

MADAGASCAR CONSERVATION & DEVELOPMENT



INVESTING IN A SUSTAINABLE NATURAL ENVIRONMENT FOR FUTURE GENERATIONS OF HUMANS, ANIMALS AND PLANTS OF MADAGASCAR

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EDITORIAL

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Madagascar at the crossroads: Youth, governance, and the rosewood reflex

September 2025 witnessed Madagascar entering a new era, following the intensification of anger which had been bubbling beneath the surface for months. The subsequent eruption heralded remarkable action in which a new generation featured prominently. As *Le Monde Afrique* reported, the first protests emerged in the streets of Antananarivo as a response to prolonged power blackouts and water shortages, with a population exhausted by Jirama's collapse and a president travelling abroad to wax lyrical about "democracy" (Caramel 2025). The movement rapidly gained momentum as longstanding structural failures, entrenched corruption, and years of empty promises consolidated a deepening sense of injustice. The crisis expanded further when farmers to north of Antananarivo watched their rice fields being forcibly buried for a solar-farm project, effectively transforming localized anger into a national uprising that spread from rural areas to cities (Rémy 2025).

Currently, the country is governed by a military-backed transitional administration, installed after the collapse of the previous government.

This particular resistance was not an isolated Malagasy phenomenon. Rather, it was part of a broader movement sweeping across the Global South. In Nigeria (Dambo et al. 2022), Kenya (Tsevreni et al. 2023), Sudan and Senegal (Khalafallah et al. 2025), Sri Lanka (Rambukwella 2025), Thailand (Htong Kham and Ng 2025), The Philippines (Sumatra 2025), Chile (Somma 2021), and Colombia (Restrepo Sanin 2022), Gen Z has emerged as the principal force demanding accountability, equity, and the effective deli-

very of operational public services. Their grievances resonate across continents: corruption, unemployment, shrinking opportunities, degraded ecosystems, and governments failing to secure even the most basic rights (Figure 1).

Gen Z mobilization in the Global North, though powerful, tends to focus on thematic issues such as climate justice, women's rights, LGBTQ+ protections, gun violence, and student rights (Tsevreni et al. 2023). The difference is not one of values but of conditions. In the North, to a large extent, institutions still function; youth protest to improve systems (e.g., Dokoupilová et al. 2024). In much of the Global South, they protest because systems have already failed. Their struggle is existential.

Gen Z's digital life reflects this divide. In the North, technology is framed around identity, wellbeing, and online culture, while in the South it becomes a tool against structural inequalities. In Kenya, for instance, Gen Z used social media to drive a nationwide movement against IMF-driven austerity, corruption and rising costs, occupying parliament and facing brutal repression (Tsevreni et al. 2023).

In Madagascar, the urgency has been both chronic and acute. The uprising exposed the extent of deterioration of daily life for most citizens: unreliable electricity, protracted water shortages, rising food prices, and a political system unable, and at times unwilling, to guarantee even basic rights. These conditions, described by *Le Monde Afrique* in its meticulous reporting, resonated across both cities and rural areas, drawing Gen Z and older generations into a shared mobilization centered around dignity, equity, and survival (Caramel 2025, Rémy 2025).

Just as the nation voiced its demands for the abolition of old patterns, an all-too-familiar malfeasance reared its hydra head: the recurrent use of natural resources as a fiscal shortcut during moments of political volatility, marked by opacity, exceptional authorizations, and elite capture (Waeber and Wilmé 2013). On 24 November 2025, *Madagascar Tribune* reported that the State was once again considering the sale of rosewood stocks (Mandimbi-soa 2025). The article triggered an intense public debate. Reader reactions revealed three dominant concerns: (1) disbelief that the "same old story" of exceptional authorizations was returning; (2) fear that reopening rosewood stock circulation would revive traffi-

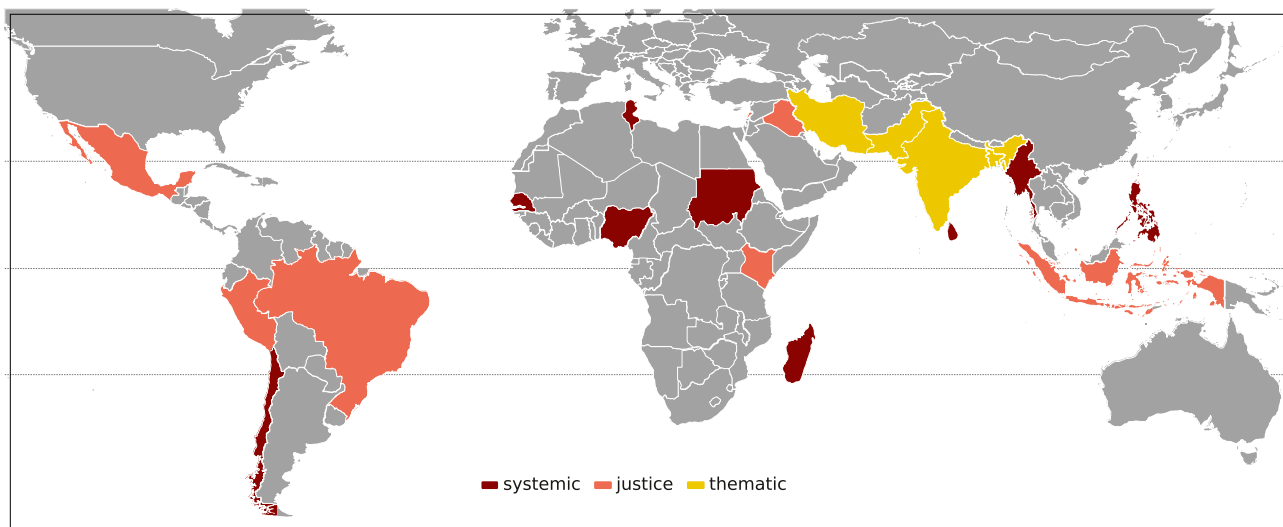


Figure 1. Selected countries illustrating Gen Z-driven mobilization within institutionally mediated political and civic systems. Countries shown represent contexts where youth mobilization operates through, or in sustained interaction with, formal political institutions. Contexts in which mobilization primarily substitutes for weak or contested state systems are intentionally excluded to avoid false comparability.

cking networks; and (3) outrage that the forests would once again serve as a budgetary shortcut while the population demands long overdue structural reforms. The detailed investigation of the 2009–2010 crisis by Randriamalala and Liu (2010) illustrated that political instability instigated massive, largely informal rosewood extraction. They documented how “exceptional” decrees authorizing forest access were systematically timed around political turning points and election cycles, so that revenues were effectively channeled toward strategic elites. During the 2009–2010 political fallout, trafficking reached an unprecedented level, far beyond that which took place during previous cycles, with hundreds of thousands of trees devastatingly felled inside national parks such as Masoala and Marojejy. While Malagasy political, military, and business elites* secured most domestic gains, the largest profits were reaped abroad, by buyers in China, which dominates the international market (Schuurman and Lowry 2009, Randriamalala and Liu 2010, Innes 2010). A decade later, the systemic risks remain. It has been demonstrated that the very existence of rosewood stockpiles fuels speculation, laundering, and thereby exacerbates pressure on remaining trees. Their analysis showed that all stockpile management options involve risk, but international trade carries the highest probability of reigniting illegal logging, corruption, and ecosystem degradation (Wilmé et al. 2020). The authors emphasized that Madagascar still lacks species-level inventories, non-detriment findings, clear traceability, and secure centralized stockpile management, all of which are core requirements of CITES.

More recently, Roberts et al. (2024) illustrated that Madagascar’s proposal to withdraw 30,000 logs from CITES control for “domestic use” would create a high-risk laundering pathway if not strictly supervised by an independent third party. Their article warned that opening national circulation under current conditions would set a dangerous precedent for other countries and could directly undermine the CITES system itself (Roberts et al. 2024).

Together, these analyses indicate a clear pattern: every time Madagascar experiences political instability, rosewood operators re-emerge to exploit any potential vacuum. Reopening the stockpiles today, even under the label of “domestic sales,” would follow the same routine and create the very conditions that fueled the 1992, 2002, 2009, or 2025 constitutional crises. The cost is immense: weakened institutions, lost revenue and damaged protected areas.

Today, however, the political setting is profoundly different. Madagascar’s Gen Z articulated demands that are fundamentally incompatible with another return to extractive crisis management. They push for functioning governance, transparency, equal opportunities, and a future in which natural resources are protected rather than liquidated to maintain the privileges of a limited elite. They have asked for the right to live with dignity, not to inherit a system that recycles corruption under new slogans.

The temptation to reopen rosewood stockpiles is characteristic of this political system. But rosewood is more than a commodity: it is a mirror that reflects power dynamics in Madagascar. Every

crisis has triggered the same reflex: exceptional decrees, opaque networks, elite capture, and institutions sidelined or bypassed. Yet this dysfunctional *modus operandi* ignores a fundamental reality: the ecosystem services provided by Madagascar’s forests, from water regulation and pollination to soil protection, carbon storage, biodiversity, and the subsistence needs of millions, are worth far more to the nation than any short-term liquidation of timber. The forest’s long-term values are national; the gains from rosewood extraction have always been private.

The question before the transitional authorities is clear: will Madagascar finally break with the detrimental political reflex, in which natural resources serve as a financial shortcut and a tool of patronage? Or, will the country once again, liquidate its most iconic species, signaling to a new generation that nothing has changed? The legitimacy of the current transitional moment will depend on that choice.

If the government aligns itself with demands of the people, Madagascar could finally exit the destructive cycle documented repeatedly over the past three decades. This would require enforcing the protection of natural resources, securing stockpiles under independent oversight, and refusing any return to so-called exceptional timber authorizations.


If, however, it turns again to its forests as a budgetary shortcut, the same, farcical political script will be reenacted: institutional decay, ecological loss, elite capture, and yet another generation betrayed. Madagascar’s Gen Z has spoken with stark clarity. The country must now decide whether to heed to their impassioned pleas, or to repeat its past.

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* **Note:** Beyond astonishing, is the sudden, public return of three notorious key figures who were extensively documented during the 2009–2010 rosewood catastrophe: Jean-Pierre Laisoa, Johnfrince Bekasy, and Jaototo Chantal Rhona (Randriamalala and Liu 2010). Laisoa alone exported 81 containers of rosewood, worth an estimated USD 16.2 million (making him one of the highest-earning operators of that period). Bekasy moved 21 containers (worth about USD 4.2 million), while Rhona, who appeared in the 2010 files as Jaototo Chantal Bhana, had 25 containers prepared for export. None of them showed the slightest concern whatsoever for the origin of the logs they had moved. Their paperwork was questionable; the source localities conveniently vague, and the aforementioned national parks of Masoala and Marojejy were disconcertingly well represented in the supply chain. In 2025, these same three individuals resurfaced in the press as spearheading a newly created association, “SOS Bois de rose” (R.O. 2025), presenting themselves as champions of “development,” “transparency,” and even national credibility. The audacity of this rebranding is as striking as it is nauseating. It rests on a callous faith in collective amnesia. That recognized architects of timber trafficking now claim to safeguard Madagascar’s reputation and present themselves as custodians of conservation is deeply lamentable.

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Position statement on the use of AI in scientific writing and publishing

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ABSTRACT

Large language models (LLMs) are rapidly reshaping scientific writing, reviewing, and publishing. Journals must respond in ways that safeguard trust while acknowledging the new realities resulting from these Artificial Intelligence-based technologies. This contribution details the position developed by the editors of *Madagascar Conservation & Development* on the use of LLMs in scholarly work and for publication in the journal. These tools can support authors by enhancing clarity, reducing language barriers, and structural inequities in global science, but recent editorial experience shows that the use of LLMs can generate errors and fabricated references, and formulate false claims that may escape traditional peer review. In volunteer-run journals, such failures impose substantial burdens on editors and reviewers. Our position is simple: LLMs may be used to support and enable authors but their results must never be trusted blindly. Authors remain fully responsible for ensuring the accuracy, originality, and validity of all content, regardless of the tools employed, and any use of LLMs must be disclosed transparently. Protecting scientific integrity remains a shared responsibility.

RÉSUMÉ

Les grands modèles de langage, ou *large language models* (LLM), transforment rapidement l'écriture scientifique, l'évaluation par les pairs et les processus de publication. Les revues doivent y répondre de manière à préserver la confiance, tout en reconnaissant les nouvelles réalités induites par ces technologies fondées sur l'intelligence artificielle (IA). Cette contribution présente la position élaborée par les rédacteurs de *Madagascar Conservation & Development* concernant l'utilisation des LLM dans les travaux scientifiques et pour toute contribution soumise à la revue. L'IA peut aider les auteurs en améliorant la clarté des textes, en réduisant les barrières linguistiques et certaines inégalités structurelles au sein de la science mondiale. Cependant, notre expérience éditoriale récente montre que l'utilisation des LLM peut générer des erreurs, produire des références inexistantes et formuler des affirmations erronées susceptibles d'échapper à l'évaluation par les pairs traditionnelle. Dans les revues reposant exclusivement sur le bénévolat, de telles défaillances se traduisent par une surcharge substantielle de travail pour les rédacteurs et les évaluateurs. Notre position est simple : les LLM peuvent être utilisés pour aider et accompagner les auteurs, mais leurs résultats ne doivent jamais être acceptés sans vérification. Les auteurs demeurent en-

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tièrement responsables de l'exactitude, de l'originalité et de la validité de l'ensemble du contenu, quels que soient les outils employés, et toute utilisation de LLM doit être déclarée de manière transparente. La préservation de l'intégrité scientifique reste une responsabilité partagée.

AUTHOR RESPONSIBILITY IN CHANGING JOURNALScape

Artificial Intelligence (AI) includes both machine-learning tools (Carbonell et al. 1983), long used for data analysis, and newer Large Language Models (LLMs), which can produce coherent text and references (Kumar 2024). In just a few years, LLMs have evolved from a technical curiosity to part of the everyday infrastructure of scientific writing, reviewing, and editorial work for many authors and publishers. Their ever-increasing usage has continuously shaped protocol design, data cleaning and analysis, manuscript drafting, reviewing, and editing, and even decisions about what work gets published (Kusumegi et al. 2025, Zhao 2025). However, since AI-based tools merely produce plausible-sounding text based on probabilities, the results can include errors and inaccuracies that seriously undermine science. Journals worldwide are having to rethink matters of responsibility, transparency, and authorship in response to this profound shift (Thorp 2023). Because *Madagascar Conservation and Development (MCD)* wishes to maintain integrity, transparency, accessibility, and equitable participation in knowledge production and dissemination, the journal has decided to articulate a carefully reasoned position on how AI may be used in manuscripts submitted for possible publication, one that protects trust while recognizing both the opportunities and challenges resulting from this new reality.

STRUCTURAL LIMITS OF VOLUNTEER-RUN JOURNALS

Since 2006, when *MCD* published its first issue, the journal has followed a clear editorial process. Each submission is screened for relevance, ethical alignment, and basic formatting. Potentially suitable manuscripts are then sent out for double-blind peer review, followed by one or more rounds of revision prior to a final decision and eventual publication. Only after reviewers and editors are satisfied that *MCD's* standards have been met does the manuscript proceed to copyediting and verification, during which references, factual claims, tables, and figures are carefully scrutinized.

While a growing number of publishers and preprint journal platforms are experimenting with AI-assisted tools for manuscript screening and research-integrity checks, and authors and reviewers are increasingly making use of the power of AI (Ghassemi et al. 2023, Zhao 2025), at *MCD* no automation is used and we have no paid staff or editorial infrastructure. Instead, the journal's operational model is based on honesty and trust among authors, reviewers, and editors.

In 2025, several manuscripts reached the latter stages of copyediting at *MCD* before the editors discovered fabricated or unverifiable references. Some included dozens of citations that looked plausible but did not actually exist. This is a well-documented outcome of LLM text generators trained to produce fluent and believable text rather than verifiable bibliographies (Ghassemi et al. 2023, Walters and Wilder 2023). These manuscripts had passed peer review and revision, indicating that even a rigorous editorial process was not sufficient to detect such errors. The problem was only revealed during final fact-checking, at the cost of substantial unpaid editorial labor. Similar cases have now been reported

across multiple journals, suggesting that it is not an isolated anomaly but rather a growing editorial issue (Brainard 2025).

Some authors use LLMs to polish grammar, clarify structure, and/or translate text, which is a legitimate form of AI-assisted writing (Katsnelson 2022, Borger et al. 2023). Others use these models to generate arguments, interpretations, methods, or text, all of which comprise AI-generated content. The editorial and research communities increasingly distinguish between these two uses of AI (Zou 2024, Bergstrom and Bak-Coleman 2025), one of which supports authorship while the other serves to replace it.

ADAPTING SCHOLARLY PUBLISHING IN RESPONSE TO NEW PRESSURES

In addition to presenting an array of challenges, LLMs can also create new opportunities. Tools that improve clarity and thereby facilitate communication can contribute to expanded participation in global science. This is especially helpful for early-career researchers and scholars writing in English when it is not their native language (Del Giglio and Pereira da Costa 2023, Berdejo-Espinola and Amano 2024). For Malagasy scientists, LLMs may reduce longstanding structural inequities in publishing (Ramananjato et al. 2025) but the promise it holds is only valid if and when the journals in which they seek to publish maintain rigorous verification standards and transparent reporting.

AI use does not constitute plagiarism per se. However, submitting AI-generated content in the form of text, figures, claims, or references without acknowledging and verifying them breaches the norms and standards of academic integrity because it removes human responsibility for accuracy and accountability in scholarship (Hutson 2025). It is neither intellectually honest nor scientifically acceptable for authors to outsource content to a computer-based model. They must remain personally and professionally accountable for every sentence, figure, citation, assumption, interpretation, and inference included in the work they claim to have produced and are seeking to publish under their own name.

A significant issue for a journal such as *MCD* is that the role, value, and appropriateness of LLMs are being judged using standards and requirements that were not factored into the creation of these models. LLM users ask these "machines" to produce truth (or something that resembles truth) even though the underlying technology was never conceived or designed to do so. AI tools compile available information into a seductive and convincing form that resembles fact-based scientific writing, but the process involved is neither transparent nor reproducible, and the results do not adhere to globally accepted scientific methods. Users of LLMs have no way of assessing whether the tool being used operates properly compared to a process developed and implemented by the authors themselves.

Across scientific publishing, a pragmatic consensus appears to be emerging regarding the use of AI in research workflows (Thorp 2023, Naddaf 2025), which can be summarized as follows:

- AI-generated output, including references, must be checked by authors.
- AI tools cannot be listed as an author.
- Responsibility for accuracy and content remains entirely with the submitting authors.
- Authors must provide journals with additional documentation (e.g., drafts or prompt histories) if concerns about AI involvement are raised.

LOOKING AHEAD

Authors submitting manuscripts to *MCD* are expected to state whether and how AI has been used, and they are solely responsible for all content. These requirements apply irrespective of the type of AI used: authors must confirm that they have read and verified all text, figures and tables, and ensure that all cited sources are true and accurate. Every reference must exist, be accessible, and support the statement or assertion being made. Doing so will ensure the reliability and accuracy of the submission while also saving valuable time and energy for *MCD*'s volunteer reviewers and editors.

Reviewers will be encouraged to flag passages that raise concerns, but many of them are already working at the limits of their capacity (Zou 2024) and they are neither expected nor equipped to investigate or assess the appropriateness of AI use. Editors may request authors to provide clarification, confirm sources, and/or correct questionable text and citations. In some cases, authors may be required to withdraw manuscripts in order to safeguard the integrity of the scholarly record (Brainard 2025).

The scholarly community will need to adjust and adapt to the newly emerging AI environment, otherwise journals such *MCD* may not survive. This is a very real possibility that must be taken seriously and something which requires immediate, coordinated action to avoid.

The principle adopted for *MCD* is straightforward: AI may be used as a supporting and enabling tool but must never be trusted blindly. Its results must always be verified and validated under the entire responsibility of the authors and its use must be disclosed in a fully transparent manner.

Embracing AI or worrying about its impacts and limitations, or the potential for its abuse are no longer the central question. This powerful new technology is already reshaping how science is performed, reported, and evaluated, from conservation research (Reynolds et al. 2025, Silvestro et al. 2025) to everyday scientific communication, peer review (Zou 2024), and academic policy (Pearson 2025). When used with care and integrity, AI can help authors write more clearly, reduce language barriers, and overcome

long-standing inequities. However, if it is used carelessly or dishonestly, without disclosure, AI will erode trust and undermine scientific credibility in general and that of authors in particular.

