 1 and 2 in 2021. However, these apparent changes in elevational distribution ranges between the two transects, and reduced number of records in 2021 may be biologically insignificant due to the small population size of each species.

Brachypteraciidae (*Brachypteracias leptosomus*, *Geobiates squamiger*, *Atelornis pittoides*, and *A. crossleyi*)

All four Brachypteraciidae species showed similar patterns in elevational range distribution changes. *Brachypteracias leptosomus, Geobiates squamiger*, and *Atelornis crossleyi* demonstrated a decrease in elevational range between 1996 and 2021 towards lower elevations. *Atelornis pittoides* shifted towards lower elevations as it was detected at Sites 2 and 3 in 2021 as opposed to Sites 3 and 4 in 1996.

Coracopsis vasa and *C. nigra*

Coracopsis vasa was detected at sites 2, 3, and 4 during the 1996 transect but was undetected during the 2021 transect. Goodman *et al*. (2000) combined *C. vasa* and *C*. *nigra* to *Coracopsis* spp. because of "difficulties in distinguishing [them] in the field" and states that "[t]he vast majority of our records concern *C*. *nigra*" and records *Coracopsis* spp. at all sites. Due to the close resemblance of these two species, combined with their detection possible only via sight and sound and mostly in the forest canopy, there is the possibility of identification errors during the 2021 transect of resulting in the lack of detection of *C*. *vasa*; but the two species exist on the massif and dominated by *C*. *nigra*.

Crossleyia xanthophrys and *Xanthomixis cinereiceps*

Crossleyia xanthophrys and *Xanthomixis cinereiceps* showed a similar pattern of increasing their elevational range distribution between 1996 and 2021. Insectivorous species densities at lower elevations may be broadly impacted by climatic factors. However, as *C*. *xanthophrys* and *X*. *cinereiceps* are high mountain specialists (Safford & Hawkins, 2013) it is normal that the contact frequency with these species was higher in the mountain mossy forest than at lower altitude forest, where these birds were rare or absent.

Conclusion

Our study in the latter portion of 2021 of the bird community at five sites along an elevational gradient (450 to 1875 m) of the Parc National de Marojejy identified a total of 80 species, 71.3% endemic to Madagascar including most of the globally threatened species that could be expected in this part of Madagascar, further confirming the importance of this protected area for bird conservation. The 2021 inventory followed in considerable detail the field techniques and dates of an earlier transect conducted in 1996. The combined data obtained during the 1996 and 2021 transects indicate that at least 91 species of birds occur on the eastern slopes of the Marojejy Massif; 11 species were recorded in 1996 and not in 2021. The various explorations at the site help to refine details on the park's bird community, most of which is forest dependent and includes taxa restricted to the northern part of the island and several globally threatened species.

The analysis of bird population trends along the eastern slopes of the Parc National de Marojejy between 1996 and 2021 indicate that four species (*Margaroperdix madagarensis*, *Coturnix coturnix*, *Caprimulgus madagascariensis*, and *Eremopterix hova*) found during the first survey in the montane ericoid thickets and montane grassland of the summit zone were not found during the 2021 exploration. The latter two species are conspicuous and presumably they no longer occur or in very low densities in the upper reaches of the massif. As a working hypothesis and awaiting the needed data for proper testing, the ecological conditions in the habitat above the forest line, particularly with the almost permanent presence of fog, which increases humidity and the lower temperature, differ from the habitats generally frequented by these species and whatever the driving factors are, they seem to have become rare or disappeared from this zone.

For dependent forest species, the majority showed no statistically significant changes in population density over the 25 year interim period but there was a general trend of reduced density. However, three taxa (*Tylas eduardi*, *Euryceros prevostii*, and *Artamella viridis*) showed decreasing population trends. These species appear more sensitive to changes in environmental conditions, most likely associated with changing ecological conditions perhaps associated with climate change, which has been documented to occur on the massif (Goodman *et al.*, 2018a). It is particularly concerning that one of these species, *E. prevostii*, is considered globally Endangered based on ongoing and rapid forest habitat clearance in its limited range, with climate change also projected to severely affect it. We suggest that anthropogenic habitat degradation cannot explain these changes as the transect zones are along the main tourist trail and not subject to different forms of exploitation. To our knowledge, this is the first published study of long-term population trends of birds occurring in moist evergreen forests of Madagascar. Given the number of quantitative surveys conducted on the island some decades ago, this is a research theme that should to be carried out at other sites to better understand the resuts of this current study and which would have important implications in terms of conservation of the Malagasy avifauna.

