Received: 13 February 2023 | Revised: 8 May 2023 | Accepted: 15 May 2023

DOI: 10.1111/conl.12960

Conservation Letters
A journal of the Society for Conservation Biology
Open Access
WILEY

LETTER

Drivers and sustainability of bird hunting in Madagascar

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Funding information
Forschungskredit of University of Zurich, Grant/Award Number: FK-21-128; International Union for the Conservation of Nature, Grant/Award Number: IUCN-SOS 2018A-117; Margot Marsh Biodiversity Foundation, Grant/Award Number: 100007134; National Science Foundation, Grant/Award Number: 1513638; National Geographic Society, Grant/Award Numbers: 55616C-20, C021–17, C280–14; Primate Action Fund

Abstract

Bird conservation depends on robust data on the densities of and threats to each species, and an understanding of the choices and incentives of bird hunters. This first comprehensive study of bird hunting and its effects in Madagascar uses 8 years of data on 87 bird species to determine bird densities and hunting pressure, incentives, choices, methods, spatial variation, and sustainability on the Masoala Peninsula of Madagascar. We find that bird hunting is common, affecting human wellbeing and, for some species, long-term population viability. Hunters caught more abundant species of lower trophic levels and consumers preferred the flavor of abundant granivores and nectarivores, while they disliked carnivores, scavengers, and species with common cultural proscriptions. Wealth increased species selectivity among consumers, whereas food insecurity increased hunting pressure overall. Projected and documented declines in at least three species are concerning, qualifying at least two for increased IUCN threatened species categories. We provide novel, data-driven assessments of hunting's threat to Madagascar's birds, identify key species of concern, and suggest both species- and consumer-specific conservation actions.

KEYWORDS

Agapornis canus, bushmeat, conservation, *Coracopsis*, density, Masoala National Park, population viability analysis, *Treron australis*

1 | INTRODUCTION

While billions of people rely on wild meat (Ingram et al., 2021), overexploitation remains the least studied driver of biodiversity loss (Mazor et al., 2018). In tropical regions, as much as two-thirds of meat comes from forest animals (Booth et al., 2021), and 39% of rural households in these regions hunt to feed their families (Nielsen et al., 2018). The lack of sufficient alternatives to wild meat in rural regions and high demand in urban centers can lead to overexploitation (Booth et al., 2021; Wright et al., 2022), threatening both provisioning ecosystem services and species viability (IPBES, 2022; IUCN, 2022).

While the need to prevent overexploitation has led to rigorous studies on the drivers and sustainability of mammal hunting (Bogoni et al., 2022; Gallego-Zamoran et al., 2020), studies on bird hunting and its effects on human and avian communities are comparatively limited. One in 10 of the world's bird species are threatened with extinction, and more birds have recently gone extinct than mammals, reptiles, and amphibians combined (IUCN, 2022). Unsustainable hunting has contributed to nearly half of these extinctions (45%) and remains the second greatest threat to the future population viability of birds (IUCN, 2022). While tropical bird abundance has declined by 58% in hunted areas (Benítez-López et al., 2017), extremely few rigorous assessments of bird hunting pressure and its effects on the densities of bird species are available to inform IUCN assessments.

Madagascar has one of the highest levels of bird endemism in the world, and the highest in Africa (IUCN, 2022). Nonetheless, more than half (54.3%) of its bird species are declining, and a quarter (25.2%) is threatened with extinction (the status of an additional 13.1% are unknown; IUCN, 2022). While there has been extensive recent research on the hunting of Madagascar's primates (e.g., Borgerson et al., 2022), comparatively little is known about the hunting of its birds. This is unexpected, given that the earliest evidence of human presence, ~10,500 years ago, comes from bird hunting (Hansford et al., 2018), and birds continue to be a highly valued natural resource (Gardner & Davies, 2014; Randriamahefasoa, 2001; Randriamiharisoa et al., 2015; Robinson et al., 2022). Birds can be traded long distances in Madagascar for food and as pets (Randrianandrianina et al., 2010; Reuter et al., 2017, 2019), and birds comprise one-third to more than half of a hunter's annual catch (in number; Borgerson et al., 2019; Merson et al., 2019). While conservation assessments and actions depend on accurate data, no thorough quantitative study has focused on bird hunting pressure, its drivers, or its effects on the density or trajectory of bird populations in Madagascar.

Here, we examined drivers and sustainability of bird hunting, using 8 years of data on 87 species from 188 km of transects used to acquire 845,239 bird observations and 1327 household interviews used to acquire 108,814 data points from 3602 annual recalls of 17,683 birds hunted on the Masoala Peninsula of Madagascar. For nearly half of Madagascar's IUCN-assessed avifauna, and two-thirds of its endemic bird species, we (1) quantify bird hunting pressure, drivers, and methods; (2) examine how bird traits and hunters' preferences affect variation in species selection; and (3) estimate the population viability of Madagascar's birds. We then use this information to provide data-driven assessments of hunting's threat to Madagascar's birds and inform actions to address hunting where rates are concerning.

2 | METHODS

2.1 | Quantifying bird hunting pressure, drivers, and methods

To evaluate bird hunting, we used 8 years (2015–2022) of paired surveys of humans and 87 species of birds at the same seventeen sites surrounding Masoala National Park and along two interior trans-park transects. Over 6 years (2015–2021), CB and BJRR interviewed 1327 participant households (164–306 per year) in 5–13 forest-adjacent communities per year. We surveyed all households in small communities, and selected 50+ study households in large communities using a gridded zigzag selection process (Borgerson et al., 2022), choosing an annual recall period because of the high seasonality and saliency of hunting practices (Golden et al., 2013). Institutional Animal Care and Use and Human Subjects Institutional Review Boards (No. 10-0010,0595 University of Massachusetts Amherst; 12–0028,13-1862,15-0002,2230 Harvard University; 18-19-1349,19-055,22-077 Montclair State University) approved all research.