Small, volunteer-run journals such as *MCD* have long functioned under structural and operational constraints. They cannot compete with large commercial publishers in terms of budgets, salaried staff, and access to automated tools to detect plagiarism, check references, and process manuscripts. AI is now amplifying these discrepancies. The volume of problematic AI-generated submissions is already increasing faster than editors can screen them and reviewers can detect erroneous information within them. The scholarly publishing system was fragile before AI-based models came onto the scene, but it is now increasingly under acute strain (Thorp 2023, Bergstrom and Bak-Coleman 2025). The only way journals such as *MCD* will be able to survive is through a coordinated effort to adapt to the rapidly surging wave of AI use (Figure 1) by implementing procedures to ensure disclosure, verification, and strengthened editorial capacity.

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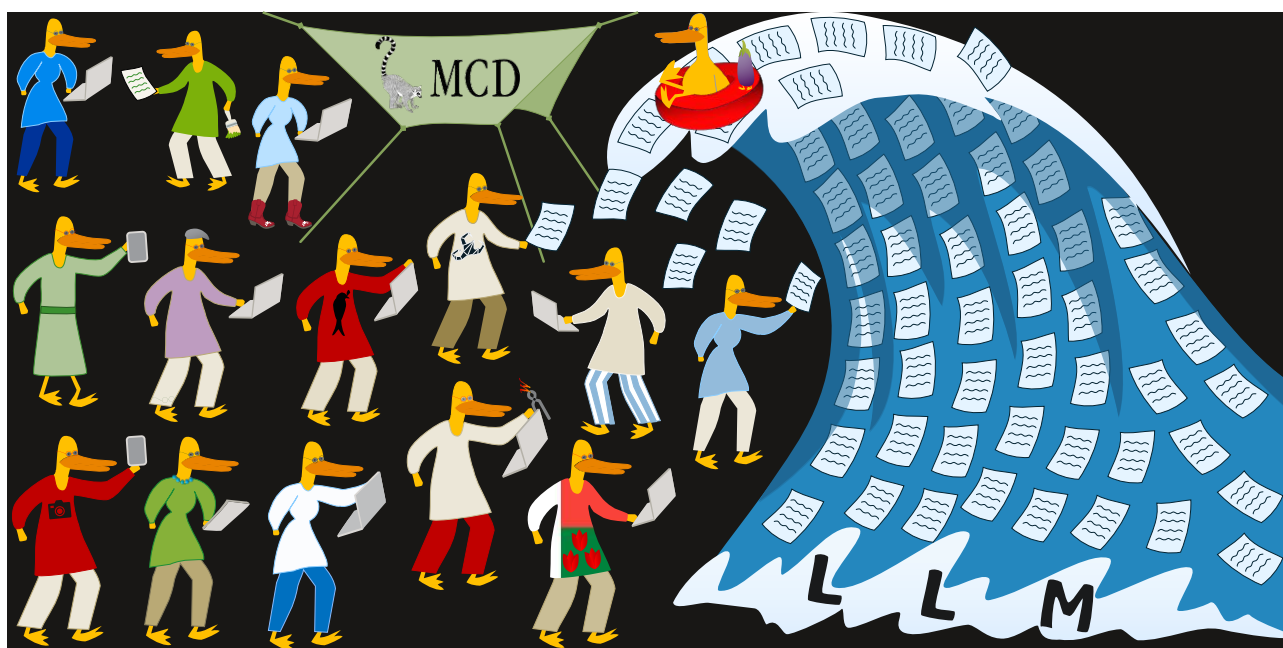


Figure 1. A wave of LLM-produced articles submerging an editorial team. (Any resemblance to actual people or to an existing journal is, of course, in no way coincidence. Special note: this image was not generated by AI)

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Description of a new haemadipsid species of genus *Chtonobdella* Grube, 1866 from Ranomafana National Park using micro-computed tomography

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ABSTRACT

The terrestrial blood feeding leeches of Madagascar represent an understudied group with recent evidence for cryptic diversity. By combining genetic and morphological data including *cox1* molecular barcoding and micro-computed tomography (μ CT) imaging, we present evidence for the presence of a new species in the genus *Chtonobdella* Grube, 1866. This description includes, for the first time, μ CT rendering of known leech species from Madagascar, which were previously described solely by dissection.

RÉSUMÉ

Les sangsues terrestres hématophages de Madagascar constituent un groupe qui reste encore peu étudié en même temps que des indices récents pointent vers une diversité cryptique. En combinant des données génétiques et morphologiques, incluant le codage moléculaire par le gène *cox1* et l'imagerie par micro-tomodensitométrie (μ CT), nous apportons des éléments attestant de la présence d'une nouvelle espèce au sein du genre *Chtonobdella* Grube, 1866. Cette description inclut, pour la première fois, une visualisation μ CT d'espèces de sangsues connues de Madagascar, auparavant décrites uniquement par dissection.

INTRODUCTION

The terrestrial leeches of Madagascar (family Haemadipsidae) represent an understudied group, with Blanchard (1917), Harding and Moore (1927), and Richardson (1975) providing the earliest records of their diversity. Early classifications relied on morphological assessment through dissection as well as documented feeding behavior. Historical records are inconclusive in determining dietary diversity of Malagasy leeches, assigned to the genus *Malagabdella* by Richardson in 1975, save for evidence presented by Rocha et al. (2012) of the first record of Malagasy leeches feeding on frogs. This genus has since been synonymized with *Chtonobdella* (Tessler et al. 2016) following subsequent revisions (Borda et al. 2007,

Tessler et al. 2016). That only four species are known to science (Borda 2006) is not indicative of their limited diversity, but rather of previously limited collection efforts.

Duognathous (two-jawed) leeches are believed to have colonized Madagascar approximately 66 million years ago during the early Cenozoic (Borda and Siddall 2011). Biogeographic and evolutionary evidence suggest this dispersal from the central Indo-Pacific to have happened after a post-Gondwanan split, allowing for the arrival of potential vertebrate hosts and the northern migration of Madagascar to its current latitude in the tropics (between 12°–25°S), enabling formation of suitable moist habitat for these terrestrial blood-sucking annelids.

Unlike their trignathous (three-jawed) relatives of the Indian subcontinent and Southeast Asia, duognathous terrestrial leeches represent endemic groups throughout the Indo-Pacific, populating such islands as Australia, Indonesia, Papua New Guinea, and Madagascar, and even with species endemic to islands as remote as Palmyra and the Juan Fernandez Archipelago (Borda and Siddall 2011). This island clade represents yet another taxonomic group endemic to Madagascar and contributes to its valued biodiversity.

Terrestrial leeches have emerged as a viable surveying tool for vertebrate biodiversity across their distribution in the tropics (Schnell et al. 2012, Schnell et al. 2018, Tessler et al. 2018, Drinkwater et al. 2021). Targeting host DNA, or invertebrate-derived DNA (iDNA) by metabarcoding leech bloodmeals has enabled researchers to document terrestrial fauna typically overlooked with other inventorying methods. Elucidating the diversity and behavior of terrestrial leeches will help improve survey design and collection methodology of leeches used for burgeoning iDNA analyses. Here, alongside molecular data, we use morphological evidence generated by micro-computed tomography (μ CT) to describe a new species from Madagascar belonging to the genus *Chtonobdella*. The field of taxonomy often benefits from advancements in imaging technology. The advent of finer scale μ CT has expanded

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possibilities for morphological description and species delimitation. Micro-computed tomography captures a series of x-ray images from all angles around a specimen and reconstructs these images to produce a digital three-dimensional model. With this technology, the internal morphology of small, soft bodied taxa which are often too delicate to recover via dissection, can be observed and documented while maintaining structural integrity of the specimens. Micro-computed tomography scanning noninvasively characterizes structural morphology at micrometer-level resolution, expanding our understanding of the intricacies of leech anatomy beyond that of traditional dissections (Tessler et al. 2016).

In addition, we use iDNA to document the leeches' feeding behavior, thereby supplying genetic, morphological, and behavioral support for their classification as a species nova. For the first time, we scan leeches from Madagascar previously described exclusively by dissections for an equal comparison of anatomy across species.

METHODOLOGY

SAMPLE COLLECTION. We collected 540 terrestrial leeches from Ranomafana National Park during June 2017 which were dissected and analyzed for biodiversity surveys via iDNA analysis in prior studies (Fahmy et al. 2019, 2020). The collections and exportation of the specimens were made possible with permit number 141/17/MEEF/SG/DGF/DSAP/ SCB.Rc issued by Madagascar's Ministry of Environment and Sustainable Development. Specimens had a portion of the posterior crop region removed, making morphological assessment of diagnostic features such as number and position of testisacs and external papillation not feasible.

DNA SEQUENCING. Each individual leech was sequenced for cytochrome c oxidase subunit 1 (*cox1*), a rapidly evolving mitochondrial gene that has been used to delimit species boundaries in leeches (Apakupakul et al. 1999, Borda et al. 2007, Kutschera and Weisblat 2015, Tessler et al. 2016, Schnell et al. 2018, Tessler et al. 2018, Iyer et al. 2019) and other taxa more generally (Shen et al. 2013). We amplified a 640 bp region of *cox1* by adding the following to GE illustra PuReTaq Ready-To-Go PCR beads: 500 µM of forward primer (LCO1490 5'-GGTCAACAAATCAT AAAGATATTGG-3') 500 µM of reverse primer (500 µM of HHCO1 5'-GCTG CAAAAATRGCAAACTACTGC-3') (Folmer et al. 1994), 23 µl water, and 2 µl DNA template. The thermocycler profile for amplification was 94°C for 1 min, 35 cycles of 94°C for 45 s, 46°C for 30 s, 68°C for 1 min, and a final cycle of 72°C for 7 min (Borda et al. 2008). Amplicons were purified using AMPure in a 0.6:1 ratio to preserve longer fragments (up to 1.8kb). They were then cycle sequenced, ethanol precipitated, and visualized on an ABI 3730xl DNA Analyzer (Applied Biosystems, Carlsbad, CA, USA). Resulting sequences had primers trimmed, were reconciled, and edited for quality using CodonCode Aligner (CodonCode Corporation).

PHYLOGENETIC ANALYSIS. We test leech species diversity with *cox1* following published protocols (Tessler et al. 2018). Sequences for leech *cox1* were evaluated phylogenetically in the context of congeners endemic to Madagascar as well as other species of the genus *Chtonobdella* (Table 1). We selected three-jawed terrestrial leeches *Haemadipsa picta* Moore, 1929, *Haemadipsa rjukjuana* (Oka, 1910) Lai, Nakano & Chen, 2011, comb. n.,

Table 1. GenBank accession numbers for *cox1* of specimens used to reconstruct phylogeny. (Cytochrome oxidase 1 (CO1) sequences are available on the National Center for Biotechnology Information's (NCBI) Sequence Read Archive with Accession numbers PV126250 – PV126259)

	Taxon	CO1	Citation
Outgroup	<i>Haemadipsa picta</i> Moore, 1929	HQ322472	Lai et al. 2011
	<i>Haemadipsa rjukjuana</i> (Oka, 1910)	HQ322461	Lai et al. 2011
	<i>Haemadipsa japonica</i> (Whitman, 1886)	LC427763	Morishima and Aizawa 2019
Ingroup	<i>Chtonobdella meyeri</i> (Blanchard, 1894)	KT968372	Tessler et al. 2016
	<i>Chtonobdella fallax</i> (Blanchard, 1917)	EU100096	Borda et al. 2008
	<i>Chtonobdella niarchosorum</i> (Borda, 2006)	HQ203185	Borda and Siddall 2010
	<i>Chtonobdella seychellensis</i> (Harding, 1913)	EU100094	Borda et al. 2008
	<i>Chtonobdella vagans</i> (Blanchard, 1917)	HQ203186	Borda and Siddall 2010
	<i>Chtonobdella bilineata</i> (Richardson, 1975)	KT968384	Tessler et al. 2016
	<i>Chtonobdella tanae</i> Tessler et al. 2016	KT968382	Tessler et al. 2016

and *Haemadipsa japonica* (Whitman, 1886) as outgroup taxa following the results of Tessler et al. 2016. Sequences were aligned with MUSCLE (Edgar 2004) and the most appropriate model fit to the data with JMODELTEST2 (Darriba et al. 2012). For maximum likelihood analysis we used the selected GTR+I+G model of nucleotide evolution to reconstruct the most likely phylogeny. Maximum likelihood analysis with bootstrapping (1000 replicates) was conducted with RaxML-HPC v.8 (Stamatakis 2014) on XSEDE using the CIPRES Scientific Gateway portal (Miller et al. 2011). Phylogenetic reconstruction was edited with FigTree v.1.4.4 (Rambaut 2010).

MICRO-COMPUTED TOMOGRAPHY SCANNING AND IMAGE RECONSTRUCTION. In preparation for µCT, six specimens grouping to the new clade of *Chtonobdella* (Figure 1) were fixed in AFA (90 mL of 70% ethanol, 5 mL glacial acetic acid and 5 ml formalin) for 48 h, rinsed in 0.2M phosphate buffer, fixed in 1% osmium tetroxide (OsO₄) for 24 h to improve contrast between soft tissues, and returned to the same buffer solution for 24 h at 4°C (Tessler et al. 2016). Specimens were then returned to ethanol after fixation. We also prepared representative specimens of known species of *Chtonobdella* from Madagascar: *C. fallax* (Blanchard, 1917), *C. vagans* (Blanchard, 1917), and *C. niarchosorum* (Borda, 2006) following the same procedure prior to scanning. Missing from this comparison is *C. morsitans* (Blanchard, 1917) with type specimens deposited at the Muséum national d'Histoire naturelle in Paris. Structural integrity of these specimens has since degraded, and their internal anatomy has not been assessed. The *cox1* region for this taxon has been sequenced and we represent it in the phylogeny, but a morphological comparison is not currently possible.

We subjected all specimens, previously stored in ethanol, to critical point drying (CPD), a procedure which reduces tension on the surface of the specimen while drying in preparation for µCT scanning. All samples were imaged with µCT at the American Museum of Natural History with resolution of 1.5 microns. Scanning was conducted in a GE v|tome|x s240 (General Electric, Fairfield,

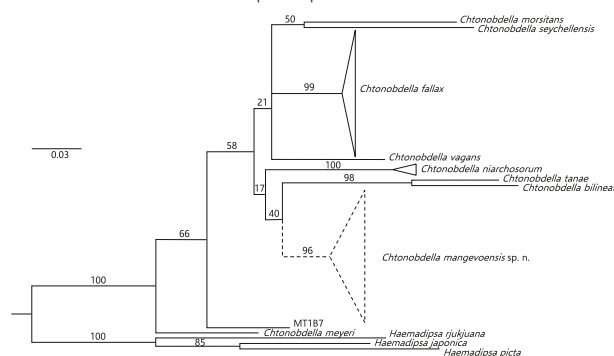


Figure 1. Molecular phylogenetic reconstruction of select members of genus *Chtonobdella* based on *cox1* with maximum likelihood bootstrap support values displayed; *Chtonobdella mangevoensis* sp. n. shown with dashed line.

CT, USA) at 100kV and 200µA with a diamond target and with exposure timing of 500ms. The holotype was scanned at a resolution of 4.82 microns/voxel. Voxel size for the remaining specimens scanned was as follows: *Chtonobdella fallax*: 6.15 microns/voxel, *C. vagans*: 5.95 microns/voxel, *C. niarchosorum*: 5.73 microns/voxel. Variability in voxel size relates to the size and thickness of each specimen (Shafiq-ul-Hassan et al. 2017). Three dimensional reconstructions of scanned images were edited with VGStudio Max 2.2 (Volume Graphics, Heidelberg, Germany) and 3DSlicer, an open-source visualization and segmentation software (Kikinis et al. 2014) and rendered in Blender (https://www.blender.org/).

RESULTS

Ninety-one percent of leeches (484/530) returned sequences for *cox1*, from which 52 were selected for phylogenetic analysis. Additional taxa analyzed are listed in Table 1. Maximum likelihood analysis reconstructed a phylogeny with strong evidence for all specimens pertaining to the new species forming a monophyletic group (Figure 1). The phylogeny also shows branch lengths that are conducive with those of other well-defined species (Tessler et al. 2016; Wang et al. 2022). Micro-computed tomography imaging of all known haemadipsids from Madagascar reflects internal anatomy uncovered previously with dissections (Borda 2006). Diagnostic male and female reproductive apparatus of the new species were easily located and successfully reconstructed and rendered with µCT. External imaging showed location of male and female gonopores (Figure 2) whereas in two-dimensional grayscale of reconstructed µCT images, location of the male gonopore was confirmed at the furrow of the fifth annulus of somite X and first annulus of XI, and female gonopore at the furrow of the fifth annulus of XI and first annulus of XII (Figure 3B). Three-dimensional reconstruction of diagnostic structures of the holotype and of previously described species visually capture morphological differences in shape, size, and location of internal anatomy (Figure 4).

SPECIES DESCRIPTION

Chtonobdella mangevoensis sp. n. (Figures 1–4)

urn:lsid:zoobank.org:pub:6C12E878-636C-41ED-94A7-7863A5F56894

<https://zoobank.org/References/6C12E878-636C-41ED-94A7-7863A5F56894>

Taxonomy: Order: Hirudinida Siddall et al. 2001; Family: Haemadipsidae Blanchard, 1893 Genus: *Chtonobdella* Grube, 1866

Type material: Madagascar, southeastern rainforests of Ranomafana National Park. Specimen collected from pristine primary forest in Mangevo field site (E047°26'50.7", S21°22'33.1"), June 2017. Specimen dissected for iDNA analysis (Fahmy et al. 2019, Fahmy et al. 2020).

Holotype: Dissected, fixed in ethanol, then stained with AFA and osmium tetroxide for µCT scanning. Subjected to Critical Point Drying and stored as a dried specimen at the American Museum of Natural History (Catalog number: AMNH_IJC 00361540).

Paratypes: 28 specimens, 18 fixed in 96% ethanol, 10 fixed in RNAlater. Dissected for iDNA analysis. Collected in Ranomafana National Park, June 2017. All specimens collected by Mai Fahmy, Aimé Tombotiana Victor, and Ny Anjara Fifi Ravelomanantsoa.

Etymology: The species is named for a field site, Mangevo, wi-

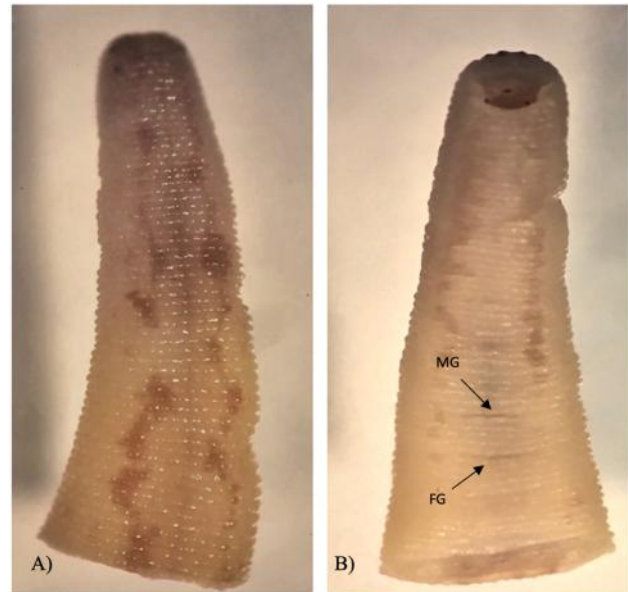


Figure 2. External morphology of holotype. (A) Dorsal view. (B) Ventral view with male (MG) and female (FG) gonopores labeled



Figure 3. Micro-computed tomography sections of the holotype of *Chtonobdella mangevoensis* sp. n. with body somites labeled (IV–XIV). (A) Coronal view showing, ejaculatory bulbs (EB), epididymal masses (EM), vaginal sac (VS), and right ovary (RO). (B) Lateral view, showing full length of vaginal sac and positioning of male and female gonopores (MG, FG). Scale bars = 0.5mm

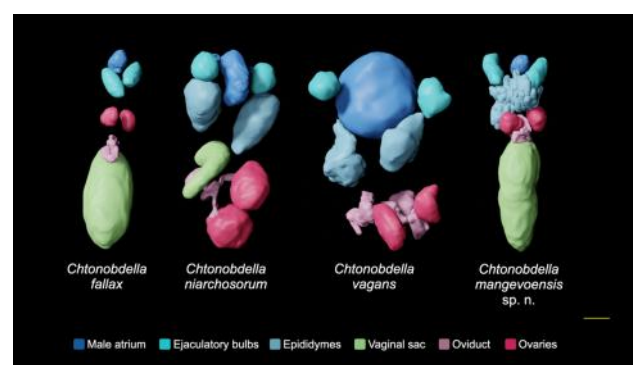


Figure 4. Three-dimensional morphometric rendering of µCT scans of diagnostic reproductive anatomy of Malagasy leeches. (Scale bar = 0.5mm. Image rendered in Blender; https://www.blender.org/)

thin Ranomafana National Park. Based on our collection efforts, it appears the species is locally endemic to this forest.