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References

Alström, P., Fregin, S., Norman, J. A., Ericson, P. G. P., Christidis, L. & Olsson, U. 2011. Multilocus analysis of a taxonomically densely sampled dataset reveal extensive non-monophyly in the avian family Locustellidae. *Molecular Phylogenetics and Evolution*, 58: 513-526.

Alström, P., Barnes, K. N., Olsson, U., Barker, F. K., Bloomer, P., Khan, A. A., Qureshi, M. A., Guillaumet, A., Crochet, P.-A. & Ryan, P. G. 2013. Multilocus phylogeny of the avian family Alaudidae (larks) reveals complex morphological evolution, non-monophyletic genera and hidden species diversity. *Molecular Phylogenetics and Evolution*, 69: 1043-1056.

Andriamasimanana, R. H. & Cameron, A. 2013. Predicting the impacts of climate change on the distribution of threatened forest-restricted birds in Madagascar. *Ecology and Evolution*, 3 (4): 763-769.

Benson, C. W., Colebrook-Robjent, J. F. R. & Williams, A. 1976. Contribution à l'ornithologie de Madagascar. *L'Oiseau et la Revue Française d'Ornithologie*, 46: 103-134, 209-242, 367-386.

Benson, C. W., Colebrook-Robjent, J. F. R. & Williams, A. 1977. Contribution à l'ornithologie de Madagascar. *L'Oiseau et la Revue Française d'Ornithologie*, 47: 41-64, 168-191.

Bibby, C. J., Burgess, N. D., Hill, D. A. & Mustoe, S. H. 2000. *Bird census techniques*, 2nd edition. Academic Press, London.

Bourque, A. 2000. Les changements climatiques et leurs impacts. *Vertigo*, 1 (2): 4042.

Cibois, A., Silka, B., Schulenberg, T. S. & Pasquet, E. 2001. An endemic radiation of Malagasy songbirds revealed by mitochondrial DNA sequence data. *Evolution*, 55: 1198-1206.

De Silva, T. N., Peterson, A. T., Bates, J. M., Fernando, S. W. & Girard, M. G. 2017. Phylogenetic relationships of weaverbirds (Aves: Ploceidae): A first robust phylogeny based on mitochondrial and nuclear markers. *Molecular Phylogenetics and Evolution*, 109: 21-32.

Evans, M. I., Duckworth, J. W., Hawkins, A. F. A., Safford, R. J., Sheldon, B. C. & Wilkinson, R. J. 1992. Key bird species of Marojejy Strict Nature Reserve, Madagascar. *Bird Conservation International*, 2: 201-220.

Fuchs, J., Lemoine, D., Parra, J. L., Pons, J.-M., Raherilalao, M. J., Prys-Jones, R., Thébaud, C., Warren, B. H. & Goodman, S. M. 2016. Long-distance dispersal and inter-island colonization across the western Malagasy Region explain diversification in brush-warblers (Passeriformes: *Nesillas*). *Biological Journal of the Linnean Society*, 119: 873-889.

García-R, J. C., Gibb, G. C. & Trewick, S. A. 2014. Deep global evolutionary radiation in birds: Diversification and trait evolution in the cosmopolitan bird family Rallidae. *Molecular Phylogenetics and Evolution*, 81: 96-108.

Gardner, C. 2022. The impact of habitat change on Madagascar's birds. In *The new natural history of Madagascar*, ed. S. M. Goodman, pp. 1603-1608. Princeton University Press, Princeton.

Gautier, L., Tahinarivony, J. A., Ranirison, P. & Wohlhauser, S. 2018. Végétation / Vegetation. Dans *Les aires protégées terrestres de Madagascar : Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their history, description, and biota,* eds. S. M. Goodman, M. J. Raherilalao & S. Wohlhauser, pp. 207-242. Association Vahatra, Antananarivo.