We asked each household if they caught and/or ate any of 87 species during the prior year and proscriptions (hereafter taboos) preventing consumption (Table 1; SM 1, 2). We examined the relative effects of household wealth and food security on both species selectivity (mean *n* species eaten) and overall hunting pressure (mean *n* birds eaten) using Poisson Generalized Linear Models (GLMs). As an indicator of short-term household wealth, we used the total spent on home repair and construction during the prior year (measured 2019–2021; SM 2). As an indicator of food security, we used a Coping Strategies Index (CSI; Care, 2008), which measured the total number of times a household

TABLE 1 Annual hunting pressure, consumer preference for the flavor, and density or abundance of 87 bird species on the Masoala Peninsula, Madagascar (2015–2022).

Species	IUCN status[a]	Hunting pressure (mean ± SD)[b]	Hunting prevalence[c]	Flavor ranking (mean ± SD)	Taboo prevalence	Density[d]/ abundance per hectare (n obs.)
Anseriformes						
e.g., *Anas erythrorhyncha*	LC	0.0008 ± 0.03	0.1%	7 ± 6.29	0.6%	–
Anas melleri	EN	0.002 ± 0.04	0.2%	4.5 ± 3.89	0.7%	–
Dendrocygna viduata	LC	0.04 ± 0.21	3.2%	2.6 ± 1.71	0.6%	0.16 (5)
Columbiformes						
Alectroenas madagascariensis	LC	0.25 ± 1.03	8.9%	12.7 ± 9.83	3.6%	0.22 (31)
Nesoenas picturatus	LC	0.75 ± 2.02	25.1%	6.4 ± 3.81	0.4%	0.22 (127)
Treron australis	LC	0.83 ± 4.31	21.9%	15.7 ± 13.71	2.7%	0.19 (82)
Galliformes						
Coturnix delegorguei	LC	<0.01 ± 0.07	0.0%	67.2 ± 8.85	0.0%	0.23 (25)
Margaroperdix madagascarensis	LC	<0.01 ± 0.03	0.1%	56.1 ± 12.33	50.8%	0.26 (33)
Numida meleagris	LC	1.24 ± 13.03	32.8%	5.1 ± 4.09	0.6%	0.73 (122)
Cuculiformes						
Centropus toulou	LC	<0.01 ± 0.05	0.1%	81.6 ± 2.17	23.0%	0.03 (143)
Coua caerulea	LC	0.03 ± 0.29	1.4%	73.2 ± 16.78	14.9%	0.12 (117)
Coua cristata	LC	0.02 ± 0.2	0.9%	51.5 ± 6.93	3.8%	0.06 (42)
Coua reynaudii	LC	0.03 ± 0.27	1.3%	57.9 ± 11.4	1.8%	0.03 (29)
Coua serriana	LC	0.02 ± 0.2	1.4%	60.6 ± 8.6	2.0%	0.38 (98)
Cuculus rochii	LC	0.01 ± 0.15	0.2%	60 ± 9.17	1.7%	0.01 (17)
Gruiformes						
Dryolimnas cuvieri	LC	0.06 ± 0.33	4.4%	19.3 ± 22.6	2.0%	–
Gallinula chloropus	LC	0.00 ± 0.00	0.0%	33.5 ± 15.55	0.0%	0.41 (75)
Mentocrex kioloides	LC	0.01 ± 0.12	0.7%	50.6 ± 10.31	2.2%	0.12 (3)
Porphyrio alleni	LC	0.03 ± 0.22	1.5%	25.4 ± 18.42	0.9%	–
Porphyrio porphyrio	LC	<0.01 ± 0.04	0.0%	30.5 ± 16.3	1.0%	–
Sarothrura insularis	LC	0.00 ± 0.00	0.0%	32.1 ± 12.65	0.9%	0.10 (4)
Zapornia pusilla	LC	0.00 ± 0.00	0.0%	20.1 ± 11.47	1.1%	–
Charadriiformes						
Glareola ocularis	NT	0.00 ± 0.00	0.0%	53.1 ± 10.65	0.0%	0.13 (3)
Rostratula benghalensis	LC	0.003 ± 0.11	0.1%	57.3 ± 14.36	1.2%	0.15 (3)
e.g., *Sterna dougallii*	LC	0.008 ± 0.28	0.2%	36 ± 9.24	1.0%	–
Caprimulgiformes						
Caprimulgus madagascariensis	LC	0.01 ± 0.16	0.8%	57.3 ± 17.09	2.3%	0.07 (18)
Apodiformes						
Apus balstoni, Cypsiurus parvus	LC	0.01 ± 0.34	0.2%	60.5 ± 13.22	0.0%	–
Suliformes						
Anhinga rufa, Microcarbo africanus	LC	<0.01 ± 0.06	0.2%	36.3 ± 15.84, 28.4 ± 11.93	1.7%	–
Pelecaniformes						
Ardea alba	LC	0.02 ± 0.69	0.2%	31.1 ± 16.48	3.2%	–
Ardea cinerea, humbloti, purpurea	LC, EN, LC	0.02 ± 0.47	0.8%	12.9 ± 7.43	1.3%	–
Ardeola idae	EN	0.01 ± 0.09	2.3%	29.3 ± 20.53	6.8%	0.05 (20)

(Continues)

TABLE 1 (Continued)