Description: *External morphology.* Dorsum light beige post fixation with darker longitudinal wavy paramedial stripes (Figure 2A). Venter light beige with darker longitudinal straight paramedial stripes, fading posteriorly (Figure 2B). Somites I-IV one-annulate; V two-annulate, VI and VII three-annulate; VIII to XXIII five-annulate. Gonopores separated by five complete annuli (Figures 2B, 3B).

Internal morphology: Ejaculatory bulbs within X and XI (Figure 3). Vaginal sac at XII, extends posteriorly to between fourth and fifth annuli of XIV (Figure 3). Male gonopore at furrow of the fifth annulus of somite X and first annulus of XI, female gonopore at the furrow of fifth annulus of XI and first annulus of XII (Figure 3B). Specimens had been dissected prior for gut content analysis, therefore posterior morphology including total number of paired testisacs, paired gastric caeca, and number of annuli on the caudal sucker could not be determined. New species is distinguished from other five-annulate leeches by the large vaginal sac extending the length of three somites (Figure 3) and curvature of full, pronounced ejaculatory bulbs (Figures 4, 5), together, not observed in other species in this genus. Large, singular epididymal mass and micromorphic male atrium distinct in their size from other species in the genus *Chtonobdella*. Dorsal patterns resemble *C. vagans* while ventral patterns resemble *C. fallax* (Borda 2006), yet molecular data and internal structures are distinct from either (Figures 1, 4).

Distribution: Lowland eastern rainforest, Ranomafana National Park, Madagascar. Found at an elevation of 714m.

Natural history: Terrestrial, sanguivorous. Known to feed on *Fossa fossana*, *Atelornis pittoides*, *Gephyromantis redimitus*, *Homo sapiens*, felids, and mongooses as determined by iDNA analysis in prior studies (Fahmy et al. 2020).

ACKNOWLEDGEMENTS

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Preparing the next generation of protected area managers in Madagascar: addressing competency gaps to advance the 30x30 target

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ABSTRACT

To curb biodiversity loss and enhance human well-being, recent decades have witnessed an expansion of protected areas, with a global goal of protecting 30% of the earth's surface by the year 2030 (often referred to as the 30x30 target). To achieve meaningful outcomes, protected areas must be staffed sufficiently with competent personnel. Madagascar's system of protected areas (SAPM by its French acronym) has expanded in area by >400% between 2003 and 2015. This study identifies priorities for growing management competencies to meet this increased staffing demand. Through competence assessment surveys and workshops involving 139 participants from 49 protected areas, we identified critical training needs: senior protected area managers require enhanced managerial skills, and technicians need improved community interaction skills. Less than 20% of senior staff have a degree in management, with a vast majority (70%) having trained in environmental disciplines. Soft skills in ethics, open-mindedness, and growth mindset are important to develop at all levels. Our results offer a pathway forward to align protected area manager training with onsite demands, establishing an enabling environment for enhanced learning in the protected area management sector. Revisiting the SAPM human resources development policy is imperative for effectiveness and expansion of Madagascar's protected areas given the ambitious 30x30 target.

RÉSUMÉ

Pour freiner la perte de la biodiversité et améliorer le bien-être humain, les dernières décennies ont vu une expansion des aires protégées, avec un objectif mondial de protéger 30 % de la surface terrestre d'ici à 2030 (souvent appelé l'objectif 30x30). Pour obtenir des résultats significatifs, les aires protégées doivent être suffisamment dotées de personnel compétent. Le système des aires protégées de Madagascar (SAPM) a vu sa superficie aug-

menter de plus de 400 % entre 2003 et 2015. Cette étude identifie les priorités pour renforcer les compétences en gestion afin de répondre à cette demande accrue de personnel. À travers des enquêtes d'évaluation des compétences et des ateliers impliquant 139 participants provenant de 49 aires protégées, nous avons identifié des besoins critiques en formation. Il s'agit des gestionnaires des aires protégées, à un niveau important dans les responsabilités, qui ont besoin de renforcement de leurs compétences managériales et des techniciens qui ont besoin d'améliorer leurs compétences en interaction avec les communautés. Moins de 20 % des cadres supérieurs possèdent un diplôme en gestion, la grande majorité (70 %) ayant été formée dans des disciplines portant sur l'environnement. Le développement des compétences transversales, telles que l'éthique, l'ouverture d'esprit et la mentalité de croissance pour un esprit de développement, est essentiel à tous les niveaux. Nos résultats offrent une voie à suivre pour aligner la formation des gestionnaires d'aires protégées avec les besoins sur le terrain, en créant un environnement propice à un apprentissage renforcé dans le secteur de la gestion des aires protégées. Il est impératif de réviser la politique de développement des ressources humaines du SAPM pour garantir l'efficacité et l'expansion des aires protégées de Madagascar, compte tenu de l'ambitieux objectif 30x30.

INTRODUCTION

Protected areas play an important role in achieving sustainable development goals (Dudley et al. 2017, Fischborn and Sandwith 2021), providing ecosystem services and multiple benefits to society (Stolton and Dudley 2015) and helping to mitigate climate change (Dudley 2010, Londono et al. 2016, Roberts et al. 2020). The parties to the Convention on Biological Diversity (CBD) have set targets to encourage all countries to increase the coverage of protected terrestrial and aquatic habitats worldwide (CBD 2010,

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2022). Although the Aichi target 11 has only been partially achieved (UNEP-WCMC et al. 2021), it inspired many countries to increase the number and size of protected areas. The Kunming-Montreal Global Biodiversity Framework Target 3 aims to protect at least 30% of lands and 30% of oceans by 2030, known as the 30x30 target, via designated protected areas and other effective area-based conservation measures (OECMs) (CBD 2022).

The ambitious 30x30 target requires that protected areas and OECMs be effective in achieving defined and specific goals, demonstrating sound planning, equitable governance, healthy relationships with local communities, adequate resources, strong processes, and ultimately outcome-based management to achieve conservation goals (Hockings et al. 2006, Visconti et al. 2019, Dudley et al. 2022). Adequate staffing—both in terms of the number of staff and their competence—is essential for achieving the 30x30 goals (Appleton et al. 2022, Rakotobe et al. 2023, Rakotobe and Stevens 2024).

Yet around the world, the increase in protected areas has often exceeded effective management capacity (Sandwith et al. 2014). Indeed, protected areas require active management to limit threats and ensure long-term ecosystem viability. Many fear that new protected areas lack sufficient resources for effective management (Di Minin and Toivonen 2015, Geldmann et al. 2018), particularly in the availability of qualified staff to carry out mission-focused objectives (Gill et al. 2017). Globally, protected areas achieve only a third of the recommended staffing levels needed for effective management (Appleton et al. 2022).

Protected areas have existed since the 19th century, yet assessment of human resource efficacy and competencies in protected area management is a surprisingly recent research topic. Competence is defined as “the proven ability to perform a task or job” (Appleton 2016:2). Although sometimes used interchangeably, a “competence” differs from a “skill” in encompassing not only the technical abilities (skills) of performing a task, but also the attitudes and deeper knowledge related to the role, including the ability to generalize knowledge, communicate with stakeholders that have different knowledge and perspectives, apply decision making in different contexts, and understand more deeply the ‘why’ for a given job. The Global Register for Competences for Protected Areas Practitioners clearly demonstrates the differences with biology or forestry professions (Appleton et al. 2016), as they combine personnel management skills with technical aspects that go far beyond monitoring fauna and flora. This role demands a range of cross-functional critical thinking skills, including effective communication and coordinated efforts, especially when engaging with local communities. Like other professionals, protected area managers must apply their knowledge, expertise, and interpersonal skills in a way that is tailored to the specific context (Müller et al. 2015, Appleton 2016).

Following a painstaking process that began with the Durban Vision in 2003, Madagascar made significant achievements in 2015 by tripling the number of protected areas and quadrupling the surface area under protection (Gardner et al. 2018). Several strategies accompanied this significant leap in land and ocean management, in particular diversification of management authorities from one parastatal national parks agency to 20+ non-governmental organizations, integration of development objectives and greater involvement of local communities in many of the new protected areas (Gardner et al. 2018). This new System of Protected Areas of Madagascar (SAPM by its French acronym) faced additional challenges amid extreme poverty around many of the protec-

ted areas, hampering participation of local communities in decision-making and management. Multiple threats to biodiversity loss and deforestation, limited law enforcement and law enforcement capacity, strategic needs for alternative livelihoods, and personnel/training required for biodiversity monitoring together result in severe challenges to overall management effectiveness (Eklund and Cabeza 2017, Gardner et al. 2018, Morelli et al. 2020). At present, Madagascar’s protected areas are critically understaffed at one third of the global recommendation, with only one staff member per 37km² (Rakotobe and Stevens 2024). A national training center was proposed at the outset of the newly created SAPM to build human resource capacity for managing new protected areas (Borrini-Feyerabend and Dudley 2005). However, this center was never established, leaving the SAPM’s expansion with unmet needs in human resources development, which are crucial for building capacity within the institutions managing protected areas (Gardner et al. 2018).

In the absence of a formalized national training program, numerous initiatives have emerged from the Ministry of the Environment and Sustainable Development (MEDD) to address gaps and enhance training for staff in newly established management institutions. For example, the Network of Conservation Educators and Professionals (NCEP) project has developed a Competency Standard for Protected Area Managers, outlining professional competencies and establishing competency-based certification schemes (Rakotobe 2015). Although these initiatives are important, they do not provide a sustainable alternative to a formalized national capacity development strategy for the SAPM.

National efforts to achieve the 30x30 target will require the strengthening and expansion of SAPM, raising important questions about the sustainability and effectiveness of both current and future human resources. Documenting competencies of protected area staff provides a solid foundation for shaping operations, improving capacity-building mechanisms, and considering outsourcing for specific capacity needs.

This article presents a study conducted as part of a project initiated by the Wildlife Conservation Society (WCS) in Madagascar aimed at clarifying the capacity-building needs of protected area managers. We share the results of our skills assessments following the expansion of SAPM and discuss the implications for preparing the next generation of protected area managers in an evolving landscape.

METHODOLOGY

In consultation with the MEDD and several protected area management institutions, we organized six workshops, grouping managers from nearby regions, and conducting surveys between June and September 2017 as detailed below. Protected area management institutions and site directors were invited to send two representatives per site to take part in the workshops.

DATA COLLECTION. Assessment of individual competencies was carried out through a survey questionnaire distributed to individuals working for protected areas. The questionnaire, in printed version, was completed individually and manually during workshops. After each workshop, the questionnaire was emailed to participants, to share with additional colleagues on a voluntary basis.

The questionnaire is comprised of two sections: 1) The respondent profile gathered information on gender, age group, education level, academic background and protected area

management experience; 2) The competency self-assessment, a series of pre-printed questions that the participant used to self-assess competency level within competency categories utilized in their professional role. Our survey instrument was based on the Malagasy competency standard for protected areas management, and modified to align with the international standard (Appleton 2016). We added the “administrator” professional level, previously absent, to include managers of groups/networks of protected areas, e.g., senior officials from regional directorates of the MEDD. We also reduced our competency categories from 19 to 11, following the international competence register (Table 1). Our self-assessment follows a three-step methodology proposed by Appleton et al. (2015). First, participants were required to specify their professional level from 1 to 4 as agent (level 1), technician (level 2), manager (level 3) or administrator (level 4). Then, in a second step, they were asked to select the top three most used competency categories in their current role. The limitation to the top three was for prioritization purposes and to limit the assessment time to one hour. The last step was a self-assessment of competencies from a 1 to 4 scale with questionnaires that correspond to individual professional level and most-used competency categories.

Inter-regional consultation workshops gathered participant perceptions of individual and managing institution capacities in the protected area sector. Participants listed perceived competency gaps, and responses were grouped by similarity without prioritization for analysis.

DATA ANALYSIS. Respondent profile responses were grouped by categories and summarized statistically. Capacity needs were calculated using the Capacity Need Index (CNI), following methodology proposed by Appleton (2015, 2016). The formula of CNI is: $CNI = \text{proportion of responses that assess the skills category as relevant for the job (1 to 4)} * \text{proportion of responses that assess competencies as 1 (low) or 2 (medium)}$.

CNI captures skills where gaps are most pronounced, as a proportion of all relevant skills using a scale between 0 and 1. The higher the CNI (closer to 1) the greater the capacity need expressed. To prioritize common competency gaps, we narrowed the responses to skills mentioned by at least 25% of participants at each professional level, focusing on the ten skills with the highest CNI. Qualitative responses obtained during discussions were grouped by similarity.

RESULTS

SCOPE. A total of 139 people took part in the study covering 49 protected areas managed by 39 institutions, including 10 public institutions (of which eight are MEDD regional directorates), 22 non-governmental organizations, five community associations (locally called VOIs), and the parastatal agency Madagascar National Parks. In all, six workshops brought together 77 managers ac-

ording to their proximity and accessibility, and 62 people responded to surveys distributed electronically. The average individual completion of the printed form was one hour. The structure of our sample enabled focused analysis on intermediate professional levels: technicians (level 2) and senior managers (level 3) as these levels represented 80% of study respondents (n=111). The highest and lowest professional levels were excluded from analysis as these categories would require a larger sample. In this study, we received 22 respondents for level 1 (Agent), and just six for level 4 (Administrator). Due to the low number of respondents, we lacked confidence that our sample was sufficiently representative of those components of the workforce.

Location and gender distribution were similar for respondents in levels 2 and 3. More than 60% of respondents were based onsite, i.e., at the protected area itself. Approximately 28% of respondents were based in main towns within regions near protected areas. Less than 10% of respondents were based in the capital, Antananarivo. These include respondents living in sites not far from the capital, and staff at the national directorate for protected areas.

The age distribution was homogeneous for level 2 (Technician) with around a third in each age bracket: under 35, 35–45 and 45–60. Perhaps not surprisingly, level 3 (Senior Manager) was dominated by people aged 45–60 (47%). Most respondents reported having an academic background in biodiversity conservation: natural sciences, environment, agronomy and forestry training at 70% for senior managers and 59.6% for technicians. In our sample, 88% of senior managers reported holding a Master’s degree, compared with 51% among technicians. Diversity of academic background was higher at the technician level. Professional experience in protected area management was relatively low at the technician level (48% reporting five years or less experience). More than 35% of senior managers and 30% of technicians reported having more than 10 years of experience in protected area management (Figure 1).

COMPETENCE AREAS. Technicians reported primarily using the following skills most frequently in their work: (1) SCD: Structuring local communities and development support; (2) CMR: Biodiversity conservation, ecological monitoring and research; and (3) EED: Environmental education.

Senior managers reported primarily using the following skills in their work: (1) SPM: Strategy, planning and management; (2) PRC: Public relations and communication; and (3) CMR: Biodiversity conservation, ecological monitoring and research.

COMPETENCE NEEDS. For technicians (Level 2), the average CNI of the ten priority skills was 0.57. The top ten priority competencies were distributed among three categories: EED (4), CMR (4) and SCD (2). For managers, the average CNI of the top ten priority competency gaps to address was 0.78, indicating a higher perceived need for training compared to that expressed by technicians (0.57). Of the ten priority skills, eight were managerial (Table 2) with five in the SPM category. The highest CNI score was for SPM 3.11 “Direct identification and implementation of measures to deal with climate change”, indicating this as a strong priority for focused training.

Table 1. Competence categories in protected area management in Madagascar.

Code	Competence Category
	<i>Managerial Competences</i>
SPM	Strategy, Planning and Management of protected area
AFM	Administrative and Financial Management
HRM	Human Resources Management
PRC	Public Relations and Communication
	<i>Technical Competences</i>
CMR	Biodiversity Conservation, Ecological Monitoring, Research
SCD	Structuring Local Community and Development support
EED	Environmental Education
ECO	Ecotourism
LAE	Law Enforcement
GIT	GIS, Information Technology

Profile of Study Participants (n=111)

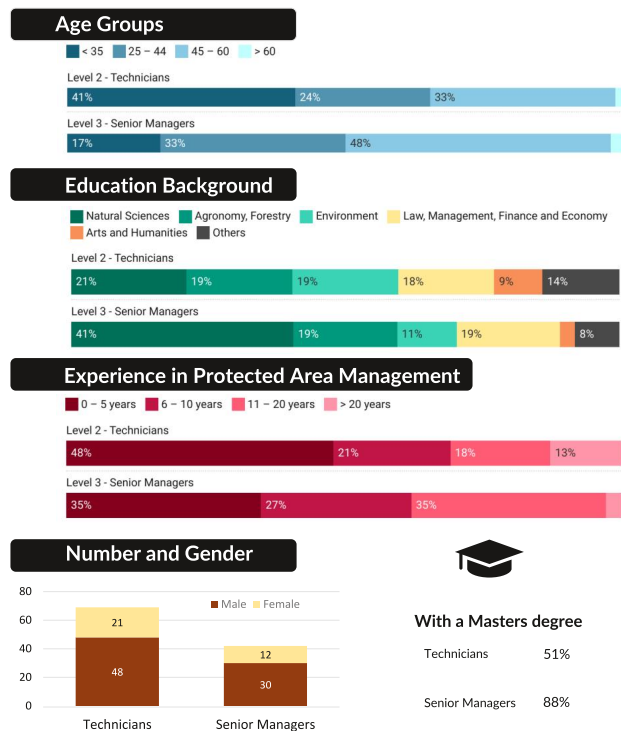


Figure 1. Profile of study participants.

Table 2. List of priority skill needs for protected area senior managers (level 3) based on Competency Need Index (CNI) calculation.

Code	Skill	CNI
EED 2.6	Organize the monitoring and evaluation of behavior change of local actors	0.73
EED 2.3	Supervise the production of training, awareness and interpretation tools	0.62
CMR 2.3	Propose conservation measures for animal and plant species and habitats	0.61
CMR 2.6	Plan, execute and report ecological restoration activities	0.61
CMR 2.4	Plan, execute and report threat management or mitigation activities	0.58
EED 2.2	Oversee the establishment of orientation and interpretation infrastructure in and around the protected area	0.54
CMR 2.2	Assess status, degree of pressures and threats to protected area conservation targets	0.52
SCD 2.10	Plan, direct and report on actions to protect cultural and historical sites, structures and objects.	0.51
EED 2.4	Organize and conduct training and information-awareness activities	0.50
SCD 2.8	Monitor support for development activities	0.49

COLLECTIVE PERCEPTIONS OF COMPETENCY GAPS. Discussions during workshops provided a collective perception of competency gaps for individuals and institutions. Gaps at the individual level were grouped into four categories: knowledge gaps, skill gaps, problems of character or attitude, and inadequate systems at the institutional level affecting individual workers (Table 3). A large proportion of answers were concerned with problems in individual character, particularly on resistance to others' ideas (closed-mindedness, lack of listening, difficulty communicating with those who are not in the protected area's world, etc.) and lack of rigor in accomplishing the work.

Regarding institutional capacities, workshop participants listed several gaps that affect the capability of the protected management institutions to deliver their mission. Institutional capacity gaps can be grouped into four categories: internal governance and leadership, operating mode, resources, and external relations or factors (Table 4). The last category received the most responses, illustrating common difficulties in work environments.

Table 3. List of staff competency gaps in protected area management in Madagascar viewed by participants of the six regional workshops (RW 1 to 6).