Goodman, S. M. (ed.). 1998. A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, new series, 90: 1-246.

Goodman, S. M. (ed.). 2000. A floral and faunal inventory of the Parc National de Marojejy, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, new series, 97: 1-286.

Goodman, S. M. & Jungers, W. L. 2014. *Extinct Madagascar: Picturing the island's past*. The University Press of Chicago, Chicago.

Goodman, S. M. & Raherilalao, M. J. 2013. Oiseaux ou Classe des Aves. Dans *Atlas d'une sélection de vertébrés terrestres de Madagascar / Atlas of selected land vertebrates of Madagascar*, eds. S. M. Goodman & M. J. Raherilalao, pp. 63-168. Association Vahatra, Antananarivo.

Goodman, S. M., Langrand, O. & Whitney, B. M. 1996. A new genus and species of passerine from the eastern rainforest of Madagascar. *Ibis*, 136: 153-159.

Goodman, S. M., Hawkins, A. F. A. & Domergue, C. A. 1997. A new species of vanga (Vangidae: *Calicalicus*) from southwestern Madagascar. *Bulletin of the British Ornithologists' Club*, 117: 4-10.

Goodman, S. M., Hawkins, A. F. A. & Razafimahaimodison, J.-C. 2000. Birds of the Parc National de Marojejy, Madagascar: With reference to elevational variation. In A floral and faunal inventory of the Parc National de Marojejy, Madagascar: With reference to elevation variation , ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 97: 175-200.

Goodman, S. M., Raherilalao, M. J. & Block, N. 2011. Patterns of morphological and genetic variation in the *Mentocrex kioloides* complex (Aves: Gruiformes: Rallidae) from Madagascar, with the description of a new species. *Zootaxa*, 2776: 49-60.

Goodman, S. M., Raherilalao, M. J. & Wohlhauser, S. (eds.). 2018a. *Les aires protégées terrestres de Madagascar : Leur histoire*, *description et biote / The terrestrial protected areas of Madagascar: Their history*, *description and biota*. Association Vahatra, Antananarivo.

Goodman, S. M., Raherilalao, M. J., Raselimanana, A. P. & Soarimalala, V. 2018b. Progrès réalisés au cours des 30 dernières années sur les vertébrés terrestres présents dans lés aires protégées. / Advances over the past 30 years on the land vertebrates occurring in the terrestrial protected areas of Madagascar. Dans *Les aires protégées terrestres de Madagascar : Leur histoire*, *description et biote / The terrestrial protected areas of Madagascar: Their history*, *description and biota*, pp. 1679-1692. Association Vahatra, Antananarivo.

Goodman, S. M., Raselimanana, A. P. & Tahinarivony, J. A. 2023. Description of the Parc National de Marojejy, Madagascar, and the 2021 biological inventory of the massif. In A floral and faunal inventory of the Parc National de Marojejy: Altitudinal gradient and temporal variation, eds. S. M. Goodman & M. J. Raherilalao. *Malagasy Nature*, 17: 5-31.

Griveaud, P. 1960. Une mission entomologique au Marojejy. *Naturaliste Malgache*, 12: 43-55.

Hawkins, A. F. A. & Goodman, S. M. 1999. Bird community variation with elevation and habitat in Parcels 1 and 2 of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation, ed. S. M. Goodman. *Fieldiana, Zoology*, new series, 94: 175-186.

Hawkins, A. F. A., Thiollay, J.-M. & Goodman, S. M. 1998. The birds of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. In A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevation variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 90: 93-127.

Hawkins, A. F. A., Safford, R. J. & Skerrett, A. 2015. *Birds of Madagascar and the Indian Ocean islands*. Christopher Helm, London.

Hending, D., Holderied, M., McCabe, G. & Cotton, S. 2021. Effects of future climate change on the forests of Madagascar. *Ecosphere*, 13 (4): e4017.