Species	IUCN status[a]	Hunting pressure (mean ± SD)[b]	Hunting prevalence[c]	Flavor ranking (mean ± SD)	Taboo prevalence	Density[d] / abundance per hectare (n obs.)
Ardeola ralloides	LC	0.02 ± 0.57	0.5%	57 ± 11.71	1.5%	–
Bubulcus ibis	LC	0.02 ± 0.56	0.7%	29.1 ± 12.62	3.0%	0.79 (39)
Egretta ardesiaca	LC	0.03 ± 0.83	0.2%	31.8 ± 15.31	1.4%	0.1 (1)
Lophotibis cristata	NT	0.16 ± 0.54	10.8%	13.8 ± 17.2	3.4%	0.33 (72)
Nycticorax nycticorax	LC	<0.01 ± 0.11	0.2%	35.7 ± 16.3	1.0%	–
Plegadis falcinellus	LC	0.01 ± 0.16	3.0%	64.9 ± 14.4	0.5%	0.04 (2)
Scopus umbretta	LC	0.00 ± 0.00	0.0%	66.4 ± 12.89	2.0%	–
Accipiriformes						
Accipiter francesiae	LC	0.02 ± 0.17	2.3%	73.3 ± 11.15	1.6%	0.04 (63)
Accipiter henstii	VU	0.01 ± 0.08	0.6%	65.9 ± 11.01	1.9%	0.01 (15)
Accipiter madagascariensis	NT	0.01 ± 0.07	0.5%	72.2 ± 11.23	0.0%	0.06 (8)
Buteo brachypterus	LC	<0.01 ± 0.03	0.1%	58.5 ± 10.63	2.0%	0.02 (16)
Eutriorchis astur	EN	<0.01 ± 0.03	0.1%	69.4 ± 16.2	1.1%	0.01 (1)
Polyboroides radiatus	LC	0.04 ± 0.23	2.8%	59.7 ± 13.23	1.6%	–
Strigiformes						
Asio capensis	LC	<0.01 ± 0.04	0.2%	59.8 ± 12.69	1.8%	–
Asio madagascariensis	LC	<0.01 ± 0.04	0.0%	55.2 ± 17.47	0.0%	0.02 (6)
Otus rutilus	LC	0.01 ± 0.17	0.7%	49.3 ± 14.28	1.9%	0.02 (4)
Tyto alba	LC	0.00 ± 0.00	0.0%	83.6 ± 1.17	30.3%	0.03 (1)
Tyto soumagnei	VU	0.00 ± 0.00	0.0%	80.9 ± 12.27	29.7%	–
Leptosomiformes						
Leptosomus discolor	LC	0.01 ± 0.30	0.4%	73.7 ± 20.84	6.9%	0.01 (6)
Coraciiformes						
Brachypteracias leptosomus	VU	0.03 ± 0.84	0.6%	60 ± 10.1	2.6%	0.18 (58)
Corythornis madagascariensis	LC	0.00 ± 0.00	0.0%	22.4 ± 6.11	8.5%	0.07 (21)
Corythornis vintsioides	LC	<0.01 ± 0.09	0.2%	20.8 ± 10.91	8.6%	0.21 (48)
Eurystomus glaucurus	LC	0.01 ± 0.11	0.5%	51 ± 11.03	2.5%	0.07 (21)
Geobiastes squamiger	VU	0.03 ± 0.84	0.6%	48.4 ± 11.34	2.6%	0.18 (58)
Falconiformes						
Falco newtoni	LC	<0.01 ± 0.05	0.2%	43.1 ± 13.89	1.5%	0.03 (21)
Psittaciformes						
Agapornis canus [e]	LC	1.32 ± 7	5.9%	40.3 ± 22.09	0.2%	0.25 (26)
Coracopsis nigra [e]	LC	1.02 ± 1.98	28.8%	22.6 ± 7.83	0.5%	0.16 (84)
Coracopsis vasa [e]	LC	0.47 ± 1.59	16.5%	17.4 ± 8.92	0.4%	0.36 (90)
Passeriformes						
Acridotheres tristis [e]	LC	0.06 ± 0.76	1.1%	21.7 ± 15.51	2.5%	0.23 (51)
Artamella viridis	LC	0.07 ± 0.58	1.8%	42 ± 13.78	1.9%	0.22 (83)
Ceblepyris cinereus	LC	0.04 ± 0.45	1.4%	55.9 ± 11.53	1.8%	0.36 (98)
Cinnyris notatus	LC	0.53 ± 2.30	7.9%	23.9 ± 6.81	1.0%	1.55 (172)
Cinnyris sovimanga	LC	1.03 ± 3.10	14.2%	14.7 ± 7.24	2.6%	0.28 (119)
Cisticola cherina	LC	0.00 ± 0.00	0.0%	36.1 ± 15.42	2.5%	0.16 (8)
Copsychus albospecularis	LC	<0.01 ± 0.05	0.2%	42.3 ± 11.49	3.5%	0.67 (160)
Corvus albus	LC	<0.01 ± 0.11	0.1%	38.2 ± 22.28	8.1%	0.2 (3)

(Continues)

TABLE 1 (Continued)