Code	Skill	CNI
SPM 3.11	Identify and implement measures to mitigate climate change effects.	0.92
CMR 3.11	Determine the value of ecological / environmental services of the protected area according to needs	0.86
SPM 3.7	Lead the establishment of a fundraising strategy	0.80
AFM 3.3	Lead the development and application of strategy and measures for the efficient use of resources for the protected area operations	0.80
SPM 3.9	Develop the protected area business plan	0.76
PRC 3.1	Lead the development and monitoring of the protected area communication strategy	0.72
SPM 3.8	Develop national and international partnerships and collaborative relationships	0.72
SPM 3.10	Lead the development of risk and disaster assessments and contingency plans.	0.72
AFM 3.6	Develop rules and procedures for the management of electrical / electronic furniture and equipment and vehicles	0.70
CMR 3.10	Contribute to national assessments of conservation status and harvest quotas	0.67

Table 4. List of institutional competency gaps in protected area management in Madagascar viewed by participants of the six regional workshops (RW 1 to 6).

Category	Issues
Knowledge Gaps	Inadequate training, with no specialty in PA management (RW1) (RW5) Poor knowledge of Code of Protected Areas COAP (RW 6) and legal texts (RW 1) Those who have diplomas do not have experience, and vice versa (RW 5)
Skill Gaps	Management and coordination capacities (RW 2) Managerial skills (RW 4) Anticipation capacities (RW 6) Data management (RW 6) Monitoring and evaluation (RW 5) Output-focused instead of impact-oriented (RW 4) Valorization of PA resources (RW 1) General PA management capacities (RW 1) Law enforcement (RW 6) Technology delay (RW 1) Lack of best practices, very little standardization (RW 4) Lobby techniques to elected officials and authorities (RW 1)
Problems of Characters or Attitudes	Closed-mindedness (RW 2) Lack of listening (RW 3) Difficulty communicating with those who are not in the PA world (RW 1) Individualistic character (RW 1) Personal interest is sometimes higher than the mission (RW 3) (RW 6) Lack of role model of integrity for youth (RW 1) Arrogance in approaches with local populations and local authorities (RW 1) Lack of rigor, tendency to let go "Moramora" (RW 4) (RW 5) (RW 1) Lack of judgment in sensitive situations (RW 4) Lack of conviction for conservation (RW 2) Do not dare speak out the truth (RW 6) Fear of facing PA opponents (RW 6) Difficulty managing sensitivities (RW 3) Lack of transparency and visibility (RW 4)
Gaps in means and organizations	Room to maneuver limited by over dependence on the central level (RW 1) Insufficient communication between PA managers (RW 2) Lack of transparency in information and management of resources (RW 3) Decrease in means available for work (RW 5)

These results indicate that protected area staff training should also include the less tangible aspects of staff attitudes and expectations.

DISCUSSION

This study is the first to detail self-identified professional development competency gaps among protected area managers at different career stages in Madagascar's expanded system of protected areas. Findings reveal managerial skill gaps among protected area executives and areas for growth among technicians, particularly in relation to interactions with local communities. Our study sample focused on technicians and senior managers, disseminating online invitations to regional workshops and questionnaires. We recognize that internet access can limit participation particularly for less-resourced protected areas, and we worked to develop a large sample of respondents from different protected area management organizations. Self-assessment studies have a bias risk since respondents may perceive or report skills differently. Yanjun (2013) found that in skills self-assessments, low performers tend to overestimate abilities and high performers tend to underestimate abilities, also termed the Dunning-Kruger effect.

We aimed to reduce the impact of such biases by using a competency standard with clearly defined competencies aligned with each professional level, helping to winnow out specific competency gaps that could be addressed. Workshop discussions represent the opinions of a smaller sample (79 individuals) and although informative, should be generalized with caution.

PREPARATION FOR EMPLOYMENT FOR MADAGASCAR'S PROTECTED AREA MANAGERS. Our results document the most frequently used skills and most greatly felt competency gaps among current Malagasy protected area managers. We found that senior managers largely feel the need for managerial skills reinforcement, with five of the ten most identified skills gaps in Strategy, Planning and Management. Indeed, less than 20% of protected area staff reported having received formal training in management-related fields. In contrast, 70% reported having received formal training in the conservation/natural history sector (natural sciences, forestry/agronomy, environment). Previous studies have conducted needs assessments based on responses expressed by individual protected area practitioners (e.g., Hausser 2013). Our study is unique in that it centers the needs assessment around the structure of a competency register. This approach demonstrates how needs differ at each professional level, offering strategic targets for professional development and capacity building throughout the protected area workforce. Although biodiversity conservation efforts often incorporate topics related to protected area management, the conservation sector lacks a systematic approach for key skills development needed for daily tasks. Effective protected area management revolves around critical managerial skills: planning, organizing, leading and evaluating functions (Worboys and Trzyna 2015) and the 30x30 target in particular requires outcomes-based management (Dudley et al. 2022). Our study documented significant capacity gaps for protected area managers in these dimensions.

For protected area technicians, we found that four of the 10 highest CNIs concerned environmental education (EED), and two focused on structuring local communities and development support (SCD). This indicates a need for capacity building in the areas of communication and community development to enhance staff capacity to engage in critical roles as social facilitators along protected area boundaries. Similar gaps were mentioned by workshop participants. Several studies have emphasized the importance of strengthening communication skills among park and protected area staff (Jacobson and McDuff 1998, Blickley et al. 2013) and elevating social sciences topics in the training of conservation practitioners (Bennett et al. 2017). In particular, Gardner et al. (2013) highlight the importance of conservation research communication with local Malagasy communities, especially for people from conservation backgrounds.

These results document gaps in academic and human resources training for conservation practice. Such a mismatch has been documented in the past (Jacobson and McDuff 1998, Muir and Schwartz 2009), particularly how many issues that protected area managers face have not traditionally been addressed in university curricula (Kopylova et al. 2011). Indeed, university training often places heavier emphasis on research skills with less attention directed to developing competencies required in the professional and interpersonal realms (Muir and Schwartz 2009). Even in training specifically directed at protected area management, Hausser (2013) documented significant content gaps. Virtual and

self-taught training courses have recently filled some of these gaps, providing content that is much more up to date with the needs of the profession and allowing practitioners to train while on the job. For instance, in 2016 only, the French-speaking Massive Open Online Courses (MOOC) on protected area management has attracted more than 7,000 learners of which 65% are from Africa (Madagascar being among the top five African countries in terms of number of enrollees) and more than half are professionals (Mauvais 2017). However, as typical to MOOC, completion rate is relatively low, with less than 10% as many enrollees do not seek a diploma but rather knowledge.

RE-EXAMINING CAPACITIES FOR SAPM SUSTAINABILITY. In a more holistic way, it is important to examine whether people who work daily with local actors are adequately trained in co-management of protected areas. Indeed, the success of SAPM expansion relies primarily on participation and engagement of local communities in the management of protected areas (Virah-Sawmy et al. 2014). This begins with establishing bonds of trust and collaboration with local actors. Strengthening community structures and co-developing environmental education activities are an essential part of growing meaningful connections to advance long-term conservation and sustainable livelihoods. When a protected area team has successfully established processes of self-determination and motivation among local communities, conservation outcomes can be sustainable (Nilsson et al. 2016).

Discussions during our workshops revealed key gaps, particularly in terms of individual characters and interpersonal skills training and conflict resolution, that hamper work with local actors and overall effectiveness of conservation efforts. These results are a reality that must be faced to move forward. Attitudes of protected area managers can be a barrier to long-term success. Ayivor et al. (2020) describe how local communities have experienced arrogance and unkindness from national park authorities in Ghana, increasing tensions between parties. Participants in one regional workshop also mentioned a similar attitude of arrogance in approaches with local populations and local authorities. Belecky et al. (2021) recognize that rangers can be both sources and victims of corruption, important aspects to address in training initiatives. Establishment of and training on an agreed code of conduct, such as the Ranger Code of Conduct (International Ranger Federation 2021) can promote and reinforce professionalism and ethical attitudes among protected area staff.

Intangibles including social and cultural capacities are recognized as essential by the World Commission on Protected Areas (IUCN-WCPA 2015). Beyond performing technical tasks, Müller et al. (2015) identified four essential skills for protected area professionals: (i) commitment (often unrecognized as a capacity), (ii) service delivery and logistical tasks, (iii) ability to build relationships and attract resources and support, and (iv) ability to adapt and renew, balance diversity and coherence. Different competency standards in management of protected areas also highlight emotional intelligence and soft skills as part of a toolkit of essential competencies (Appleton 2016).

Our research has documented that several institutional weaknesses, such as poor operating systems and insufficient funding (see also Eklund et al. 2022) are system-wide influences that impede success for protected area staff. Several studies encourage institutions to review human resources strategies to identify opportunities to maintain, improve and sustain engagement and

performance and personnel growth (IUCN-WCPA 2015, O'Connell et al. 2019, Porzecanski et al. 2022) indicating that providing staff training is not enough. Rather than merely considering capacity needs assessments results as training topics, they can feed into the institutional capacity development strategy and any initiative to improve the overall PA system (Müller et al. 2015, Dudley et al. 2022).

Madagascar has established the SAPM commission, a consultative and collaborative body designed to foster cooperation between MEDD, stakeholders involved in protected areas and other ministerial departments. The commission offers an inter-institutional platform of in-depth discussions on protected area issues. In response to these discussions and member requests, several guidelines have been produced (e.g., harmonized protected area management plan format) with impacts at the system level. The commission has excellent potential to develop a systematic approach to capacity building for Madagascar's protected areas workforce and respond to current staffing gaps with a national and inclusive workforce strategy (Rakotobe et al. 2023, Rakotobe and Stevens 2024).

CONCLUSIONS

The 30x30 target promotes the idea that increasing the amount of land/ocean that is under environmental protection through protected areas and OECMs will improve biodiversity conservation outcomes and ultimately enhance human health and wellbeing. This assumes that these protected areas are managed effectively, and that depends largely on adequate staffing, enhanced training for protected area managers, and systems that work together to achieve ambitious and well-defined outcomes (Appleton et al. 2022, Rakotobe and Stevens 2024).

For Madagascar to succeed in protected area management, a renewed workforce development strategy must be developed (Rakotobe et al. 2023). The 30x30 target stipulates that protected areas are no longer the sole prerogative of conservation institutions and elite university graduates, but rather a collective responsibility requiring new organizations that engage a broader society including local communities and the private sector. Academic institutions and professional training centers must ensure that curricula harmonize with real-world challenges, recognizing the essential role of interdisciplinary training across social and natural sciences. The SAPM must expand human resource engagement strategies to local communities as part of their external workforce. Our findings help prioritize training needs by documenting skills gaps and behavior issues that protected area managers have identified; these can be integrated within national training centers as the CNFTF in Angavokely or the CNFEREF in Kirindy for forestry technicians and also in university programs that produce senior managers and technicians (e.g., School of Forestry and Agronomy, natural sciences and geography departments). Conservation NGOs could also consider these topics for timely workshops or online trainings for their staff. Revisiting the concept of a national Center of Excellence for Protected Area Management, proposed nearly two decades ago (Borrini-Feyerabend and Dudley 2005), to foster sector-relevant skills and community building in a decentralized approach can elevate the centrality of biodiversity conservation training in a megadiverse country like Madagascar. This reflection should also be extended to the capacity development of all types of stakeholders involved in OECMs management. A renewed national conservation workforce strategy is imperative to consolidate efforts and build a stronger environmental future.

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The influence of cultural prohibitions on wildlife hunting and consumption in western Madagascar

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ABSTRACT

Unsustainable hunting is a leading driver of species decline globally, particularly in biodiversity hotspots like Madagascar, where wildlife conservation challenges intersect with severe humanitarian needs. In the Menabe Region near Kirindy Mitea National Park, wildlife hunting persists despite various prohibitions. While national legal frameworks, often developed with limited local input, seek to regulate hunting and consumption behaviors, regional studies have consistently shown that these laws alone are insufficient in safeguarding vulnerable species. In contrast, food prohibitions, such as species-specific taboos (or traditional *fady* in the case of Madagascar), are culturally derived prohibitions and ethical relations that shape how Malagasy individuals perceive and engage with wild and domestic animals. Previous research has highlighted the potential of *fady* to protect particular species while also acknowledging the complex nature of *fady* adherence in conservation contexts. This paper considers the impact of both locally rooted belief systems and national regulatory structures on wildlife use in a village near Kirindy Mitea National Park, where communities are navigating intersecting challenges of food insecurity and reliance on wild meat for sustenance. We carried out quantitative surveys of heads of households regarding their personal beliefs and adherence to taboos and laws, and expanded upon this information through focus groups and semi-structured interviews with key informants. While *fady* discouraged consumption in some species, it did not significantly impact hunting behavior. Similarly, stricter hunting laws are associated with reduced consumption but have little impact on hunting practices, primarily due to poor law awareness. These findings underscore the limitations of top-down conservation policies and the need to support community-led conservation approaches that are informed by local priorities, challenges, and existing governance structures. Ef-

fective conservation policies must simultaneously recognize and address structural challenges, like food insecurity, that shape decision-making. These findings suggest the need for ongoing, community-engaged qualitative research into the material and sociocultural contexts that inform decision-making about wildlife use.

RÉSUMÉ

La chasse non durable entraîne le déclin des populations de nombreuses espèces dans le monde, notamment à Madagascar, un hotspot de la biodiversité confronté à de graves défis écologiques et humanitaires. Bien que des lois imposées au niveau central visent à régulariser la chasse et les comportements des consommateurs, des études régionales ont montré que ces lois, à elles seules, ne suffisent pas à protéger les espèces vulnérables. En revanche, les interdictions alimentaires, telles que les tabous spécifiques à certaines espèces (*fady* de consommation dans le contexte malgache), sont des interdits d'origine culturelle qui influencent la perception et l'utilisation de la viande sauvage et domestique par les Malgaches. Des recherches antérieures ont mis en évidence le rôle potentiel des *fady* dans la protection de certaines espèces, tout en reconnaissant la complexité de leur respect dans un contexte de conservation. Cet article examine l'influence des interdictions culturelles et légales sur l'utilisation de la faune dans un village proche du parc national de Kirindy Mitea, dans la région de Menabe, à l'ouest de Madagascar. Ce village est caractérisé par un niveau élevé de chasse aux animaux sauvages, combiné à une insécurité alimentaire et une malnutrition significatives, mais l'effet des interdictions sur l'utilisation de la faune y a été peu étudié. Nous avons mené des enquêtes quantitatives auprès de chefs de ménage sur leurs croyances personnelles et leur adhésion aux *fady*, et complété ces informations par

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des groupes de discussion et des entretiens semi-structurés avec des informateurs clés. Bien que les *fady* influencent négativement la consommation, ils n'ont pas d'effet significatif sur la capture des animaux. De même, des lois plus strictes sur la chasse sont associées à une réduction de la consommation, bien que les résultats soient nuancés. Toutefois, les lois de conservation imposées d'en haut étaient peu connues dans la communauté et n'ont pas réduit la capture et la consommation de la faune sauvage. Nous recommandons des études qualitatives supplémentaires pour mieux comprendre les conditions dans lesquelles les individus consomment des espèces qu'ils considèrent comme immanquables ou culturellement interdites, afin d'expliquer leur prise de décision en matière d'utilisation de la faune.

INTRODUCTION

The unsustainable hunting and consumption of wildlife are major drivers of global population loss (Ripple et al. 2016), with a recent analysis that at least 48% of vertebrate species are declining globally (Finn et al. 2023). Wildlife exploitation, particularly unsustainable hunting, can lead to localized extinctions and cascading ecological consequences (Ripple et al. 2016). Responding to biodiversity loss requires solutions that begin with the needs, knowledge, and priorities of local communities.

Wild meat consumption is influenced by complex and interwoven social, ecological, and personal factors, which result in varying preferences, aversions, and prohibitions (Birch 1999). Taboos, which are culturally defined prohibitions, shape dietary practices worldwide (Birch 1999, Fessler and Navarrete 2003, Meyer-Rochow 2009). These taboos, rooted in beliefs about danger, immortality, or religious impurity, play a significant role in regulating dietary practices across societies (Rozin 1987, Landim et al. 2023). They may apply to entire groups of people, such as religious communities, or can affect individuals during a specific life phase, such as pregnant women (Colding and Folke 1997, Landim et al. 2023). Although created and enforced socially, taboos often become internalized through expectations and fear of stigma, guiding behaviors even sometimes without exterior enforcement. These social rules are created and enforced by individuals (Colding and Folke 1997, 2001, Fessler and Navarrete 2003, Meyer-Rochow 2009). When these norms are violated, not only are external (i.e., social) rules breached, but internal rules aiding one's sense of self and connection to the physical and spiritual world (Lambeck 1992, Meyer-Rochow 2009).

Taboos that restrict the use of a particular species may reflect long standing human-environmental relationships that also result in decreased hunting pressures, indirectly offering conservation benefits (Colding and Folke 2001, Cinner 2007, Jones et al. 2008), especially given that more than 100 documented species that are subjects of taboo (Landim et al. 2023). In some cases, such as restrictions on shellfish in Jewish traditions or beef in Hindu communities, prohibitions may organically align with beneficial ecological outcomes (Meyer-Rochow 2009). Globally, 30% of species-specific taboos pertain to threatened species, often safeguarding those that are endemic or otherwise ecologically important (Colding and Folke 1997, 2001). While global parallels (see Landim et al. 2023 for individual citations) highlight the cultural dimensions of food taboos, Madagascar offers a particularly complex and locally embedded case through the system of *fady*, traditional prohibitions with deep ancestral and spiritual roots.

Fady are important and dynamic prohibitions deeply ingrained in Malagasy society, conferring spiritual, ancestral, and physical well-being (Ruud 1960, Lambeck 1992). *Fady* includes various behavioral prohibitions and social expectations, from breaches of 'good manners' punished by social disapproval to strict taboos enforced by ancestral forces (Lambeck 1992). *Fady* are highly diverse and vary by region, origin, household, and even individual. Some are strict ancestral prohibitions (*sandrana*), while others may be negotiable (*fadin-drazana*) (Jones et al. 2008). *Fady* can also be a health proscription received through spiritual command by a human spirit medium (*ombiasa*) (Golden and Comaroff 2015a). Others relate to wider community norms on what is edible or not (*fadin-pairahamonina*); however, some authors do not frame this category as *fady*, but more simply shouldn't be done (*tsy azo atao*) (Jones et al. 2008). These examples, however, are not exhaustive given the complexity and richness of the *fady* system.

There have been multiple documented instances of *fady* protecting a wild species from hunting and consumptive behaviors. For example, some ancestral *fady* (*fadin-drazana*) prohibit the consumption of lemurs because of their perceived morphological and behavioral similarities to humans and their representation of ancestors (Loudon et al. 2006, Jones et al. 2008). Other stories of species saving ancestors (e.g., dolphins, sea turtles, and rays rescuing sailors) have led to inherited ancestral *fady* prohibiting the consumption of the subject of the *fady* (Lilette 2006). Some *fady* include fears of spiritual and physical repercussions, like in the Sofia region, where rashes and sores occur after eating octopus and can only be cured by spiritual remedies (Cinner 2007). Others are health-related (*fadin'ody*), such as Tanala pregnant women avoiding crayfish (*Astacoides*) to prevent having multiple births (Jones et al. 2008). Species-specific *fady* are vast, and many overlap with formal conservation efforts (complete list within Appendix A); here, we focus on ancestral and health-promoting taboos. While *fady* may align with conservation in some cases, Keller (2009) cautions against framing Malagasy cultural systems exclusively through the lens of just taboo, which simplifies a much broader cultural landscape. Following Keller's ideas, this study seeks to understand how *fady* and conservation laws shape wildlife use in ways that reflect community realities, perspectives, and knowledge.