Humbert, H. 1955. Une merveille de la nature à Madagascar. Première exploration botanique du Massif du Marojejy et de ses satellites. *Mémoires de l'Institut Scientifique de Madagascar*, Série B, Biologie Végétale, 6: 1-272.

IUCN. 2023. The IUCN Red List of Threatened Species. Version 2022-2. https://www.iucnredlist.org.

Johansson, U. S., Bowie, R. C. K., Hackett, S. J. & Schulenberg, T. S. 2008. The phylogenetic affinities of Crossley's babbler (*Mystacornis crossleyi*): Adding a new niche to the vanga radiation of Madagascar. *Biology Letters*, 4: 677-680.

Jønsson, K. A., Fabre, P.-H., Fritz, S. A., Etienne, R. S., Ricklefs, R. E., Jørgensen, T. B., Fjeldså, J., Rahbek, C., Ericson, P. G. P., Woog, F., Pasquet, E. & Irestedt, M. 2012. Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Sciences of the USA*, 109: 6620-6625.

Jury, M. R. 2022. The climate of Madagascar. In *The new natural history of Madagascar*, ed. S. M. Goodman, pp. 91-99. Princeton University Press, Princeton.

Kirchman, J. J., Hackett, S. J., Goodman, S. M. & Bates, J. M. 2001. Phylogeny and systematics of the ground rollers (Brachypteraciidae) of Madagascar. *Auk*, 118: 849-863.

Langrand, O. 1990. *Guide to the birds of Madagascar*. Yale University Press, New Haven.

Langrand, O. 1995. *Guide des oiseaux de Madagascar*. Delachuaux et Niestlé, Lausanne.

Langrand, O. & Wilmé, L. 1997. Effects of forest fragmentation on extinction patterns of the endemic avifauna on the Central High Plateau of Madagascar. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 280-305. Smithsonian Institution Press, Washington, D. C.

Marks, B. D. & Willard, D. E. 2005. Phylogenetic relationship of the Malagasy Pigmy Kingfisher (*Ispidina madagascariensis*). *Auk*, 122: 1271-1280.

Morris, P. & Hawkins, F. 1998. *Birds of Madagascar: A photographic guide*. Yale University Press, New Haven.

Nakamura, M., Yamagishi, S. & Olamiya, T. 2001a. Breeding biology of the Sickle-billed Vanga *Falculea palliata*, which is endemic to Madagascar. In *Ecological radiation of Madagascan endemic vertebrates with special reference to coevolution between birds and reptiles*, eds. S. Yamagishi & A. Mori, pp. 48-52. Kyoto University, Kyoto.

Nakamura, M., Yamagishi, S. & Nishiumi, I. 2001b. Cooperative breeding of the White-headed Vanga *Leptopterus viridis*, an endemic species in Madagascar. *Journal of the Yamashina Institute for Ornithology*, 33: 1-14.

Nakamura, M., Okamiya, T., Hasegawa, M. & Hasegawa, M. 2009a. Cooperative breeding in the endemic Madagascan Chabert's Vanga *Leptopterus chabert*. *Ornithological Science*, 8: 23-27.

Nakamura, M., Tateno, M. & Rakotomanana, H. 2009b. Breeding ecology of the Tylas Vanga *Tylas eduardi* in southeastern Madagascar. *Ornithological Science*, 8: 15-22.

Nicoll, M. E. & Langrand, O. 1989. *Madagascar: Revue de la conservation et des aires protégées*. World Wide Fund for Nature, Gland.

Payne, R. B. & Sorenson, M. D. 2003. Museum collections as sources of genetic data. *Bonner zoologische Beiträge*, 51: 97-104.

Rabarisoa, R., Rakotonomenjanahary, O. & Ramanampamonjy, J. 2006. Waterbirds of Baie de Baly, Madagascar. In *Waterbirds around the world*, eds. G. C. Boere, C. A. Galbraith & D. A. Stroud, pp. 374-375. The Stationery Office, Edinburgh.

Rabarisoa, R., Ramanampamonjy, J., Razafindrajao, F., Rene de Roland, L.-A., Jeanne, F., Bacar, O., Laubin, A. & Bignon, F. 2020. Status assessment and population trends of the Madagascar Pond-Heron (*Ardeola idae*) from 1993-2016. *Waterbirds*, 43: 45-54.