Species	IUCN status[a]	Hunting pressure (mean ± SD)[b]	Hunting prevalence[c]	Flavor ranking (mean ± SD)	Taboo prevalence	Density[d]/ abundance per hectare (n obs.)
Cyanolanius madagascarinus	LC	<0.01 ± 0.05	0.1%	50.9 ± 12.23	2.3%	–
Dicrurus forficatus	LC	<0.01 ± 0.06	0.2%	82 ± 1.33	67.8%	0.21 (171)
Euryceros prevostii	EN	0.02 ± 0.26	0.8%	34.6 ± 11.35	4.0%	0.21 (115)
Foudia madagascariensis	LC	2.94 ± 6.96	25.1%	10 ± 6.39	1.5%	3.14 (142)
Foudia omissa	LC	0.33 ± 1.92	4.1%	11.3 ± 3.56	1.1%	0.61 (59)
Hypsipetes madagascariensis	LC	1.09 ± 2.53	22.7%	33.4 ± 17.12	0.8%	0.61 (401)
Lepidopygia nana	LC	0.17 ± 1.33	1.9%	14.1 ± 3.03	2.0%	1.5 (45)
Leptopterus chabert	LC	0.01 ± 0.35	0.2%	44.9 ± 11.42	2.6%	–
Motacilla flaviventris	LC	0.00 ± 0.00	0.0%	47.3 ± 9.96	3.6%	0.29 (33)
Oriolia bernieri	EN	0.00 ± 0.00	0.0%	66 ± 9.91	0.0%	0.04 (6)
Ploceus nelicourvi	LC	0.02 ± 0.23	0.8%	43.2 ± 16.11	3.9%	0.1 (71)
Schetba rufa	LC	0.00 ± 0.00	0.0%	65.1 ± 10.88	2.4%	–
Terpsiphone mutata	LC	0.09 ± 0.57	3.3%	37.8 ± 13.66	4.7%	0.23 (78)
Vanga curvirostris	LC	<0.01 ± 0.06	0.2%	62.2 ± 16.05	2.7%	0.34 (60)
Zosterops maderaspatanus	LC	0.22 ± 1.5	3.2%	61.6 ± 16.7	1.8%	0.7 (81)

[a]IUCN status: CR = critically endangered; EN = endangered, VU = vulnerable.

[b]Hunted per household (1327) per year.

[c]Percentage of households which ate this species during the prior year.

[d]Species with more than 25 observations were used to calculate densities, abundances with less than 25 observations should be treated with caution.

[e]Also captured to keep as a pet. While three-quarters (75.0%) of households recently ate at least one wild bird, only 3.1% owned one as a pet; of those 58.7% owned *Coracopsis nigra*, 16.3% *Agapornis cana*, 16.3% *Coracopsis vasa*, and 8.7% *Acridotheres tristis*.

used behavioral strategies to cope with insufficient food during the prior week (measured 2015–2021).

To determine the contribution of individual bird species to diets, we multiplied its body mass (Razafindratsima et al., 2018) by the mean number eaten annually per household (SM 1). We asked consumers about how they acquired each bird they ate (purchased, actively pursuit-hunted, opportunistically hunted, passively snare-trapped, or received as a gift), the tool they used to acquire it (gun, dog, hand, slingshot, thrown object, or stick), and the land type in which they caught it (forest, town, trail (through any land type), lowland rice field, hillside rice field, or other fallow or active hillside farm lands). These interviews resulted in 108,814 observations from 3602 individuals' annual recalls of 17,683 birds caught.

2.2 | Selection in bird hunting

2.2.1 | Bird traits

We examined the effects of trophic level (determined from diet; Razafindratsima et al., 2018), adult body mass (log transformed; Razafindratsima et al., 2018), and availability on hunter preference and hunting outcomes. We used distance sampling methods, analyzed using Rdistance, to assess the density (species with > 25 observations) or abundance (< 25) of bird species from 2015–2022. BR and DR established 188 km of transects, bisecting village, agricultural, and forested landscapes. These included thirty-four 2-km long community transects (each walked 10+ times per year; 34 times in 2015–2018, and 10 in 2018–2022) and two transects (120 km) bisecting Masoala National Park (walked twice per year in 2016 and 2021).

2.2.2 | Consumer preferences

We calculated the prevalence of taboos (log transformed) at the species-level using responses from all 1327 participant households. To examine consumers' preference for the flavor of each species, we held 10 focus-groups (2022) where 6–10 participants ranked photographs of 85 locally recognized birds (87 taxa; assuming equal portion sizes).

2.2.3 | Analysis

We deployed a single piecewise structural equation model in R (SEM) to examine the direct and cascading effects of bird traits on hunters' preferences and species-specific hunting outcomes, that is, the annual number and amount of each species eaten (a priori predicted unidirectional relationships SM 3). The model included four Gaussian GLM 'pieces' and transformed variables using the lme4 package. To account for a possible correlated error between body mass and trophic level, we fitted a corresponding error term. We did not eliminate nonsignificant relationships. We included 85 of the 87 species. For 23 species, we imputed abundance with the median value for the genus, family, or order, respectively, using the lowest taxonomical level available. Analogously, we imputed taboo prevalence for *Glareola ocularis* and *Oriolia bernieri* and missing data on body mass and gram eaten for *Margaroperdix madagascarensis*. We excluded two species with multiple missing data (SM 1).