Fady can shape wildlife use even when they do not explicitly prohibit hunting, but nonetheless influence how people engage with particular species (Ruud 1960, Lambeck 1992, Jones et al. 2007, 2008, Jenkins et al. 2011). Regional studies indicate that when adhered to, species-specific *fady* can reduce consumption of the animal, inherently reducing hunting pressure. However, there has been documented erosion of *fady* in younger generations (Jones et al. 2008, Randrianandrianina et al. 2010, Jenkins et al. 2011, Reuter et al. 2016, Anania et al. 2018). These dynamics have generated discussion among conservationists aiming to align conservation frameworks with locally grounded systems of environmental stewardship. Yet, Madagascar's high cultural and dietary diversity complicates this alignment. What works in one region may not translate to another without close consideration of the community context. While national assessments of hunting pressure are limited, several regional studies reveal significant use of mammal and bird species to meet economic and nutritional needs (García and Goodman 2003, Golden 2009, Randrianandrianina et al. 2010, Jenkins et al. 2011, Razafimanahaka et al. 2012, Golden et

al. 2014, Borgerson et al. 2019, 2022, 2023, Thompson et al. 2023). Wildlife consumption, which drives hunting pressure, is influenced by several factors including taboo adherence, perceived inedibility, and meat preference (Reuter et al. 2016). However, other research has found no significant link between individual taboos and regional consumption patterns (Golden and Comaroff 2015b), pointing to the need for additional localized studies on how cultural beliefs influence wildlife use.

In this study, we examine *fady* regarding wildlife use, specifically those followed for health or ancestral reasons, in a community neighboring Kirindy Mitea National Park. As taboos represent culturally specific prohibitions imposed within a family or community, we also acknowledge conservation laws as culturally specific prohibitions imposed onto a community, which might similarly influence conservation behavior. Species outside strictly protected zones (e.g., Strict Nature Reserves, National Parks, or Special Reserves with IUCN protection status I, II and IV) are separated into four categories of protection based on Decree No. 2006-400, ranging from no restrictions to complete prohibition of capture. However, awareness of conservation law varies regionally (Keane et al. 2011), and even when individuals are aware of regulations, they may preferentially comply more with social norms when those norms and laws conflict (Rachlinski 1999). Relative compliance with laws often depends on their integration with social practices and ongoing management (Vuola and Pyhälä 2016), and conservation approaches rooted in community-led decision-making tend to reflect local values and thus more enduring support (Rakotoson and Tanner 2006).

Here, we use data from interviews, surveys, and focus group discussions to explore how cultural and legal prohibitions influence the hunting and consumption of wildlife. We hypothesize that (i) cultural prohibitions (*fady* and other aversions) influence only a species' consumption because *fady* typically restricts only the consumption of an animal. Thus, that species may technically be hunted for a second person to consume without breaching the prohibition. Furthermore, we hypothesize that (ii) policy (laws and hunting regulations) will influence only the hunting of a species, since only the hunting, and not the consumption, of a protected species is expressly prohibited by Malagasy law (Decree No. 2006-400). This data will help assess the impact of emic and etic cultural prohibitions on wildlife use and inform regional and national policies that align with Indigenous values, creating formal institutions that are effective yet complementary to existing informal practices.

METHODOLOGY

STUDY SITE. This study was carried out in communities living adjacent to Kirindy Mitea National Park in Madagascar's southern Menabe Region. This area is characterized by a dry forest with a mix of spiny and deciduous ground coverage as well as over 100 bird species, 31 reptile species, and 34 mammal species, including eight lemur species. Many communities in the Menabe Region, including this one, rely on both agricultural and pastoral activities with limited opportunities for wage labor (Thompson et al. 2023). Households in this region face food insecurity, child malnourishment, and multidimensional poverty; 95% of households are 'impoverished,' and 77% are 'severely impoverished' (Romanello et al. 2023). Most households rely on wild animals for food security and cultural practices, many of which are listed as conservation priorities (Thompson et al. 2023). For example, lemur consumption is reportedly higher here than in other study sites in

Madagascar, with almost 50% of households eating lemurs in the year prior (Romanello et al. 2023).

ETHICAL NOTE. We received full informed consent from each participant in this study, using the local dialect of Malagasy. Detailed ethical considerations, including the participant exclusion criteria, participant rights, and matters of participant anonymity, can be found in Thompson et al. (2023). The Stony Brook University Internal Review Board reviewed and approved all research methods (IRB #1183799-4). Our study was conducted with the requisite permits and approval at the national, regional, and local through the facilitation of the Madagascar Institute for the Conservation of Tropical Environments (Permit #171/18/MEEF/SG/DGF/DSAP/SCB.Re).

DATA COLLECTION. We collected information using (i) structured interviews with household representatives on food prohibitions and wildlife use, and used (ii) semi-structured focus groups, and (iii) semi-structured key informant interviews with local hunters to contextualize and ground information learned in structured interviews. We held all interviews from September 2018 to March 2019 in the local dialect of Sakalava Malagasy. Self-identified heads of households were interviewed, and their wildlife-related beliefs and awareness of conservation law were explored (detailed below). We defined a household as individuals who eat together in the same kitchen, and we reached 66 of the community's 89 households (74.2%). Focus group participants were then identified based on their experiences in the community, and their insights were used to understand community-level taboos and animal use practices. Experienced hunters were also identified for interviews to discuss specific hunting practices, meat sales, and evolution of animal use, thereby further grounding the information obtained in structured interviews with household representatives.

Community members consulted in household interviews were first asked about species-specific taboos they personally adhere to (not necessarily the household). First, we asked whether each species (Table 1) was prohibited for them to eat (1 = yes or 0 = no). If a species was considered prohibited by the respondent, they were asked to categorize the reason for the prohibition by selecting one of the following: ancestral *fady*, health *fady*, perceived inedibility, dislike, or other. Medicinal *fady* are those in which the consequences of breaking the *fady* result in harm to health; ancestral *fady* are those imposed through generational ties (*fadin-drazana* or *sandranana*); perceived inedibility are species which the interviewee believes it can't be consumed; and dislike meaning the interviewee does not prefer the taste of the meat. Categorizing the reason for consumption prohibition allowed us to filter out *fady* (e.g., followed for medical or ancestral reasons) from unrelated personal preferences, such as dislike or perceived inedibility.

For medicinal *fady*, additional details were requested regarding how the taboo was treated, how long the respondent had been proscribed this taboo, and the duration they were expected to follow it. We also asked participants about the applicability of the taboo across different ages (babies, children, adults, or the elderly), the sexes affected by the taboo (female, male), and the life stages during which it is relevant (options including pregnancy, lactation, infancy, childhood, adulthood, as an elder, when the parents were alive, when the parents were deceased, or other specified stage).

To assess knowledge of conservation regulations, each household representative received a conservation awareness score based on correctly identifying each species' protection status and, where applicable, naming of the legal hunting season. To do this, we first asked the participants about species' conservation status, with respondents categorizing it as protected, game, or nuisance. If the animal belonged to a game species, respondents were asked to specify the months during which it could be caught. We allotted 1 point for knowing the animals' hunting status (allowed or not allowed to hunt) and 1 point for identifying the correct hunting season (0.5 points for partial response). We obtained environmental laws via Malagasy Ordonnance n° 60-128, which categorizes all wildlife in Madagascar into respective protection statuses. In our study sample, seven species are categorized as Protected Class I, five as Protected Class II, four as Game, and one as Nuisance (Table 1) (Ministère de l'Environnement, des Eaux et Forêts et du Tourisme 2006). We calculated conservation awareness scores and categorized species based on Malagasy conservation status (0 = Protected Class I, 1 = Protected Class II, 2 = Game, 3 = Nuisance). We combined this data with data from another individual-level survey on wildlife utilization, in which we asked each participant about hunting and consumptive behaviors for each species in the year prior (Thompson et al. 2023).

To examine the effects of different prohibitions on hunting and consumption, we last asked household interview respondents about their food acquisition and consumption practices. This data on taboos and legal proscriptions was combined with data from another individual level survey on wildlife utilization. During this interview, we asked each participant about hunting and consumptive behaviors (Thompson et al. 2023). Specifically, we asked about the use of five species of lemur, three tenrecs, two birds, one swine, three endemic carnivores, one tortoise, and two bats (Table 1). Since respondents typically could not distinguish microbats at the species level, we asked broadly about them. Locally identified bats include *Hipposideros commersoni*, *Myotis goudoti*, *Eidolon dupreanum*, *Scotophilus robustus*, and *Miniopterus gleni*. Although we did not include the pale fork-marked lemur (*Phanerpallescens*) in this measure, we included it in a version data after identifying it as locally relevant. We excluded the spotted fanaloka

(*Fossa fossana*), also known as a Malagasy civet, for similar reasons. For this study, hunting refers to species capture and consumption refers to eating terrestrial wild animals during the year prior, as defined by the respondents' own memory.

Focus group discussions included 6–12 individuals of similar gender, age, and occupation, with all participants in a single group coming from different households in the community. Each discussion group lasted approximately 60 minutes and occurred in a neutral location. Discussion groups, led by KETT reviewed hunting practices, food availability, food insecurity mitigation practices, and financial stressors. Recorded quotes and explanations from these focus groups to provide sociocultural context to individual and household interview data results. We also conducted semi-structured interviews with four hunters, who were recognized as subject matter experts, focusing on hunting practices and *fady* related to hunting. Focus group discussion data, similar to key informant interviews, was used to contextualize individual interview responses and interpret patterns in hunting and consumption behavior. Rather than imposing thematic categories and codes, we allowed insights from collective discussions to guide interpretation and contextual understanding.

VARIABLE ANALYSIS. First, since we aim to determine whether an individual hunted or ate a species rather than the number of animals hunted or consumed, we converted the number of animals hunted or consumed into binary data. From this data, we calculated which species were hunted and consumed for each respondent and across the community. We then created binary data for each *fady* category: ancestral *fady*, health-related *fady*, perceived inedibility, and dislike. Each was coded as 1 if the respondent identified that reason as the cause of aversion, and was coded as 0 otherwise. To generate a conservation law awareness score, each respondent received 0–2 points per species: 1 for correctly identifying its legal protection status and 1 for naming the hunting season (0.5 for partial responses). Scores were then summed across all species to create an overall law awareness score, treating all species equally regardless of their given ecological risk. Species with no legal hunting season were marked as 'prohibited year-round', and any indication of allowed months was

Table 1: Species in the household-level annual surveys with conservation information, hunting status, and calculated conservation awareness scores. (Higher scores indicate a higher awareness of associated wildlife laws; * = likely not in the area; (1) from IUCN 2025; (2) from Ministère de l'Environnement, des Eaux et Forêts et du Tourisme 2006; (3) see methodology; (4) insectivorous bats include the following species which are locally identified but indistinguishable: *Hipposideros commersoni*, *Myotis goudoti*, *Eidolon dupreanum*, *Scotophilus robustus*, and *Miniopterus gleni*)

Species	Malagasy name	IUCN status (1)	Malagasy protection status (2)	Hunting season (2)	Average conservation awareness score (3)
Reptilia, Testudinidae					1.56
<i>Pyxis planicauda</i>	Kapiky	CR	Protected I	Prohibited	1.56
Aves					0.22
<i>Numida meleagris</i>	Akanga	LC	Game	1 May–30 Jun	0.36
<i>Carocopsis vasa</i>	Tsiotry	LC	Protected II	1 May–30 Jun	0.08
Mammalia, Chiroptera					0.08
<i>Pteropus rufus</i>	Fanihy	VU	Game	1 May–1 Sep	0.03
Insectivorous bats (4)	Angavo, Kitroto, Kinakina		Protected II	1 May–1 Sep	0.13
Mammalia, Suidae					1.26
<i>Potamochoerus larvatus</i>	Lambo	LC	Nuisance	Unrestricted	1.26
Mammalia, Eupleridae					0.17
<i>Mungodictis decemlineata</i>	Andrao, Bokiboky	EN	Protected I	Prohibited	0.21
<i>Cryptoprocta ferax</i>	Fosa	VU	Protected II	1 Apr–30 Jun	0.18
<i>Fossa fossana</i>	Fanaloka	VU	Protected II	1 Apr–30 Jun	0.11
Mammalia, Lemuriformes					1.48
<i>Lepilemur ruficaudatus</i>	Boenga	CR	Protected I	Prohibited	1.73
<i>Eulemur rufifrons</i>	Gidro	VU	Protected I	Prohibited	1.71
<i>Lemur catta</i> *	Maky	EN	Protected I	Prohibited	1.70
<i>Propithecus verreauxi</i>	Sifaka	CR	Protected I	Prohibited	1.71
<i>Phanerpallescens</i>	Tanta	EN	Protected I	Prohibited	0.76
<i>Microcebus murinus</i>	Fitilivahy	LC	Protected I	Prohibited	1.33
<i>Cheirogaleus medius</i>	Kelybehohy	VU	Protected I	Prohibited	1.42
Mammalia, Tenrecidae					0.94
<i>Tenrec ecaudatus</i>	Trandraka	LC	Game	1 Apr–31 May	0.91
<i>Setifer setosus</i>	Sora	LC	Protected II	1 Apr–31 May	0.96
<i>Echinops telfairi</i>	Tambotriky	LC	Game	1 Apr–31 May	0.96

scored as incorrect. To integrate legal protection categories into our statistical model, we assigned ordinal numeric codes: 0 = Protected Class I, 1 = Protected Class II, 2 = Game, 3 = Nuisance.

We used general linear models, and a rare events logistic regression model when appropriate, to assess how cultural and legal prohibitions influence hunting and consumption in our study community. Rare events logistic regression was used because the hunting variable had a very low event rate (2%), which a standard logistic regression would underestimate event probability. While consumption occurred at an event rate of 15%, which is not considered rare, hunting occurred at an event rate of 2%, requiring a rare events logistic regression model. For the rare events model, we performed regressions for dichotomous dependent variables with the Zelig package in R Statistical Software v4.1.1 using a Re-Logit model (Imai et al. 2007). When certain ReLogit models were performed, particularly in the case of *fady* (ancestral and health origin reasons), model overfitting occurred, indicating this model was too complex for our sample size. Given this, general linearized regression models were used. When neither model produced unrealistic parametric estimates or uninterpretable results with similar AIC scores, we conducted Fisher's Exact Tests, which are robust to small and uneven sample sizes.

RESULTS

HUNTING AND CONSUMPTION. Sampled community members hunted an average of $0.9 \pm SD1.2$ animals per individual (median=0, range=0–8) and consumed an average of $1.9 \pm SD2.6$ animals (median=0, range=0–11) during the prior year. Forty-two (63.6%) respondents reported not hunting any species, while one (1.5%) reported hunting 11 species during the previous year.

The most hunted taxa were tenrecs (mean=10.1% of catch), with the greater hedgehog tenrec (*Setifer setosus*) being hunted by the highest number of individuals in our community (11 respondents, 16.7%, Figure 1, Table 2). Though the common tenrec (*Tenrec ecaudatus*) occupies a similar ecological niche, it was hunted by substantially fewer individuals (2 respondents, 3.0%). Bird species and the tortoise were also caught at moderate levels, while lemurs were generally caught in numbers less than other species (Table 2). Only the fosa (*Cryptoprocta ferox*) and Verreaux's sifaka (*Propithecus verreauxi*) were not hunted at all.

Regarding consumption, birds were the most commonly eaten taxa, with the helmeted guinea fowl (*Numida meleagris*) most consumed wild meat, despite moderate hunting levels (21 individuals, 31.8%, Figure 1, Table 2). Although only two individuals hunted it, a quarter of respondents (25.7%, n=17) ate bush pig meat (*Potamochoerus larvatus*). While lemur consumption was relatively low across all species within our sample, a more comprehensive study of lemur hunting in this community suggests more extensive lemur consumption than was captured in our current dataset (Romanello et al. 2023). The most consumed lemurs were red-tailed sportive lemur (*Lepilemur ruficaudatus*) and Verreaux's sifaka, each of which was consumed by seven households (10.6% of study households). The tortoise and bat taxa were both consumed at low to moderate levels. The fosa was the only species reported as not consumed.

INFLUENCE OF FADY ON HUNTING AND CONSUMPTION. Several *fady*, among other food aversions, were reported by community members surveyed. We distinguish these in the text and visualizations. '*Fady*' refers specifically to cultural taboos

Table 2: Hunting and consumption levels of species utilized near Kirindy Mitea National Park, Madagascar (2018–2019).

Species	Hunters	Percent Hunters (n=66)	Consumers	Percent Consumers (n=66)
Reptilia, Testudinidae (N=66)	5	7.6%	7	10.6%
<i>Pyxis planicauda</i>	5	7.6%	7	10.6%
Aves (N=132)	11	8.3%	34	25.8%
<i>Numida meleagris</i>	5	7.6%	21	31.8%
<i>Coracopsis vasa</i>	6	9.1%	13	19.7%
Mammalia, Chiroptera (N=132)	4	3.0%	4	3.0%
<i>Pteropus rufus</i>	3	4.6%	3	4.6%
Insectivorous bats	1	1.5%	1	1.5%
Mammalia, Suidae (N=66)	2	3.0%	17	25.8%
<i>Potamochoerus larvatus</i>	2	3.0%	17	25.8%
Mammalia, Eupleridae (N=132)	3	3.0%	8	25.8%
<i>Mungodictis decemlineata</i>	3	4.6%	8	12.1%
<i>Cryptoprocta ferox</i>	0	0.0%	0	0.0%
Mammalia, Lemuriformes (N=330)	13	3.9%	29	8.8%
<i>Lepilemur ruficaudatus</i>	3	4.6%	7	10.6%
<i>Eulemur rufifrons</i>	3	4.6%	5	7.6%
<i>Propithecus verreauxi</i>	0	0.0%	7	10.6%
<i>Microcebus murinus</i>	4	6.1%	5	7.6%
<i>Cheirogaleus medius</i>	3	4.6%	5	7.6%
Mammalia, Tenrecidae (N=198)	20	10.1%	26	13.1%
<i>Tenrec ecaudatus</i>	2	3.0%	11	16.7%
<i>Setifer setosus</i>	11	16.7%	4	6.1%
<i>Echinops telfairi</i>	7	10.6%	11	16.7%
Total (N=1056)	58	5.5%	125	11.8%

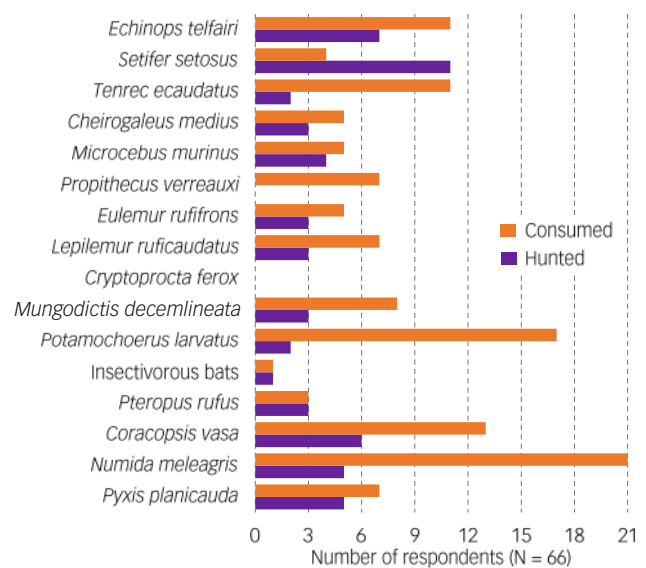


Figure 1: The number of respondents which hunted and consumed wildlife species near Kirindy Mitea National Park, Madagascar (2018–2019).

(as characterized by Jones et al. (2007, 2008), while 'aversions' include more general food avoidances like perceived inedibility and personal dislike. While *fady* was not as frequent as perceived inedibility, *fady* significantly influenced behavior, with community members each reporting a mean of 1.80 species as *fady* (median = 2, SD ± 2.0). The maximum number of individual *fady* by a respondent was 12 species, and 16 respondents said they had no *fady* for consuming any species. Respondents most perceived Malagasy Eupleridae as *fady*, with approximately half viewing the consumption of fosa (53.0%, n = 35) and spotted fanaloka (*Fossa fossana*, 43.9%, n = 29) as *fady*. Almost all attributed these *fady* to ancestrally-derived teachings, obligations, or prohibition (Figure 2 and Table 3). Although the vonsira (*Mungodictis decemlineata*) is similar in appearance and ecological niche to the spotted fanaloka and fosa, *fady* adherence in our study village was notably much lower. Several respondents cited bush pig consumption as *fady*, most of whom noted health-related reasons. Some community members reported insectivorous bats as *fady* (15.1%, n = 10), but none reported the Madagascar flying fox (*Pteropus rufus*) as such. *Fady* existed in relatively low numbers across all lemur species except for the ring-tailed lemur (*Lemur catta*) and the pale fork-

Table 3: Instances of aversions (broken down into fady and other aversions) near Kirindy Mitea National Park, Madagascar (2018–2019).