Raherilalao, M. J. & Goodman, S. M. 2003. Diversité de la faune avienne des massifs d'Anjanaharibe-Sud, du Marojejy et de la Forêt de Betaolana, et importance du couloir forestier dans la conservation des oiseaux forestiers. Dans Nouveaux résultats d'inventaires biologiques faisant référence à l'altitude dans la région des massifs montagneux de Marojejy et d'Anjanaharibe-Sud, eds. S. M. Goodman & L. Wilmé. *Recherches pour le Développement, Série Sciences biologiques*, 19: 203-230.

Raherilalao, M. J. & Wilmé, L. 2008. L'avifaune des forêts sèches malgaches. Dans Les forêts sèches de Madagascar, eds. S. M. Goodman & L. Wilmé. *Malagasy Nature*, 1: 76-105.

Raherilalao, M. J., Gautier, F. & Goodman, S. M. 2002. Les oiseaux de la Réserve Spéciale de Manongarivo, Madagascar. Dans Inventaire floristique et faunistique de la Réserve Spéciale de Manongarivo, Madagascar, eds. L. Gautier & S. M. Goodman. *Boissiera*, 59: 359-381.

Raherilalao, M. J., Raselimanana, A. P., Soarimalala, V. & Goodman, S. M. 2016. Evaluation biologique et écologique de la flore et de la faune du Parc National de Marojejy, Madagascar. Rapport non publié. Association Vahatra, Antananarivo.

Rakotondrafara, M. L., Randriamarolaza, L. Y. A., Rasolonjatovo, H., Rakotomalala, C. L. & Razanakiniana, F. S. 2018. Evolution des paramètres climatiques à Madagascar. Dans *Les aires protégées terrestres de Madagascar : Leur histoire*, *description et biote / The terrestrial protected areas of Madagascar: Their history*, *description and biota*, pp. 199-206. Association Vahatra, Antananarivo.

Rand. A. L. 1932. Mission Franco-Anglo-Americaine à Madagascar : Notes de voyage. *L'Oiseau et la Revue Francaise d'Ornithologie*, nouvelle serie, 2: 227-282.

Rand, A. L. 1936. The distribution and habits of Madagascar birds: Summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. *Bulletin of the American Museum of Natural History*, 72: 153-499.

Reddy, S., Driskell, A. C., Rabosky, D. L., Hackett, S. J. & Schulenberg, T. S. 2012. Diversification and the adaptive radiation of the vangas of Madagascar. *Proceedings of the Royal Society B: Biological Sciences*, 279: 2062-2071.

Rene de Roland, L. & Thorstrom, R. 2022. Accipitriformes and Falconiformes: Hawks, eagles, kites, and falcons. In *The new natural history of Madagascar*, ed. S. M. Goodman, pp. 1668-1679. Princeton University Press, Princeton.

Safford, R. J. & Duckworth, J. W. (eds.) 1990. *A wildlife survey of Marojejy Reserve, Madagascar*. ICBP Study Report No. 40. International Council for Bird Preservation, Cambridge, United Kingdom.

Safford, R. J. & Hawkins, A. F. A. (eds.) 2013. *The birds of Africa, volume 8: The Malagasy Region*. Christopher Helm, London.

Safford, R. J., Goodman, S. M., Raherilalao, M. J. & Hawkins, A. F. A. 2022. Introduction to the birds. In *The new natural history of Madagascar*, ed. S. M. Goodman, pp. 1553-1602. Princeton University Press, Princeton.

Sheldon, B. C. & Duckworth, J. W. 1990. Rediscovery of the Madagascar Serpent-eagle *Eutriorchis astur*. *Bulletin of the British Ornithologists' Club*, 110: 126-130.

Sinclair, I. & Langrand, O. 1998. *Birds of the Indian Ocean islands*. Struik Publishers, Cape Town.

Sinclair, I., Langrand, O. & Andriamialisoa, F. 2006. *A photographic guide to the birds of the Indian Ocean islands: Madagascar, Mauritius, Seychelles, Reunion and Comores*. Struik Publishers, Cape Town.