2.3 | Population viability of Madagascar's birds

To identify species which may be hunted unsustainably, we used population viability analyses (Vortex 10). We created baseline models using demographic and population data for 63 of the 87 species (those which were both consumed and seen during transect surveys), including generation length, mean clutch size, age of first reproduction, years dependent on parent bird, lifespan, and adult survival proportion from birth to maximum lifespan (Bird et al., 2020). The population of each bird species and its annual catch was calculated within 10 km of Masoala National Park (methods, Borgerson et al., 2022). We constructed and ran 20,000 simulations for each species to yield estimates of (1) baseline extinction risk and mean expected population sizes in the absence of hunting (10,000 simulations); (2) extinction risk under current hunting pressure simulated by the annual removal of a constant number of individuals per-generation at empirically derived mean catch rates over the study period (5000 simulations; hereafter constant model); and (3) extinction risk under current hunting pressure simulated by the annual removal of individuals at a constant percentage of per-generation population size (hereafter referred to as the population-dependent model) derived from empirically derived mean catch rates over the study period (5000 simulations). See SM 4 for full model details for each species under each set of assumptions. We recommend a cautious interpretation of the results of these models, especially given the error margins of rarely sampled and poorly studied birds. We considered hunting concerning when declines exceeded 50% in the population-dependent model within 100 years. We suggest considering an elevation in the threatened status of a species (which has a robust density estimate) to Vulnerable or Endangered when the decline of a species currently listed as Least Concern, met IUCN criteria A3 for Endangered (reduction ≥50%, met within three generations; IUCN, 2022) and to Near Threatened when populations declines were both ≥50% within 25 years in population-dependent model and met or exceeded Endangered criterion in the constant model. We also examined whether measured empirical annual abundance for any species declined significantly during the study.

3 | RESULTS

3.1 | Bird hunting pressure, drivers, and methods

Bird hunting was common across households and species, with 75.0% of the total 1327 households having eaten wild birds during the year prior. Households ate a mean 12.87 ± 22.38 (median = 3) individual birds belonging to 2.70 ± 3.23 (median = 2) species annually. Variation in bird consumption was high; while a quarter of households did not eat birds during the prior year, half ate 1–16, and few (10%) ate more than 39. People ate most (85.6%) bird species present in the region (Table 1). While the most commonly eaten birds were Least Concern, many threatened species were also eaten in small numbers, including Endangered helmet vanga (*Euryceros prevostii*), Meller's ducks (*Anas melleri*), Madagascar pond herons (*Ardea humbloti*), Madagascar serpent eagle (*Eutriorchis astur*), Vulnerable Henst's goshawk (*Accipiter henstii*), scaly and short-legged ground rollers (*Brachypteracias* leptosomus, *Geobiastes squamiger*), and Near Threatened Madagascar crested ibis (*Lophotibis cristata*; Table 1). Most (85.0%) households had a member with taboos against eating a median of two (mean 3.72 ± 6.50) bird species. While taboos on five species were especially common, all but three bird species were taboo for at least one person in the study sample (Table 1). Although taboos are inherited (and not widely held cultural norms across all individuals in an area), and most taboo species were hunted by other households or even individuals within that household, species' taboo prevalence was still negatively correlated with hunting pressure (Est: −0.37; CL: −0.91 to 0.02; $\chi^2 = 5.05(1, 83)$; $p = 0.03$).

Poverty and food insecurity decreased the species selectivity of hunters (GLM, Poisson: $\chi^2 = 28.27$; $p < 0.0001$) and increased the number of birds a household ate ($\chi^2 = 274.45$; $p < 0.0001$). While wealth ($\chi^2 = 28.40$; $p < 0.0001$) significantly contributed to the model explaining the number of species a household ate, food security did not ($\chi^2 = 0.08$; $p = 0.78$). Wild birds provided a mean 806 g of meat per person (>6 months old) per year, accumulating to 2964 g

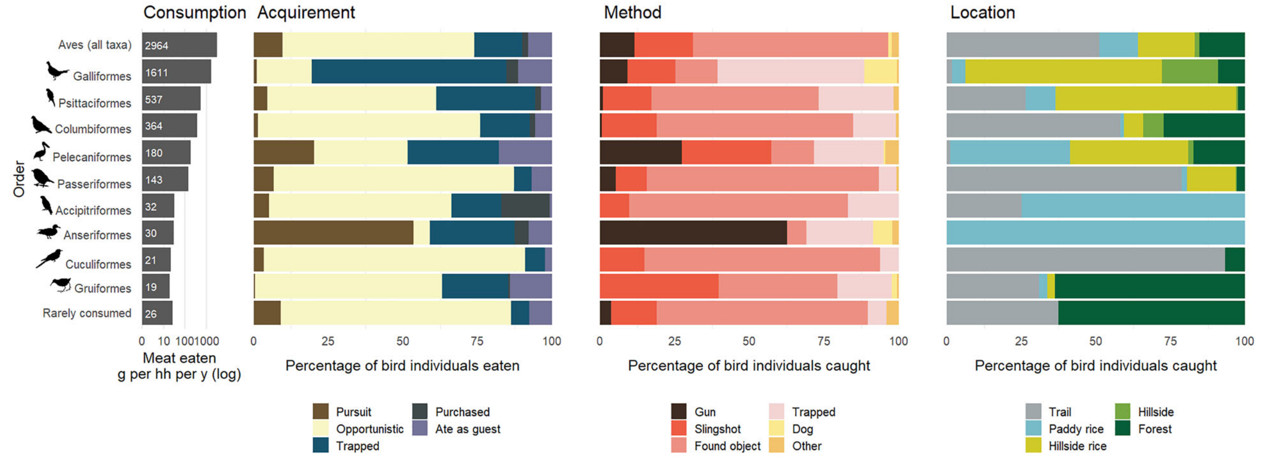


FIGURE 1 Patterns in the acquisition of, methods for, and location of 87 species of birds and the meat they provided (in grams; by taxa) in 13 villages near the Masoala National Park (2015–2021).

of meat per household annually. Nutritionally, the most important birds (those which provided the most meat per household per year) were helmeted guinea fowl (*Numida meleagris*; 1611 g), followed by black parrots (*Coracopsis nigra*; 251 g), greater vasa parrots (*Coracopsis vasa*; 247 g), and Madagascar green pigeons (*Treron australis*; 195 g; SM 1, Figure 1). Threatened birds provided 131 g of meat per household annually, with the Madagascar crested ibis (*L. cristata*, Near Threatened) providing the most in both number (mean 0.16 per household annually) and meat (mean 93 g) of threatened species, followed in mass by Henst's goshawk (*Accipiter henstii*, Vunerable, 0.02, 21 g), and ground rollers (*Brachypteracias* leptosomus, 0.03, 6 g; *Geobiastes squamiger*, 0.03, 5 g).