Species	All aversions	Fady: ancestral & medicinal reason	Other aversions: Dislike & inedible	Aversion Reason 1: Ancestor	Aversion Reason 2: Medical	Aversion Reason 3: Don't like	Aversion Reason 4: Inedible
Reptilia, Testudinidae (N=66)	5 (7.6%)	3 (4.6%)	5 (7.6%)	4			1
<i>Pyxis planicauda</i>	5 (7.6%)	4 (6.1%)	1 (7.6%)	4			1
Aves (N=132)	0	0	0				
<i>Numida meleagris</i>	0	0	0				
<i>Coracopsis vasa</i>	0	0	0				
Mammalia, Chiroptera (N=132)	57 (43.2%)	10 (7.6%)	47 (43.2%)	8	1	3	43
<i>Pteropus rufus</i>	4 (6.1%)	0 (0%)	4 (6.1%)				4
Insectivorous bats	53 (80.3%)	10 (15.2%)	43 (80.3%)	8	1	3	39
Mammalia, Suidae (N=66)	14 (21.2%)	14 (21.2%)	0 (21.2%)		12		
<i>Potamochoerus larvatus</i>	14 (21.2%)	14 (21.2%)	0 (21.2%)		12		
Mammalia, Eupleridae (N=198)	91 (46%)	66 (33.3%)	25 (46%)	63		1	24
<i>Mungodictis decemlineata</i>	7 (10.6%)	2 (3%)	5 (10.6%)	2			5
<i>Cryptoprocta ferox</i>	47 (71.2%)	35 (53%)	12 (71.2%)	33			12
<i>Fossa fossana</i>	37 (56.1%)	29 (43.9%)	8 (56.1%)	28		1	7
Mammalia, Lemuriformes (N=462)	79 (17.1%)	23 (5%)	56 (17.1%)	17	1	2	54
<i>Lepilemur ruficaudatus</i>	2 (3%)	1 (1.5%)	1 (3%)	1			1
<i>Eulemur rufifrons</i>	3 (4.6%)	2 (3%)	1 (4.6%)	1			1
<i>Lemur catta</i>	7 (10.6%)	6 (9.1%)	1 (10.6%)	4			1
<i>Propithecus verreauxi</i>	5 (7.6%)	4 (6.1%)	1 (7.6%)	1	1		1
<i>Phaner pallescens</i>	33 (50%)	6 (9.1%)	27 (50%)	6		2	25
<i>Microcebus murinus</i>	15 (22.7%)	3 (4.6%)	12 (22.7%)	3			12
<i>Cheirogaleus medius</i>	14 (21.2%)	1 (1.5%)	13 (21.2%)	1			13
Mammalia, Tenrecidae (N=198)	0	0	0		1		
<i>Tenrec ecaudatus</i>	0	0	0				
<i>Setifer setosus</i>	0	0	0				
<i>Echinops telfairi</i>	0	0	0		1		
Total (N=1254)	248	118	133	92	15	6	122

Table 4: Regression results indicating the relationships between hunting or consumption and taboo, perceived inedibility, protection status, and knowledge of conservation laws.

Behavior	Predictor	Test	P value	95% Confidence interval
Hunting	Taboo	Fisher's Exact Test for count data	0.068	0.068–1.097
Consumption	Taboo	Fisher's Exact Test for count data	0.004	0.134–0.767
Hunting	Perceived inedibility	Relogit	0.155	
Consumption	Perceived inedibility	Relogit	0.303	
Hunting	Protection status	GLM	0.976	
Consumption	Protection status	GLM	0.000	
Hunting	Protection status x Conservation score	GLM	0.565	
Consumption	Protection status x Conservation score	GLM	0.284	

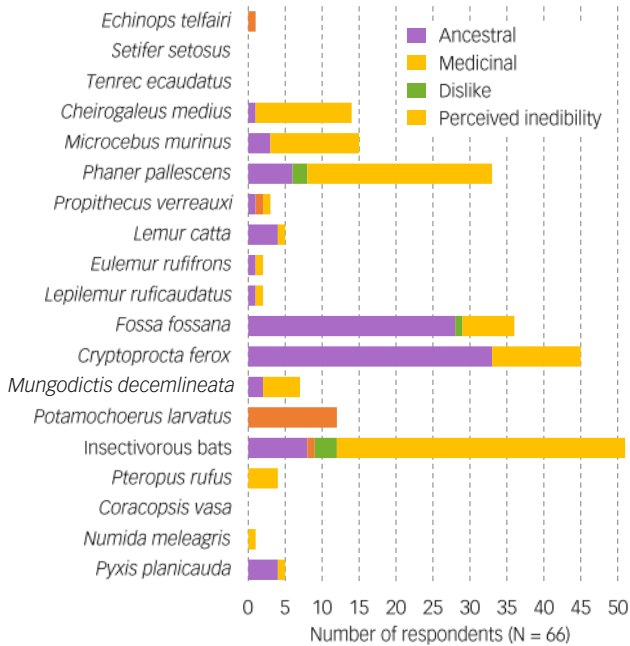


Figure 2: Reason for species aversion near Kirindy Mitea National Park, Madagascar (2018–2019).

marked lemur (*Phaner pallescens*), which were subject to *fady* for some individuals (Table 3). Individuals who cited the fork-marked lemur as *fady* did not provide a definitive origin, and there were no apparent significant factors influencing whether one adhered to the *fady* or did not. Besides one individual who cited health reasons for Verreaux's sifaka consumption taboo, all other respondents claimed ancestral forces shaped their *fady* for lemur consumption. No respondents surveyed bird species as subject to a consumption *fady*, and only two reported a tenrec as subject to a consumption *fady*, both of which were the lesser hedgehog tenrec (*Echinops telfairi*).

We found that the odds of eating a species for those who report adhering to a *fady* were approximately 65.2% less than for those who do not cite a *fady* (odds ratio= 0.345, p = 0.004) (Table 4). On the other hand, *fady* did not affect hunting (p = 0.0683). When we attempted to subset *fady* by “ancestral” and “health” reasons, sample sizes for some species were too small to allow for statistically valid model estimates, highlighting the limits of categorizing complex cultural beliefs. This includes *Propithecus verreauxi* for which only four respondents report *fady*, with only two of which cited a reason, and *Mungodictis decemlineata* for which two respondents report *fady*, both citing ancestral reasons (Table 3).

INFLUENCE OF PERCEIVED INEDIBILITY ON HUNTING AND CONSUMPTION. Other food aversions, specifically perceived inedibility, were more common in our study village than *fady*, with each individual citing 1.94 aversions (median = 2.0, SD ± 1.6). Individuals more frequently viewed a wild animal as inedible than expressing dislike for its consumption (Figure 2). The most commonly cited “inedible” species were insectivorous bats (n= 39, 59.1%), while only a few respondents thought the Madagascar flying fox was inedible (n= 4, 6.1%). Some respondents (n= 25, 37.9%) also believed certain lemurs, especially the pale fork-marked lemur (*Phaner* spp.), were inedible, while they considered other lemur species edible. No respondents reported aversions to consuming birds or tenrecs. Inedibility did not predict hunting or consumption (p = 0.155, p = 0.303), suggesting no significant relationship between perceived inedibility and these behaviors (Table 4).

ENVIRONMENTAL LAW AND AWARENESS. Participants' knowledge of hunting laws and regulations varied highly by species (Table 1). Most respondents were aware of lemur hunting

laws, with a mean law awareness score of 1.89 out of 2. The flat-tailed tortoise (*Pyxis planicauda*) also had a relatively high awareness score (1.56). The Madagascar flying fox had the lowest awareness score (0.03). Introduced species, bats, and bird species all had relatively low scores, while tenrecs had moderate scores (Table 1).

Based on the general linear regression model, we observed that a one-unit increase in protection status was associated with a significant increase in the odds of consumption (Table 4), meaning that as species moved towards the legal side of the protection status spectrum, respondents were 50.8% more likely to consume it. On the other hand, protection status had no significant effect on hunting. We also explored whether awareness of conservation status affected behaviors more than protection status alone, but neither model detected a significant association.

DISCUSSION

This study explored how Malagasy belief systems and legal frameworks shape wildlife use decisions, guided by two hypotheses: that cultural prohibitions, such as *fady* and other aversions influence consumption, and that formal hunting laws primarily influence hunting. Our findings partially aligned with these expectations. Cultural dimensions of food prohibitions, particularly *fady*, predict reduced consumption and support the idea that culturally-rooted values influence behavior, supporting our first hypothesis, but challenge assumptions about formal deterrents, as protection status was associated with consumption rather than hunting. These results highlight the nuanced, and sometimes counterintuitive, ways cultural and legal prohibitions shape wildlife use. The gap between legal frameworks and lived practice also underscores the need enforcement strategies that are locally derived.

FREQUENCY AND PATTERNS OF *FADY* ADHERENCE AND ITS INFLUENCE ON WILDLIFE UTILIZATION. Wildlife consumption *fady* are common in the study community, and adherence to these beliefs predicted wildlife consumption, but not hunting. This is likely because individuals adhering to a consumption *fady* can still hunt and sell that species to other consumers. Though our sample was too small to subset *fady* by reason (ancestral vs. health) and test their individual influence on behavior, species-specific patterning in our focus groups offered deeper insights into how these patterns are understood locally.

Fosa and spotted fanaloka were the most common subjects of consumption *fady* by respondents. Across Madagascar, carnivorous hunting behavior and taboos vary (Jones et al. 2007, Golden 2009, Farris et al. 2015, Merson et al. 2019). In our study, no one reported hunting or consuming fosa. This lack of variability in our sample precluded statistical analysis, but community discussions suggest that the high prevalence of *fady* related to fosa does in fact influence the decision to avoid this species. Across Madagascar, underlying perceived similarities to dogs also deter consumption in other regions (Merson et al. 2019). A similar sentiment may apply to fosa in this region, as one individual explained, "*Satria mitovy ny alika, ary ny Malagasy tsy homana alika*" ("Because it's [fosa] similar to dogs, and Malagasy people do not eat dogs"). Carnivorous capture and killing is often driven in part by retaliation for livestock predation (Merson et al. 2019). No respondent in our study cited livestock predation as a reason for hunting, possibly because of lower livestock ownership than in other regions.

Though the spotted fanaloka was the subject of taboo by many, participants did not provide in-depth explanations of *fady* for fanaloka and we lacked sufficient utilization data to explore trends regarding this species.

Although bush pigs are the subject of many consumption-related taboos, roughly a quarter of respondents consumed bush pig during the prior year. While most *fady* species in our study had ancestral origins, those who reported a bush pig *fady* all cited health-based reasonings. Quotes from surveys indicate that these *fady* were proscribed by a local ombiasy (Malagasy traditional healer) and were related to fertility (Appendix B). For example, one interviewee explained, "*Nanomboka aho niteraka ny zanako voalohany, tsy neken'ny ombiasy miahy hihinanana lambo intsony,*" ("Ever since the birth of my first child, the ombiasy has not allowed me to eat bush pig"). Some respondents stated that the *fady* applied to everyone, while others said it applied to only women of birthing age. This could possibly explain why hunting and consumption of bush pig was still relatively high among the community despite high reported taboo adherence. Other communities in Madagascar also have taboos or strong aversion against bush pigs (Randrianandrianina et al. 2010), but the emic origins of this *fady* are unclear. Goodman and Raselimanana (2003) observed hesitation to hunt and eat bush pigs in another community near Kirindy Mitea but also could not determine the origin and did not examine the nuances of who can or cannot eat this meat and when. Globally, pigs (both wild and domestic) are one of the most commonly eaten yet tabooed animals (Lobban 1994, OECD no date); this can appear self-contradictory if belief systems are oversimplified. In some regions, hunters have driven bush pigs out, while in other communities bush pigs are a fast-reproducing and potentially sustainable source of protein. Near Kirindy Mitea, however, the bush pig population is abundant and interactive with the domestic pig population, possibly increasing hunting opportunities (Rakotoarivony et al. 2024). Understanding cultural beliefs surrounding bush pig consumption can help inform recommendations for alternative protein sources, reducing the overutilization of more vulnerable species.

While lemur taxa are subjects of *fady* less frequently than other species, participants frequently cited inedibility as a reason to avoid lemur meat, especially that of the pale fork-marked lemur. Examples of lemur-specific consumption *fady* have been recorded across the island (Appendix A), especially for larger-bodied lemurs such as sifakas (*Propithecus* spp.). Regardless, lemur aversions, including *fady*, are less common here than in other regions (Jones et al. 2007, Randrianandrianina et al. 2010, Jenkins et al. 2011). Fork-marked lemurs' perceived inedibility is consistent with findings across many, but not all, regions of Madagascar, where these lemurs are rarely eaten because of their bitter flavor and low densities (Borgerson et al. 2022). In a key informant interview, one hunter explained that he only captures one individual per group of lemurs to prevent killing all reproductive females. This *fady*, a long-standing ancestral rule, indicates conservation ethics in its origin. Other hunters similarly explained that they attempt not to hunt any pregnant females, mothers, or babies. Such *fady* that stem from conservation concerns are relatively rare, both in our study community and on the island more broadly. Across Madagascar, *fady* that can be attributed to conservation concerns represent less than 1% of observed beliefs (Golden and Comaroff 2015b).

Unlike much of Eastern Madagascar, where the greater hedgehog tenrec (*Setifer setosus*) is commonly subject to consumption *fady* (Golden and Comaroff 2015a,b), this study village does not observe this *fady*. In areas with high *fady* prevalence, there is also a significant occurrence of zoonotic transfer of bubonic plague, with many attributing the persistence of the disease to the consumption of hedgehog tenrecs. As a result, local stories recount ancestors falling severely ill after eating hedgehog tenrecs, sometimes dying (Golden and Comaroff 2015b). If instances of plague are less common near Kirindy Mitea National Park, it may explain the relatively lower rates of health-related prohibitions against hedgehog tenrec consumption. Future research might benefit from combining community-narratives with epidemiological data to better understand health-related taboos.

FREQUENCY AND PATTERNS OF PERCEIVED INEDIBILITY AND EFFECTS ON WILDLIFE USE. In the community, perceiving meat as inedible was more common than *fady*, but was unable to predict hunting or consumption (Table 4), possibly reflecting heightened food insecurity across the village. Future work, as discussed below, should further investigate conditions in which people eat foods seen as inedible. Because only six individuals cited dislike of a wild animal, we could not perform any tests to verify how dislike predicts wildlife use decisions.

While insectivorous bats were frequently perceived as inedible, most considered the frugivorous Madagascar flying fox acceptable to eat. Overall, few respondents hunted or consumed either bat taxa; however, it was observed that children in our study village often hunted small insectivorous bats for fun but did not consume them. Across Madagascar, while insectivorous bat consumption is low, frugivorous bats are commonly hunted, eaten, and traded taxa (Jenkins and Racey 2008, Reuter 2015). Future studies should explore how communities conceptualize each subgroup, how beliefs vary between them, why these beliefs persist, and how they influence daily decisions. In regions, various bat species are subjects of *fady*, but the conservation relevance of the beliefs remains unclear (Randrianandrianina et al. 2010, Teixeira Rocha 2018). Teixeira Rocha (2018) identified a community-level *fady* arising from ancestral prohibitions due to insectivorous bats' morphological similarity to rodents, but we found no evidence of a similar origin in our study community.

Fady significantly influenced the odds of an individual consuming an animal, but perceiving the species as inedible did not (Table 4). Globally and throughout time, people have eaten foods perceived as inedible or distasteful during times of nutritional duress and famine (Kamp 2019, Winchcombe 2023), and in Africa particularly, this phenomenon may be exacerbated as a byproduct of conditions created by colonization (Goody and Goody 1995, Minnis 2021). Under dire circumstances, the need for sustenance can often outweigh social or moral prohibitions, even if they were once internalized. While there is little research on this in Madagascar, similar effects may be present in our study community, where most households (94.2%) in our study village experience some level of food insecurity, with almost half (49.4%) relying on less preferred or cheaper food items (Thompson et al. 2023). The heightened need for food likely explains why perceived inedibility does not predict hunting or consumption. Quantitative studies exploring the relationship between food insecurity and consuming "inedible" foods can provide further insights.

CONSERVATION AWARENESS AND EFFECTS ON WILDLIFE UTILIZATION. Protection status did appear to influence consumption (and not hunting), but increased knowledge of laws did not influence the odds of either wildlife use decisions. Although Malagasy law (Ordonnance n°60-128) explicitly prohibits hunting and does not prohibit consumption, our results suggest that legal status only influences whether or not someone consumes wildlife. One explanation for these convoluted results is that our constructed score may not have fully captured respondents' knowledge of conservation laws. Laws cannot be meaningfully prohibitive if individuals are unaware of them, so these convoluted results might indicate that our constructed score may not have fully captured knowledge of these laws. For most species we studied, knowledge of conservation law, quantitatively evaluated by survey responses, was low, similar to observations from other sites within Madagascar (Keane et al. 2011). However, simply being aware of the laws does not correspond to adherence. Another possible explanation for the lack of association is that our constructed conservation knowledge score may have inadequately captured true understanding of the law. Because we ascribed points in only a few categories, based on partial or full recall and without assessing its interpretation, our score may have failed to capture respondents' full understanding of the law. Future studies should thoughtfully create a way to assess how both awareness and attitude inform wildlife, such as models designed to more completely measure individuals' knowledge of conservation laws, environmental issues, and sentiments towards them (Al Amin et al. 2021).

EMIC PROHIBITIONS AND CONSERVATION PROTECTION. In our study village, emic prohibitions (*fady*, perceived inedibility) overlap with conservation aims for species in some instances but not others. While taboo predicts species consumption, other aversions do not influence behavior in any other way, highlighting the existing yet perhaps overstated protection emic prohibitions can offer. Our study shows that while emic proscriptions can influence behaviors, their influence is more nuanced and variable than many conservationists claim it to be for three main reasons. First, Madagascar's cultural and ecological diversity leads to significant variation in responses to social prohibitions. *Fady*, often specific to single communities, families, or individuals, is challenging to generalize. *Fady* are deeply personal and often passed down through family oral traditions unique to specific households or villages. For example, this study identified *fady* that overlapped with conservation priorities for vulnerable species, but were specific only to an individual household (Appendix A, *Pyxis planicauda*). As such, conservation programs and policies cannot rely on generalized assumptions about cultural beliefs may result in externally imposed policies that misunderstand or are not aligned with indigenous systems. Second, discussions of indigenous belief systems within poverty and food security contexts are also important to better understand their effects on behavior. Economic and nutritional pressures may force people to seek nutrition in ways against their beliefs or broader social preferences, highlighting the elasticity of these norms under duress. Madagascar is the fifth most food-insecure country in the world (The Economist Intelligence Unit 2024), with 80.7% of Malagasy individuals experiencing multidimensional poverty (World Bank Group 2023). In our study village, almost all households faced multidimensional poverty (Romanello et al. 2023). Thirdly, and though outside the scope of this

study, internal migration within Madagascar has been documented to decrease the regional-level prevalence of certain *fady* (Jenkins et al. 2011, Golden and Comaroff 2015a.). Future studies may want to include stresses like food and income insecurity in addition to individual demographic factors and settlement patterns in their exploration of belief systems.

CONCLUSION

Cultural and legal prohibitions have become increasingly a central topic of conservation narratives, particularly for their roles in shaping human-environmental relations. This study explored how cultural prohibitions, particularly *fady*, and formal conservation laws influence wildlife consumption and hunting behaviors in a community adjacent to Kirindy Mitea National Park. The findings suggest that while cultural prohibitions, especially ancestral and health-based taboos, offer some reduction on species use, taboos were highly individual and not broadly shared, limiting their reliability as conservation tools. We found that *fady* significantly decreased the likelihood of consuming wildlife but had no effect on hunting (supporting hypothesis 1). Legal protection status increased the odds of consumption but not hunting (partially supporting hypothesis 2), likely because the respondents' knowledge of hunting laws was uneven and did not predict their behavior. These findings highlight that while cultural and legal prohibitions influence wildlife use behaviors, and cannot be assumed to produce predictable outcomes.

Conservation efforts must avoid assuming either traditional beliefs or formal rules will yield predictable outcomes. Instead, policies should be rooted in how people actually navigate wildlife use decisions-making under current conditions, including migration, and limited conservation education and food insecurity. As our data has shown, even traditionally deeply held beliefs may bend under pressure, and even well-written laws may be insufficient in the absence of knowledge or legitimacy.