Sultan, B., Lalou, R., Sanni, A. S., Oumarou, A. & Samouré, M. A. 2015. *Les sociétés rurales face aux changements climatiques et environnementaux en Afrique de l'Ouest*. IRD Edition, Marseille.

Tadross, M., Randriamarolaza, L., Rabefitia, Z. & Zheng, K. Y. 2008. *Climate change in Madagascar: Recent past and future*. World Bank, Washington, DC.

Tahinarivony, J. A. 2023a. Typologie des habitats en fonction du gradient altitudinal : Cas du Parc National de Marojejy. In A floral and faunal inventory of the Parc National de Marojejy: Altitudinal gradient and temporal variation, eds. S. M. Goodman & M. J. Raherilalao. *Malagasy Nature*, 17: 102-135.

Tahinarivony, J. A. 2023b. Etude descriptive de l'évolution de la végétation du Parc National du Marojejy entre 1995 et 2022. In A floral and faunal inventory of the Parc National de Marojejy: Altitudinal gradient and temporal variation, eds. S. M. Goodman & M. J. Raherilalao. *Malagasy Nature*, 17: 73-87.

Thiollay, J.-M. 1998. The diurnal raptors (Falconiformes) of the Réserve Spéciale d'Anjanaharibe-Sud: Abundance, distribution, and conservation. In A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 90: 1-246.

Urano, E., Yamagishi, S., Andrianarimisa, A. & Andriatsarafara, S. 1994. Different habitat use among three sympatric species of couas *Coua cristata*, *C. coquereli* and *C. ruficeps* in western Madagascar. *Ibis*, 136: 485-487.

Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T. F.

& Achard, F. 2018. Combining global tree cover loss data with historical national forest-cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, 222: 189-197.

Weiskopf, S. R., Cushing, J. A., Morelli, T. & Myers, B. J. E. 2021. Climate change risks and adaptation options for Madagascar. *Ecology and Society*, 26 (4): 36.

Wilmé, L. 1996. Composition and characteristics of bird communities in Madagascar. In *Biogéographie de Madagascar*, ed. W. R. Lourenço, pp. 349-362. ORSTOM Editions, Paris.

Wilmé, L. Goodman, S. M & Ganzhorn, J. 2006. Biogeographic evolution of Madagascar's microendemic biota. *Science*, 312 (5776): 1063-1065.

Wink, M. 2008. Taxonomy and genetics: Phylogenetic and phylogeographic relationships. In *The Little Owl: Conservation, ecology and behaviour of* Athene noctua*,* eds. D. van Nieuwenhuyse, J.-C. Génot & D. H. Johnson, pp. 38-44. Cambridge University Press, Cambridge, United Kingdom.

Younger, J. L., Strozier, L., Maddox, J. D., Nyári, Á. S., Bonfitto, M. T., Raherilalao, M. J., Goodman, S. M. & Reddy, S. 2018. Hidden diversity of forest birds in Madagascar revealed using integrative taxonomy. *Molecular Phylogenetics and Evolution*, 124: 16-26.

Younger, J. L., Dempster, P., Nyári, A. S., Helms, T. O., Raherilalao, M. J., Goodman, S. M. & Reddy, S. 2019a. Phylogeography of the Rufous Vanga and the role of bioclimatic transition zones in promoting speciation within Madagascar. *Molecular Phylogenetics and Evolution*, 139: 1-11.

Younger, J. L., Block, N. L., Raherilalao, M. J., Maddox, J. D., Wacker, K. S. Kyriazis, C. C., Goodman, S. M. & Reddy, S. 2019b. Diversification of a cryptic radiation, a closer look at Madagascar's recently recognized bird family. *Biorxiv*. doi: https://doi.org/10.1101/825687.

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Appendix 1. Number of contacts for bird species in 1996 and 2021 at the five surveyed sites along an elevational gradient in the Parc National de Marojejy.