People primarily caught birds using a found object (77.6%), which was thrown when the birds were seen opportunistically during other tasks (63.7%), primarily along trails (31.9%), in town (26.6%), or in hillside shifting-agricultural farmlands (25.6%; Figure 1). Both the location and methods of bird hunting varied, however, in species-specific ways (Figure 1, SM 1, 5). While pigeons, doves, and couas were primarily caught along trails, parrots were caught in hillside shifting-agricultural rice fields, goshawks in lowland rice fields when they sought small avian prey, crested ibis and rails in forests, and sunbirds in communities near homes (SM 1, 5). And while larger parrots, pigeons, doves, hawks, and sunbirds were opportunistically caught as individuals using mostly thrown objects, small parrots and crested ibis were instead trapped (the former as flocks using sticky resin traps and the latter as individuals using snare traps). Diet also affected the hunting method used (GLM, Poisson); People opportunistically caught nectarivores ($T = 2.26$, $p = 0.001$) and frugivores ($T = 3.83$, $p = 0.03$), while they trapped granivores ($T = -2.63$, $p = 0.01$) and herbivores ($T = -2.01$, $p = 0.048$).

3.2 | Selection in bird hunting

We could predict nearly half ($R^2 = 0.46$) of species selection (the variation in the number of each species of bird eaten per year) using the traits of birds and preferences of hunters (Figure 2, SM 3). The best predictor of a species' hunting pressure was its abundance. Abundance varied widely across species (from 0.01 to 3.14 birds per ha^2), and the more abundant a species was, the more it was eaten (Figure 2). Lower trophic level also had a significant positive effect on species selection, both directly on catch and indirectly through its effect on the flavor of a species' meat. Depending on the species, birds could either be preferred or avoided because of their flavor (Table 1). Overall, consumers were more likely to prefer the flavor of a familiar abundant species and dislike the flavor of birds that were commonly taboo or were of higher trophic levels ($R^2 = 0.37$; Figure 2). Consumers disliked the flavor of carnivores and scavengers and a preferred the flavor of granivores and nectarivores (Figure 3).

3.3 | Population viability of Madagascar's birds

The hunting of most species appeared sustainable. However, we identified at least three species of concern: the black parrot (*Coracopsis* nigra), Madagascar green pigeon (*Treron australis*), and grey-headed lovebird (*Agapornis canus*; Figure 4). These three species are all currently listed as Least Concern. Yet, the projected decline of black parrots in the region, 77.5% in three generations (24 years), exceeds IUCN criterion A3 for Endangered species status. This was reinforced by the significant measured decline at our sites in the annual abundance (which should be interpreted with caution) of black parrots by 81.4% ($R^2 = 0.82$,

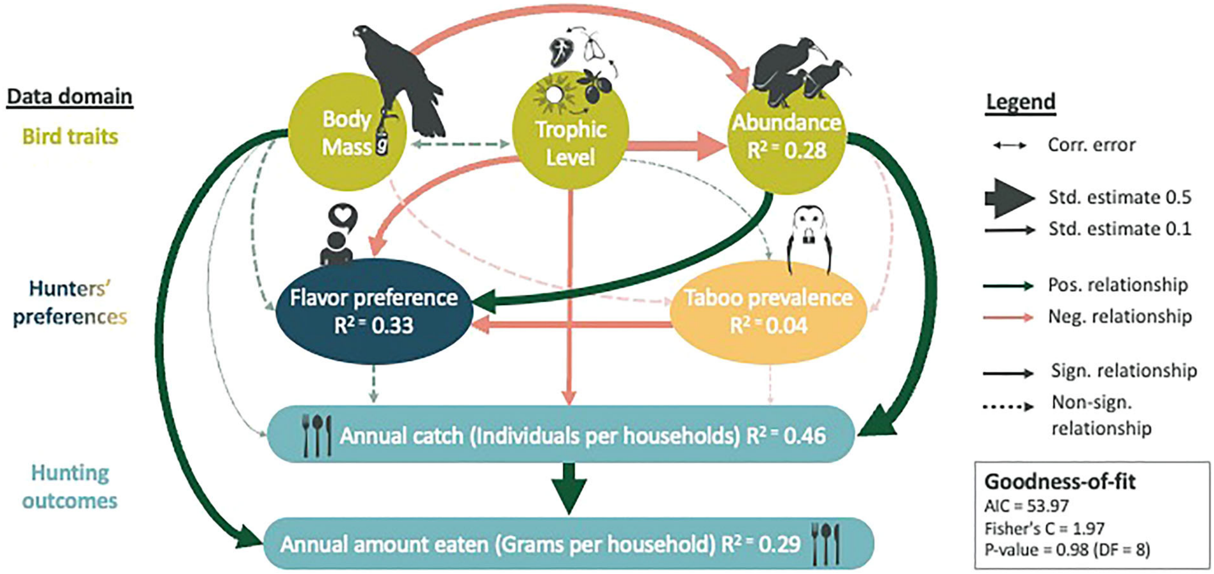
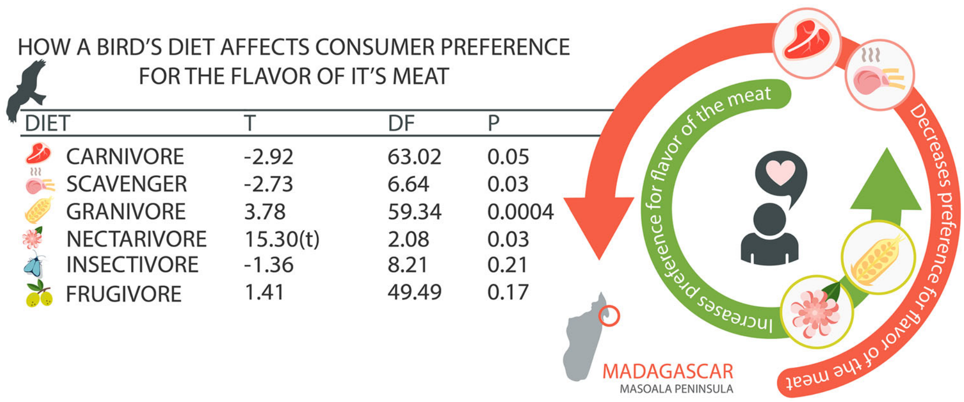