Our study also underscores the need for conservation research and policies to go beyond quantitative metrics, and center community narratives, lived experiences and cultural nuances of indigenous communities. Sustainable conservation will require co-created approaches that will require culturally grounded, informed, and integrated experiences of rural communities. Adaptive and collaborative conservation frameworks should reflect how people actually navigate environmental choices and respond to current challenges, and honor the ways people manage amid uncertainty and change.

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ty and a commitment to ethical, collaborative engagement that respects Malagasy knowledge. This research was funded through grants and fellowships secured by Dr. Thompson, including the Safina Center's Kalpana Chawla Launchpad Fellowship, the Lemur Conservation Action Fund, Primate Conservation Inc., and the Interdepartmental Doctoral Program in Anthropological Sciences (IDPAS) at Stony Brook University.

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Distribution and habitat use by the eastern woolly lemur, *Avahi laniger* (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar

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ABSTRACT

Lemurs are one of the key species for conservation in Madagascar. While much research has focused on diurnal lemurs, nocturnal species such as the eastern woolly lemur (*Avahi laniger*) remain understudied. To address this gap, we conducted a population and habitat study of *A. laniger* in the Ambohidray Protected Area (PA) of, in two forest zones: (i) core area, interior and (ii) buffer zone outside PA. Vegetation structure was assessed using 50 m × 2 m standard botanical plots. Six diurnal and nocturnal observations were conducted along ~1 km transects. The distance sampling method, specifically the Conventional Distance Sampling (CDS) approach, was used during nighttime observations to assess population density, which resulted in a total sampling effort of 38.7 km. To model how habitat variables, as well as distance, influence lemur detection probability, we use the Multiple Covariate Distance Sampling (MCDS) method. We observed 58 individuals and estimated a population density of 63 individuals/km² with our best MCDS fit model. Our model suggests preference for habitats with small crown diameter and semi-open canopy cover. Encounter rates were higher in the buffer zone (2.26 individuals/km) than in the core zone (1.03 individuals/km). *A. laniger* was detected in trees with a diameter at breast height (DBH) of 11–20 cm, a height of 9–16 m, and relatively small crowns. Vegetation structure, including DBH, tree height and plant diversity differed between zones. These findings suggest *A. laniger*'s adaptation is shaped by more than habitat structure, and that Ambohidray PA serves as a vital refuge for the species.

RÉSUMÉ

Les lémuriens jouent un rôle crucial dans les efforts de conservation à Madagascar. Cependant, les connaissances sur les lémuriens nocturnes, tels que *Avahi laniger*, restent limitées. Pour combler cette lacune, une étude écologique de cette espèce a été menée dans l'Aire Protégée d'Ambohidray. Cette étude s'est concentrée sur deux zones distinctes : le noyau dur et la zone tampon de l'aire protégée. La végétation a été analysée en établissant des parcelles standard de 50 m x 2 m dans les zones étudiées. Des observations directes diurnes et nocturnes le long de transects ont été réalisées. La méthode d'échantillonnage par distance (*distance sampling*), en particulier l'approche CDS (*Conventional Distance Sampling*), a été utilisée lors des observations nocturnes pour évaluer la densité de la population. La méthode MCDS (*Multiple Covariate Distance Sampling*) a été utilisée afin d'évaluer l'influence des variables de l'habitat ainsi que la distance sur les taux de rencontre afin d'améliorer la précision de l'estimation de la densité et d'évaluer son influence sur les taux de rencontre. Une densité de population de 63 individus/km² a été estimée à partir du nombre d'observation (n = 58) en utilisant le modèle le mieux ajusté. La visualisation graphique de la fonction de détection indique que l'espèce préfère un habitat caractérisé par des arbres avec un faible diamètre de la couronne associé à une couverture de canopée semi-ouverte. *A. laniger* était plus fréquemment rencontré dans la zone tampon (2,26 individus/km) que dans le noyau dur (1,03 individus/km). L'espèce a été le plus souvent observée dans des arbres ayant un diamètre à hauteur de poitrine (DHP) de 11 à 20 cm, une hauteur comprise entre 9 et 16 m, de faibles diamètres de couronne (<5 m) et une canopée semi-ouverte. Des différences dans la structure de la végétation

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(DHP et hauteur maximale des arbres) ainsi que dans les indices de diversité (indice de Shannon = 3,8 vs. 3,3 ; Jaccard = 0,39 ; Sørensen = 0,24 et Bray-Curtis = 0,60) entre les zones ont été constatées. Le noyau dur présentait une diversité spécifique significativement plus élevée que la zone tampon. La hauteur des arbres était significativement plus grande dans le noyau dur tandis que le DHP des arbres y était plus faible. Ces résultats montrent que la Nouvelle Aire Protégée d'Ambohidray constitue un refuge pour *A. laniger* et suggèrent que l'adaptation de cette espèce aux habitats fragmentés est influencée non seulement par la structure de l'habitat, mais aussi par d'autres facteurs écologiques ou anthropiques. En fournissant ces informations, cette étude offre une base importante pour le suivi écologique de cette espèce dans cette aire protégée.

INTRODUCTION

Understanding the population dynamics and basic ecology of species is essential for the implementation of successful practices for their conservation (Courchamp et al. 2015), as well as for effective management of a protected area. The abundance and density measurements of an animal population can indicate species rarity and extinction risk (Purvis et al. 2000). With increasing anthropogenic pressures, such as increased land fragmentation and hunting, establishing population records as well as understanding the associated habitat will measure for the effects and outcomes of conservation strategies in the future (Gerber et al. 2012). Additionally, population viability assessments, including considerations of population size and fragmentation, are essential for evaluating the impact of these pressures on species survival (Frankham et al. 2014).

The Ambohidray PA is a protected area created in response to the Durban Vision ratified by the Malagasy government in September 2003 to triple the national surface area of protected areas. The objective of these PAs are: (i) to conserve all of Madagascar's unique biodiversity, (ii) to conserve the cultural heritage of the Malagasy, and (iii) to maintain ecological services and promote the sustainable use of natural resources for poverty reduction (Andriamalala and Gardner 2010). Ambohidray was officially created on May 5, 2015 (Decree N. 2015-808), and is classified as a Category V "Protected Landscape" according to the IUCN classification. Yet very few studies on the fauna and flora of Ambohidray have been carried out since its inauguration.

Lemurs are an emblematic group of fauna in Madagascar (Durbin 1999). However, given the fact that lemurs are tightly linked with their natural habitat (Eppley et al. 2020); they are very sensitive to fragmentation, hunting, and human disturbances (Rakotondravony and Rabenandrasana 2011, Hending et al. 2024). Recent anthropogenic activities such as deforestation for agriculture or gold mining has reduced forest cover by 40%, with an 80% reduction in Madagascar's central highlands forest between 1950–2000 (Harper et al. 2007). With these increased threats to lemur habitat, lemurs are among the key animals of conservation concern in Madagascar. Approximately 98% of lemur species are listed under an IUCN (2020) category of threat, making their conservation a global concern.

Despite the numerous studies on lemurs, the nocturnal species such as the eastern woolly lemur (*Avahi laniger*) are less studied, which is considered a neglected group of primates (Joly 2011). *Avahi* species are the only nocturnal lemur species belonging to the family Indridae while *A. laniger* is native to the nor-

thern half of the Malagasy eastern humid forests (Mittermeier et al. 2023). *A. laniger* typically lives in monogamous family groups that maintain long-lasting bonds (Thalman 2006). With a home range covering an area of one to two hectares (Ganzhorn et al. 1985), *A. laniger* can be sensitive to habitat fragmentation. However, studies suggest that *A. laniger* can tolerate some degree of forest fragmentation, though the extent of this tolerance remains unclear (Lehman et al. 2006, Rakotondratsimba et al. 2013). This ecological flexibility makes *A. laniger* a useful model for understanding how lemur species may respond to different levels of anthropogenic disturbance. Although primarily folivorous, *A. laniger* occasionally consumes fruits (Mittermeier et al. 2023), contributing modestly to seed dispersal and forest regeneration. Additionally, *A. laniger* serves as prey for native predators such as the fosa (*Cryptoprocta ferox*, Norsia & Borgognini-Tarli 2008) and nocturnal birds of prey (*Accipiter henstii*, Karpanty 2006), playing a vital role in sustaining the forest food web. Through population density surveillance, the threat status of *A. laniger* on the IUCN Red List was elevated from *Least Concern* (Rakotondratsimba et al. 2013) to *Vulnerable* in July 2013 (Schwitzer et al. 2013). This change in threat status suggests that the population dynamics of *A. laniger* are shifting. This species like all in the woolly lemur genus, has never been kept in captivity with any success (Mittermeier et al. 2023). Therefore, documenting the ecology and distribution of *A. laniger* is essential not only to guide future conservation actions and inform management strategies in the region but also to fill gap in scientific understanding.

This study focusses on the population of *Avahi laniger* within the Ambohidray PA in central eastern Madagascar. In this study, we focus on two key zones within the Ambohidray PA: the core and buffer zones. The core zone is strictly protected with minimal human disturbance, while the buffer zone allows certain economic activities, resulting in a higher level of anthropogenic pressure. These zones provide a valuable comparison for assessing the population and ecological dynamics of *A. laniger* under different disturbance regimes. The main objectives were to provide knowledge on the current population and ecological associations of *A. laniger* to help establish conservation policy for land managers and serve as a reference for future ecological monitoring. Specifically, we aimed to: (i) estimate the population density of *A. laniger* in the Ambohidray PA by incorporating habitat variables as covariates to improve the accuracy of the density model; (ii) assess patterns of spatial distribution of the species between the core and buffer zones; (iii) identify key tree species and structural characteristics (DBH, crown diameter, height, canopy cover) associated with *A. laniger* presence; and (iv) assess differences in habitat characteristics between the core and the buffer zone of the PA.

METHODS

FIELD METHODS. Study location. The study took place in the southern part of the Ambohidray PA in Central-Eastern Madagascar (E048°17' to 048°19', S18°34' to 18°37'). The Ambohidray PA has an IUCN conservation status of category V—a Protected Landscape—and is jointly managed by the Plant Biology and Ecology Department of the Faculty of Science (Mention Biologie et Écologie Végétales, MBEV), University of Antananarivo and the local community of Ambohidray referred as VOI Miray (*Vondron'olona Ifotony*, meaning "local community"). The Ambohidray PA is located between Moramanga and Ambatondrazaka and acces-

sible 40 km north of Moramanga by following the national road 44 (Figure 1). The PA is made up of several forest blocks with a total area of 1,241 ha and a total perimeter of 22.15 km. The eastern part consists of continuous forest, whereas the central, northern, and western are fragmented, occupied by cultivated areas, rice paddies and degraded areas. The Ambohidray forest is classified as a tropical, hot, and humid environment with annual precipitation of approximately 1,681 mm. The average annual temperature is 18°C, with seasonal variations (wet season: October to April; Tadross et al. 2008). This complex evergreen forest is rich in tree and shrub species.

Study design. The Ambohidray PA is divided into four zones, with boundaries proposed by the managing organization, MBEV at the time of the PA's creation: core hard zone (here after as core zone), buffer zone, ecotourism zone, and peripheral zone (Figure 2). This zonation was applied during our study. This study focuses on the differences between the core and buffer zones, representing two areas experiencing different anthropogenic disturbance pressure (core = lower, buffer = higher). The core zone is strictly protected, and biodiversity conservation is a priority. The buffer zone is an area where various economic activities are permitted but regulated to ensure better conservation of biodiversity and the sustainability of its use. This distinction is based on the official zoning of the protected area, which designates the core zone as strictly protected, prioritizing biodiversity conservation, and the buffer zone as a regulated area where certain economic activities are allowed to promote sustainable use of natural resources (CO-AP 2015, 2017). In addition to this zoning framework, our field observations confirmed this pattern. We recorded significantly more signs of human activity in the buffer zone, including rice fields, *Eucalyptus* plantations, and degraded areas, compared to the core zone. By comparing these zones, this study aims to assess the species' response to different environmental conditions and inform conservation strategies for the sustainable management of Ambohidray PA. We conducted this research in these locations for this study under permit number N. 087/21/MEDD/SG/DGGE/DAPRNE/SCBE.Re.

In each zone type, transects of approximately 1 km in length (Meyler et al. 2012) were installed following a north-south orientation. Every 50 m interval of the transect line was marked by a colored ribbon to facilitate their identification and orientation during observations. Each transect line was spaced at least 200 m apart (Meyler et al. 2012; Figure 2). In total, 13 transects were established, with eight transects in the core zone (453 ha) and five transects in the buffer zone (408.5 ha). Transects were planned based on field visits to assess forest continuity and accessibility and were finalized using QGIS, ensuring a minimum spacing of 200 m between them. Transect lines were established at least 24 hours prior to the first lemur observation to avoid any disturbances to the animals. The study took place from 26 June 2021 through 6 September 2021 during the dry season for the central Madagascar region.

LEMUR OBSERVATION. We used "Line-transect-distance sampling" (Buckland 2001, Meyler et al. 2012) to estimate the density of the *Avahi laniger* population across Ambohidray PA. This method involves the direct observation of lemurs along transect lines while considering the perpendicular distance between the animal and transect line. Over the course of our study, we visited each transect six times, three during the day and three during the night. For the density estimation, we used only the nighttime observation when *A. laniger* was active, which resulted in a total sampling effort of 38.7 km. Both nighttime and daytime observations are used to characterize the habitat preference of the species. Daytime observations took place either in the morning between 0730–1030 or in the afternoon between 1430–1730 and nighttime observations began around 1830. Lemur eyeshine was first detected using headlamps, followed by the use of a more powerful light to confirm species identity. Transect observations were conducted by a team of three people who walked each transect line at a slow pace of ~ 0.5 km/h. Visits to the same transect were separated by at least two days to minimize disturbance of the animal and its habitat (Buckland 2001). For each group of lemurs observed, we recorded the identity of the transect, and GPS

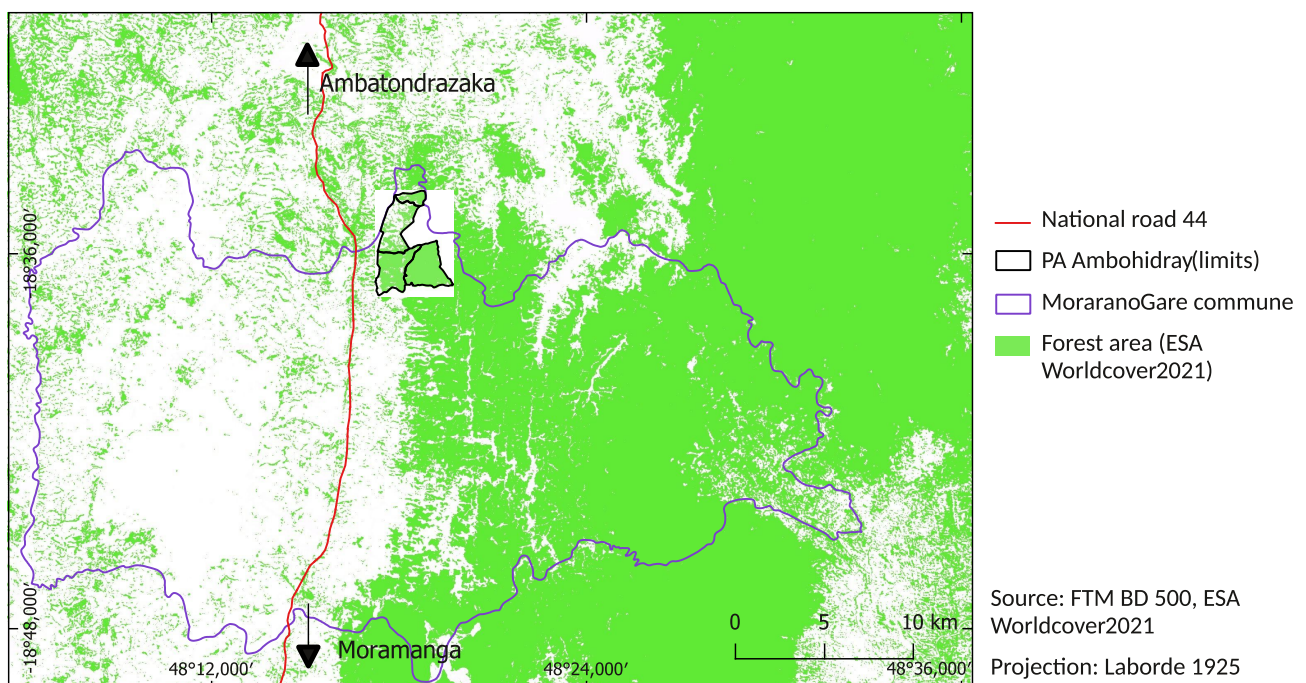


Figure 1. Geographic location of the Ambohidray Protected Area

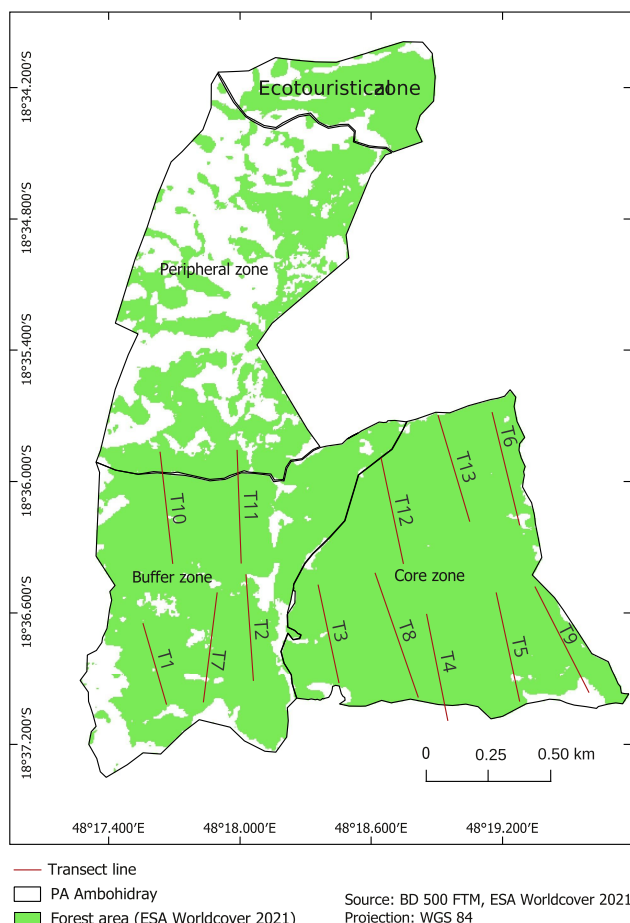


Figure 2. Ambohidray PA with its four management zones and transect lines (red lines labeled TN) implemented in the buffer zone and the core area.

coordinates of the observation point, as well as the species identities, and the estimated perpendicular distance between lemurs and transect line. Additionally, we marked the tree at the observation site for later habitat characterization.

CHARACTERIZATION OF HABITAT. To characterize the vegetation, we established standardized plots that were first divided into 50 m x 2 m “botanical plots” which were further subdivided into 2 m x 2 m subplots to facilitate data collection (Figure S1). The botanical plots were established every 150 m along each transect line, positioned 2 meters to the side of the transect line, to characterize the vegetation of the study area (Figure S2). This plot size and arrangement provide a practical balance between detail and field efficiency, allowing for effective detection of microhabitat variability along ecological gradients. Smaller, repeated plots are often preferred over fewer large plots for more accurate habitat characterization across heterogeneous environments (Dengler 2017).