	1996					2021				
	Site 1 (19 points)	**Site 2 (22 points)**	**Site 3 (22 points)**	**Site 4 (16 points)**	**Site 5 (11 points)**	**Site 1 (15 points)**	**Site 2 (15 points)**	**Site 3 (15 points)**	**Site 4 (15 points)**	**Site 5 (11 points)**
Species	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts
Nesoenas picturatus	1					1	2			
Alectroenas madagascariensis		1				2				
Coua caerulea	9	5	6	5	1	5	4	6	10	6
Coua reynaudii	2	7	3	4	4		3	1	3	2
Coua serriana	8	5	7				2			
Centropus toulou	12	3	1			2	1			3
Cuculus rochii	7	19	19	3	1	2	2	1	2	
Mentocrex kioloides	2	1					2			
Sarothrura insularis					7		1			2
Lophotibis cristata						1	1			
Accipiter francesiae							1			
Accipiter henstii				1						
Accipiter madagascariensis								1		
Buteo brachypterus								1		
Otus rutilus		2								
Leptosomus discolor		2				2				
Corythornis madagascariensis						4	1		1	
Eurystomus glaucurus				1						
Brachypteracias leptosomus	3	2	1	1			1	1		
Atelornis crossleyi			2	2	1					
Atelornis pittoides			1	1			1	1		
Coracopsis nigra	10	9	13			4	3	5	1	
Philepitta castanea	1	3	7			2	2	2		
Neodrepanis coruscans	5	7	6					2		
Neodrepanis hypoxantha			21	3					1	
Coracina cinerea	7	1	2			1	4			
Newtonia amphichroa	2	2	12	10	8	2	7	7	13	2
Newtonia brunneicauda	10	16	14	17	2	5	7	5	4	
Tylas eduardi	3	9	17	7	5	1		3	4	
Calicalicus madagascariensis	22	13	14	4	1	5	5	6		
Leptopterus chabert	1								1	
Mystacornis crossleyi		3	9	3		1	1			
Cyanolanius madagascarinus		2	6	2			1			
Vanga curvirostris		3	1	5	2	1	2	4	4	
Pseudobias wardi						1				1

Appendix 1. (followed)

	1996					2021				
	Site 1 (19 points)	**Site 2 (22 points)**	**Site 3 (22 points)**	**Site 4 (16 points)**	**Site 5 (11 points)**	**Site 1 (15 points)**	**Site 2 (15 points)**	**Site 3 (15 points)**	**Site 4 (15 points)**	**Site 5 (11 points)**
Species	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts	Number of contacts
Euryceros prevostii	3	2	3	1				1		
Artamella viridis	5	6	7	2	2	1	2			
Dicrurus forficatus	8	2	1			6	2	1	1	
Terpsiphone mutata	15	8	8	1		2	5	5		
Neomixis striatigula	13	11	3	14		9	8	8	6	
Neomixis tenella	17	10	9			2				
Neomixis viridis	13	8	6	2		5	1			
Nesillas typica			33	18	30	2		8	13	38
Bradypterus brunneus					1				4	3
Oxylabes madagascariensis	1	6	3	4		8	8	1		
Bernieria madagascariensis	7	6	6			3	13	6		
Cryptosylvicola randrianasoloi			12	18	14			1	1	8
Xanthomixis cinereiceps									3	
Xanthomixis zosterops	7	5		6		10	12	2		
Crossleyia xanthophrys			2							
Randia pseudozosterops	8	6	2	7		5	5	4	7	
Hypsipetes madagascariensis	19	14	23	21	6	20	22	12	14	16
Zosterops maderaspatanus	20	18	12	12	3	8	25	8	4	1
Hartlaubius auratus						1				
Copsychus albospecularis	11	6	1			6	9	3		
Monticola sharpei			4	12	5			1	1	
Saxicola torquatus					9					3
Cinnyris notatus	9	5	6			4	9	1	3	
Cinnyris sovimanga	40	33	60	38	29	66	44	38	39	34
Nelicurvius nelicourvi	1	5	3			3	3	1		
Foudia madagascariensis			1	3						
Foudia omissa	2	4			1			1		1
Lepidopygia nana	1									
Total number of species	**36**	**39**	**41**	**31**	**20**	**35**	**37**	**33**	**23**	**14**