FIGURE 2 Structural equation model depicting the effects of multiple bird traits on hunters' preferences and subsequently hunting outcomes for 85 bird species of northeastern Madagascar.Arrows represent unidirectional relationships between variables and are scaled on the standardized regression coefficient. Positive relationships are denoted by dark green arrows, negative by pink, significant by solid, and dashed are not significant. Correlated errors included in the model are symbolized by a two headed arrow. Goodness-of-fit metrics are displayed in the grey box. Additionally, R^2 values for each latent and response variable are provided.



DIET	T	DF	P
CARNIVORE	-2.92	63.02	0.05
SCAVENGER	-2.73	6.64	0.03
GRANIVORE	3.78	59.34	0.0004
NECTARIVORE	15.30(t)	2.08	0.03
INSECTIVORE	-1.36	8.21	0.21
FRUGIVORE	1.41	49.49	0.17

FIGURE 3 Effect of a bird's diet on consumer preference for the flavor of their meat in 13 villages near the Masoala National Park (2022).

$F(1, 5) = 18.57$, $p = 0.01$ (87.29–0.04 per year)). The projected decline of green pigeons (53.5% in the coming 25 years), may further warrant Near Threatened status. While Henst's goshawk (VU, *Accipiter henstii*) hunting was also concerning, we determined this using abundance, and not density, and it should be interpreted with caution.

4 | DISCUSSION

Bird hunting in rural Madagascar is common and nearly all species are hunted. While people across the socioeconomic spectrum eat wild birds, wealth increased species selectivity and food insecurity increased hunting pressure. Households eat more than a dozen birds annually, providing nearly a kilogram of undressed meat per person. Most were caught opportunistically, with a thrown object, and, consistent with previous research (Borgerson et al., 2022; Chaves et al., 2020; Dunn & Smith, 2011), consumers ate more abundant species, regardless of their smaller size, because of their ease of catch. A bird's diet contributed most to its perceived flavor and consumers preferred the taste of granivores and nectarivores while disliking carnivores and scavengers. Beyond the effects of diet on consumer preference for flavor and fat content, these diets also directly increased the number caught, potential due to the spatiotemporal predictability of food plants (Borgerson, 2016), and hunter incentives, when