Within each subplot (2 m x 2 m), vegetative habitat characteristics were documented. Specifically, we recorded the species identity, height, diameter of crown, and diameter at breast height (DBH) for all woody plants with a circumference at chest height (CBH) greater than 10 cm. Height measurements of the woody plants were categorized into seven height classes for analysis: 0–1 m, 1–2 m, 2–4 m, 4–8 m, 8–16 m, 16–32 m, and > 32 m (Daniels et al. 1992). DBH estimates were subsequently grouped into five classes for analysis: 0–2.5 cm, 2.5–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, and > 30 cm (Honoré Djadagna Ahy 2024). Crown diameter was estimated and assigned to one of four width categories: < 5

m, 5–10 m, 10–15 m and > 15 m (Mitchell et al. 1991). These classification systems were selected because they have been applied in tropical forest ecology studies (Boinski et al. 2002, Honoré Djadagna Ahy 2024), allowing for standard assessment of forest structure. Canopy cover was estimated following the protocols of Paletto and Tosi (2009) which consist of taking digital photographs of the canopy. Photos of the canopy were taken in the middle of each subplot with a digital camera (Powershot Sx50). Photos were analyzed with the open-source software Canopydigi developed by Goodenough and Goodenough (2012). This method has demonstrated to provide accurate and repeatable estimates of canopy density (Morales et al. 2016). The photos were converted to monochrome (BMP format) using ReaConverter Lite, and processed in Canopydigi to create “false color” images. Dark pixels representing the canopy were identified, and the software calculated the percentage of canopy cover. Additional details on how the photos were uploaded, transformed, and analyzed can be found in Supplement Text 1. The cover was classified into five groups: open ($\leq 20\%$), relatively open (21–50%), semi-open (51–70%), relatively closed (71–90%), and closed ($> 90\%$). Grouping canopy cover into categories allowed for a clearer ecological interpretation of habitat openness and facilitated comparisons across plots.

We used the same 50 m x 2 m botanical plots for *Avahi laniger* microhabitat characterization. Botanical plots were established at locations where the species was observed during both daytime and nighttime surveys. The tree supporting *A. laniger* was positioned at the center of the plot (Figure S2), and we recorded its species identity, height, crown diameter, and CBH. These plots were used solely for canopy cover estimation, with photos taken following the same methodology described above.

DATA ANALYSIS

Lemur density estimates. To estimate the density of *Avahi laniger* from transect observation, we applied the Conventional Distance Sampling (CDS) method (Buckland 2001), which models the detection probability as a function of the perpendicular distance from the transect line to each *A. laniger* sighting. The CDS method estimates animal density (D , individuals per km²) using the equation:

$$D = \frac{NT}{2(L \cdot ESW)}$$

where NT is the number of detected animals, LT is the total transect length, and ESW is the effective strip width. To implement this method, we used the distance package in R Studio (version 4.1.1) (Miller et al. 2019, R Core Team 2021). Detection functions were modeled using different key functions (e.g., half-normal, uniform, exponential (Miller et al. 2019), and the best model was selected based on the lowest Akaike Information Criterion (AIC) (Akaike 1974). Data were truncated at 10% of the maximum observed distance to eliminate extreme values (Buckland 2001). The ESW was estimated, and model fit was both visually with Q-Q plots and statistically with the Cramér-von Mises test to evaluate how well the fitted detection function matched the observed data (Burnham et al. 2004, Miller et al. 2019). Variance and confidence intervals for density estimates were calculated from the fitted model.

We expanded the previous model to assess how detection probability varied with both distance and additional habitat covariates, including canopy cover, height, DBH and crown distance of the trees. These habitat variables were obtained through microhabitat characterization of *Avahi laniger*. We tested the multiple-covariate distance sampling (MCDS) models by first considering

each variable individually, then combining two variables, and finally testing combinations of three variables (Buckland et al. 2004, Marques et al. 2007). The AIC was again applied to choose the best model, selecting the one with the lowest AIC score. Once the best-fit model was identified, we used it to estimate the population density of *A. laniger*. To understand how changes in the covariates influence detection probabilities, we generated visualizations of the detection functions based on the interaction of habitat variables (Marques et al. 2007).

Lemur distribution within core vs. buffer zone. As the number of observations was insufficient for accurate estimates, the CDS was not applied to compare density estimates or abundance between the core and buffer zones. Minimum of 40 observations was required for reliable effective strip width (ESW) and density estimates (Buckland et al. 2001). Instead, we used encounter rates (the number of individuals observed per kilometer surveyed) to compare the relative distribution of *A. laniger* between the two zones (Murphy et al. 2016). Mean encounter rates were calculated separately for each zone, and statistical comparisons were made using a one-way ANOVA to assess potential differences in lemur distribution across the core and buffer zones.

Habitat characteristic differences within core vs. buffer zones. The data used for this analysis were collected from botanical plots established along each transect in both the core and buffer zones. Based on these data, we first examined potential difference in the plant genera diversity of the two zones by calculating the Shannon diversity (Heusèr, 1998) (i.e., alpha diversity within a site). We additionally applied the Hutcheson t-test to compare the Shannon diversity results between the core and buffer zones. To determine the dissimilarity between the two areas, we evaluated the beta diversity (i.e., between sites) using the Jaccard (1908), Sørensen (1948), and Bray-Curtis (1957) indices. Because some individuals were identified only to the genus level, these indices were calculated based on generic composition, which may underestimate species-level turnover. To examine how the association between habitat variables and the plant genera may vary between core and buffer zones, we used a linear mixed effects models with habitat variables as fixed effects and plant genera or species as a random effects.

RESULTS

AVAHI LANIGER POPULATION DENSITY. We observed 36 groups of *A. laniger* composed of 58 individuals (Core zone = 14 groups – 25 individuals and buffer zone = 22 groups – 33 individuals). Each group refers to a distinct sighting recorded during nocturnal surveys, and the number of individuals was based on direct visual confirmation. Using the CDS method, the best-fit model was the half-normal key function with no adjustment (Figure 3A) yielding an estimated density of 37 groups/km² and 59 individuals/km² for the entire study area (Table 1). When incorporating the habitat covariates with the CDS method (i.e., the MCDS mo-

del), the best-fit model to improve the detection function was a half-normal key function with no adjustments and the addition of crown diameter and canopy cover covariates (Figure 3B). From this best-fit model (Cramer-von Mises: test statistic = 0.08, p-value = 0.6), we obtained a density of 41 groups/km² and 63 individuals/km² (Table 1). Additional model summaries can be found in Table S1. The plot detection function indicates that the encounter rates peak where trees supporting *A. laniger* have a relatively small mean crown diameter (4 m in the dataset) and are associated with a semi-open canopy cover (64%) (Figure 3C). Certain combinations of these two covariates not present in the dataset produced irregular or "non-normal" detection curves. These were excluded from the interpretation, as they likely resulted from the model extrapolating beyond the observed data range.

SPATIAL DISTRIBUTION OF ENCOUNTER RATES IN CORE AND BUFFER ZONES. *Avahi laniger* was observed in all transects except on transect four (T4) in the core zone. Encounter rates varied among transects and differed significantly between zones (Table S2). The species was more frequently encountered in the buffer zone, where the mean encounter rate was higher (2.26 individuals/km) compared to the core zone (1.03 individuals/km) (ANOVA, t-test = 5, p = 0.01).

AVAHI LANIGER HABITAT PREFERENCE. The most common tree species that *A. laniger* were observed in were *Labourdonnaisia laciniata* (vernacular name: *Menahihy*), *Syzygium cuneifolium* (*Rotramena*), *Garcinia chapelieri* (*Fantsikahitra*), *Brexiella cymosa* (*Ranga*), *Syzygium cumini* (*Rotrafotsy*). Tree characteristics that had higher occurrences of *A. laniger* were trees with a DBH of 11–20 cm, max height between 9 and 16 m, little crown diameter < 5 m, and a canopy coverage that is semi-open or relatively open (Table S3).

VEGETATION ANALYSIS. From our vegetation survey of 2,805 tree observations in the core zone, and 1,405 tree observations in the buffer zone, we identified 110 unique plant genera (Table S4, core = 101 unique plant genera, buffer = 94 unique genera). The Shannon diversity was calculated to test the diversity of plant genera within each zone and then applied to the Hutcheson t-test, which found significant differences between plant genera in

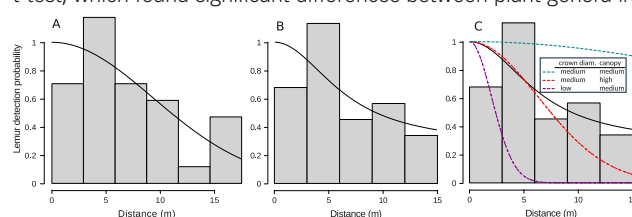


Figure 3. (A) The estimated conventional distance sampling (CDS) detection function for *Avahi laniger* based on the best-fit model. (B) The estimated multiple covariate distance sampling (MCDS) detection function for *A. laniger* based on the best-fit model. (C) Visualization of the detection function based on the interaction between the two habitats covariates (crown diameter and canopy cover).

Table 1. Best-fit detection model without (-) and with covariates for an area of 8.9 km² and covered area of ~ 1 km². (Model types are D = density per km², A = abundance in core zone, E = expected cluster size; the best-fit density estimate for cluster and individual *Avahi laniger* are in bold)

Model	Level	Covariates	Estimate	Se	Coeff variation	Lower & upper CI
D	Cluster	-	37.6	11.1	0.3	20.7 -68.5
A	Cluster	-	336.0	99.2	0.3	184.5 -611.7
D	Individual	-	60.0	15.2	0.3	36.0 -99.9
A	Individual	-	535.5	135.3	0.3	321.7 -891.4
E	NA	-	1.6	0.2	NA	1.2 -1.9
D	Cluster	Canopy cover + crown distance	41.2	14.6	0.4	20.2 -84.0
A	Cluster	Canopy cover + crown distance	367.8	130.4	0.4	180.5 -749.4
D	Individual	Canopy cover + crown distance	63.9	24.1	0.4	30.2 -135.4
A	Individual	Canopy cover + crown distance	570.5	215.1	0.4	269.5 -1208.1
E	NA	Canopy cover + crown distance	1.6	0.2	NA	1.1 - 2.0

the core and buffer zone (t-statistic = -8.93, df = 535.05, p-value < 0.001). The buffer is less diverse than the core zone (3.3 vs. 3.8, respectively). The dissimilarity metrics (Jaccard = 0.39, Sørensen = 0.24, Bray-Curtis = 0.60) are greater than zero and suggest differences in plant diversity between the core and buffer zones. The linear mixed effects models testing the association of habitat variables by zone (with genus as a random effects) found evidence of differences in plant characteristics between the core and buffer zones. For the fixed effects, tree DBH and maximum height were significantly different between the zones (Table S5). The strongest relationship was for maximum tree height with the core zone having significantly taller trees than the buffer zone (genus fixed effects: estimate = 0.56, se = 0.16, df = 1629.73, t-statistic = 3.51, p-value < 0.001). The next strongest relationship was between tree DBH with the core zone having lower tree DBH than the buffer zone (genus fixed effects: -0.87, se = 0.32, df = 1617.6, t-statistic = -2.75, p-value < 0.01). We did not find significant differences in tree crown distances between zones (Table S5). Similarly, canopy cover percentages showed little variation, with the core area averaging 64.2% and the buffer zone 64.7%, both exhibiting a semi-open canopy.

DISCUSSION

This study provides updated information on the current population status of *Avahi laniger* in the Ambohidray PA, intended to support conservation planning and management decisions. Our study found an estimated density of 41 groups/km² and 63 individuals/km² with our best-fit MCDS model. The result of the multiple covariates distance sampling allows us to know the potential habitat preference of *A. laniger*, which is a combination of small crown diameter and semi-open canopy cover. Notably, in our study, the occurrence of *A. laniger* was higher in the buffer zone compared to the core zone.

When compared to other regions of Madagascar, the estimated density of 63 individuals/km² in the Ambohidray PA is relatively high. Previous studies that employed similar methods to estimate *Avahi laniger* populations have reported densities ranging from 13 to 41 individuals/km² (Rakotondratsimba et al. 2013, Sabin 2013, Rakotomalala et al. 2017). However, these studies were conducted in forests across Madagascar, each subject to varying levels of anthropogenic pressures. In general, *A. laniger* appears to reach higher population densities in fragmented or disturbed forests compared to large, intact forest areas. For example, in the Ankadivory Classified Forest (Tsinjoarivo-Ambatolampy), a relatively small forest fragment of less than 20 ha and under significant anthropogenic pressure, Rakotomalala and collaborators (2017) reported a density of 31.98 ± 9.05 individuals/km². Similarly, in the VOI forest of Ambodiriana Manompana, a predominantly primary forest covering 2.25 km², Sabin (2013) estimated a density of 41 individuals/km². In contrast, Rakotondratsimba and collaborators (2013) recorded a much lower density of only 13 individuals/km² in the extensive (~8,000 ha) and largely undisturbed humid evergreen forest of Torotorofotsy. An exception to this trend is found in the Ambatovy–Analamay forest, where extremely high densities of 235 and 172 individuals/km² were recorded in plots with natural forest in good condition, and 140 individuals/km² in a degraded plot (Ralison 2010). Although large-scale mining was planned for the area, extraction activities had not yet resumed at the time of the inventory; however, road construction linked to the project had already begun, providing access to the forest plots.

This area is where a large scale mining activities have been occurring. These findings suggest that *A. laniger* may reach higher densities in disturbed or fragmented forests. However, this apparent pattern may be influenced by methodological and ecological biases (Buckland 2001) related to forest size, disturbance level, and transect coverage. In smaller forests like Ambohidray, transects may cover a larger proportion of the total area, increasing the likelihood of detection and potentially inflating density estimates. Furthermore, habitat fragmentation can concentrate individuals in the remaining patches of suitable habitat (Irwin et al. 2010), leading to artificially high local densities that reflect habitat limitation rather than true preference.

In our study, *Avahi laniger* was encountered more frequently in the buffer zone, although it was also present in the core. The lack of strong negative response to forest degradation resembles the pattern observed in forest remnants of north-eastern Madagascar (Schübler et al. 2018). This suggests that *A. laniger* may be more sensitive to habitat area than to degradation level. In contrast, on the Masoala Peninsula, *Avahi mooreorum* showed significant differences in abundance across distinct forest types (Sawyer et al. 2017). Its specialized locomotion and dietary requirements may make it more vulnerable to habitat disturbance. However, it is important to note that the comparison in that study was between clearly different forest types, while our study focused on varying levels of disturbance within a single forest type. The results of these studies suggest that *A. laniger* can thrive in general fragmented habitats, and similar patterns were observed in the Ambohidray PA, where the species displayed relatively high densities and a preference for the buffer zone. However, the sensitivity of population density estimates to factors such as fragmentation, forest type, and sampling methods warrants further investigation.

We were able to detect higher occurrences of *Avahi laniger* individuals in trees that had a DBH of 11–20 cm, max tree height between 9 and 16 m, small crown diameters, and a canopy coverage that is semi-open or relatively open. The woody plants most commonly used by *A. laniger* in our observations—such as *Syzygium* spp. (*rotarafotsy* and *rotramena*), *Garcinia chapelierii* (*fatsika-hitra*), and *Labourdonnaisia laciniata* (*menahihy*)—have also been reported as components of its diet (Harcourt 1991, Ganzhorn et al. 1985, Faulkner and Lehman 2006). Previous studies have documented that *A. laniger* typically rests on vertical tree trunks supported by thin branches at heights ranging from 5 to 10 m (Harcourt 1991) and more generally at heights ranging from 2 to 10 m (Ganzhorn et al. 1985). Furthermore, Ganzhorn (1989) reported that trees where *A. laniger* were found in the National Park Analamazoatra had a mean DBH of 15.62 cm, a mean height of 9.17 m, and a mean crown diameter of 3.11 m. Interestingly, the trees used by *A. laniger* in Ambohidray PA do not appear to have distinct characteristics compared to those in other localities. This suggests that the species may demonstrate flexibility in its habitat use, potentially adapting to various types of trees across different regions.

We were able to detect a significant difference in plant diversity between core and buffer zones (3.8 vs. 3.3, respectively). Beta diversity metrics also indicated differences between the zones (Bray-Curtis = 0.60, Jaccard = 0.39, Sørensen = 0.24), but these differences varied in magnitude across the indices. The linear mixed-effects models indicated significant differences in tree characteristics between zones, with taller trees in the core zone and

trees with larger DBH in the buffer zone. The canopy cover percentages were nearly identical between the zones, with both exhibiting a semi-open canopy. No significant differences were observed in tree crown diameter between the zones. Although the core zone has taller trees overall, particularly within the preferred height range of *Avahi laniger* (11–20 m), the species shows a preference for the buffer zone. This preference may seem surprising, as the core zone contains more trees of the preferred height range for this species. The density and distribution of lemurs are influenced by factors beyond vegetation characteristics, including food availability, competition, predation pressure, and habitat disturbance. The presence of the species in both habitat types with higher encounter rates in the buffer zone despite the significant difference in plant diversity, may indicate that the species can tolerate variation in plant diversity between habitats (Norscia et al. 2006). This magnitude of difference of plant diversity may not be large enough also to be spatial patterns of the species. Additionally, higher light levels and limited temperature variation in the buffer zone likely improve leaf quality (Ganzhorn 1995), making it a more valuable food source for folivores. Coexisting species like *A. laniger* and *Indri indri* exhibit different activity patterns, allowing them to share similar habitats (Ganzhorn 1989), while competition with nocturnal lemurs such as *Lepilemur* spp. for food quality and habitat selection (Ganzhorn 1993, Thalmann 2001, Ralison 2010) may push *A. laniger* to fragmented habitats near edges. Although habitat fragmentation happen in the buffer zone, *A. laniger* may occasionally use these areas to reduce competition for resources making the buffer zone a refuge for the species.

How land is managed can be informed by ecological studies that focus on key species important to the cultural and ecological characteristics of Madagascar. Our findings serve as a reference for future ecological monitoring as anthropogenic pressures increase throughout Madagascar's landscape, particularly affecting species such as the *Avahi laniger*. Variation in abundance across the species' range is likely linked to habitat characteristics, such as canopy cover and tree height, which influence the species' fitness responses. Despite these differences in tree characteristics, they do not seem to affect *A. laniger*'s occurrence, suggesting the species can tolerate a range of tree characteristics. Although there are differences in plant diversity between the two zones, these metrics may change over time due to forest degradation or conservation efforts, which could influence habitat suitability for *A. laniger*. Continuous monitoring is essential to understand how these dynamics impact the species' distribution over the long term.

Although our study was able to achieve some of the objectives we sought to address, there is additional methods that could fill remaining knowledge gaps. An important aspect of an ecological study is understanding how a species can respond to seasonal changes which can alter their food preferences and behavior. Because of logistical constraints, our study took place only during the dry season. Many lemur species, including *Avahi laniger* are active throughout the year (Harcourt 1991). However extending the study into the rain season, when more food is available in Madagascar's rainforest (Campera et al. 2021) would allow for a more comprehensive understanding of *A. laniger* population dynamics. As the transition from *Least Concern* to *Vulnerable* on the IUCN Red List suggests, this species is experiencing population-level threats that may be the result of habitat change from anthropogenic pressures such as conversion of land to agriculture or mining

activities. A more nuanced study that takes into consideration the type and magnitude of anthropogenic stress on lemur habitat and populations may be more appropriate to inform policy on land management and conservation. Also, *A. laniger* does not represent all lemur species in the Ambohidray PA, and other considerations beyond our results should be incorporated into non-*A. laniger* ecological studies such as those focused on *Propithecus diadema*, *Indri indri*, *Hapalemur griseus*, *Eulemur fulvus*, *Lepilemur mustelinus*, *Cheirogaleus* spp., and *Microcebus* spp.

IMPLICATIONS FOR CONSERVATION MANAGEMENT. The higher density of *Avahi laniger* in the buffer zone compared to the core zone suggests that this area could play a critical role in species conservation. Given that the buffer zone is subject to anthropogenic pressures, such as human disturbance and habitat fragmentation, effective management strategies could focus on enhancing the ecological conditions within these zones. For example, management efforts could prioritize reducing disturbances in the buffer zone to maintain its role as a refuge for *A. laniger*. Moreover, the distinct tree characteristics observed in both zones— such as tree height and DBH— indicate the importance of maintaining diverse tree structures for the species' habitat. Forest restoration initiatives that focus on promoting a variety of tree sizes and canopy cover in degraded areas may improve the suitability of the landscape for *A. laniger*, especially in the buffer zone where the species seems to thrive. Finally, continuous monitoring of the species' distribution and habitat use in both the core and buffer zones is crucial for assessing the effectiveness of conservation measures over time. By tracking how changes in vegetation structure, fragmentation, and human activity impact the species, management practices can be adapted to ensure *A. laniger*'s persistence in the Ambohidray NA.

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