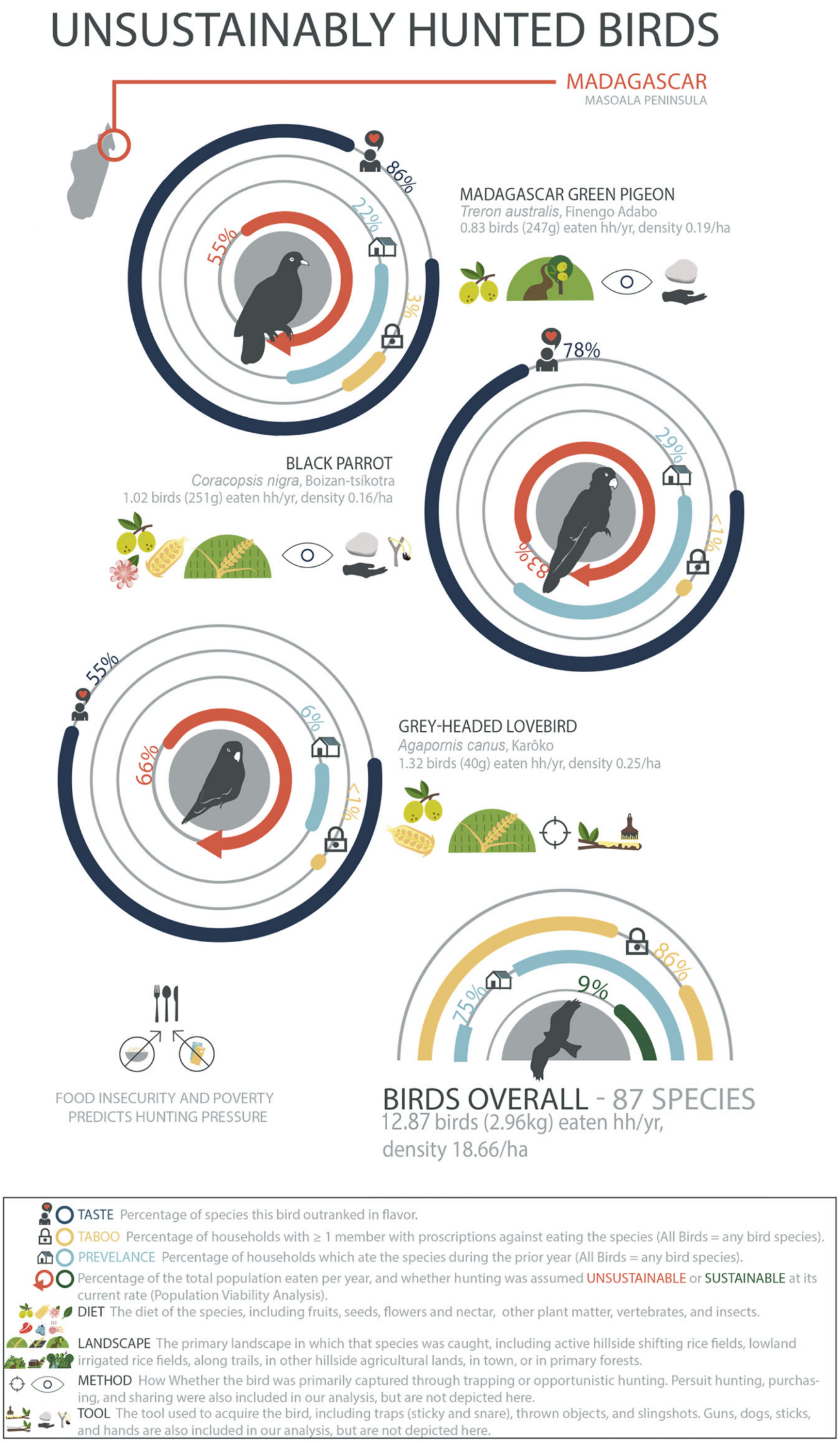


FIGURE 4 Unsustainably hunted birds on the Masoala Peninsula, Madagascar (2015–2021).

such animals forage on crops (Araneda et al., 2002; Horgan et al., 2020).

While many species appeared sustainably hunted, at least eight threatened species were eaten. Further, our population viability analysis identified concerning rates of hunting for three species currently listed as Least Concern (IUCN, 2022): the black parrot (*Coracopsis nigra*), Madagascar green pigeon (*Treron australis*), and grey-headed lovebird (*Agapornis canus*). Population declines which consider hunting are far greater than declines previously projected for the Madagascar green pigeon, and despite the previously assumed stable population size for black parrots (Bird et al., 2020; IUCN, 2022), their populations significantly declined throughout our study. The projected local declines of the black parrot and green pigeon were especially concerning, as they met or exceeded

IUCN criteria for Endangered and Near Threatened statuses (respectively), in all models. While food insecure households primarily hunted these species to improve their nutrition (all three ranked amongst the top providers of wild bird meat in grams), these species were also preferred for their flavor and, unlike most species, were occasionally purchased and shared. This diverse pressure resulted in with 55.0–82.7% of their local population eaten per year. Efforts to improve the sustainability of pigeon hunting should focus on opportunistic catch along trails, while those tailored to parrots would need to reduce both targeted and opportunistic hunting in seasonal shifting hillside rice fields. Because these species appear to be widely caught using similar methods across much of Madagascar (Garder & Davies, 2014; Jenkins et al., 2011), where population densities are unknown, declines may be geographically broad but underreported. Further, lovebirds and parrots (CITES Appendix II species) were the most owned wild pets in rural households, consistent with findings from urban Madagascar (Reuter et al., 2017; Rodríguez et al., 2020), and assessments of international exports (UNEP-WCMC CITES Trade Database, 2022). Although a consistent decline in the international trade of black parrots may indicate an increasing difficulty of acquiring the birds in the wild (Reuter et al, 2017, 2019).

In addition to hunting pressure, Malagasy bird species are threatened from high rates of habitat loss (Gardner et al., 2016; Hawkins, 1999, Martin et al., 2021; Murphy et al., 2018; Santini et al., 2019; Tracewski et al., 2016) and from predation by introduced species such as feral cats (Murphy et al., 2018). While the at-risk birds we identify here are not primary forest dependent, hunting is second to forest loss as a threat to birds overall (IUCN, 2022). Indeed, primary forests have nearly twice the diversity of bird species, as well as a higher share of endemic species, when compared to other land-use types in the region (Martin et al., 2021). Similar to lemurs, the relative effects of habitat loss and hunting on birds may be species-specific (Borgerson, 2015), or may be compounded for birds specialized to lowland forests which are most subject to habitat conversion in Madagascar. Efforts to mitigate habitat fragmentation may benefit from ensuring the sustainable hunting of frugivorous seed dispersers, such as the Madagascar green pigeon, an important seed disperser for many nonlemur-dispersed pioneer plant species (Bollen et al., 2004).

5 | CONCLUSIONS

By understanding why hunters catch birds, the traits that determine targeted species, how these species are hunted, and the effects of these factors on bird population trajectories across biodiversity hotspots, we can understand and mitigate bird threats and ensure timely conservation action. In northeastern Madagascar, the hunting of at least three bird species is concerning while most hunting appears sustainable. Programs which focus their efforts on improving rural wealth and food security are most likely to reduce overall bird hunting, while conservation actions should be informed by species-specific hunting and consumption patterns. Rigorous assessments of bird hunting pressure and its effects on the densities of bird species across tropical regions are a high priority for future research, as these are essential to inform IUCN assessments and to ensure timely conservation action for the world's birds.

ACKNOWLEDGMENTS

We would like to extend our deepest gratitude to the communities in which we work, the editor, the anonymous reviewers, the Republic of Madagascar, and Madagascar National Parks for their continued support.

FUNDING

This research was funded by the National Geographic Society (C280–14,C021–17,55616C-20), Margot Marsh Biodiversity Foundation, Primate Action Fund, National Science Foundation (1513638), International Union for the Conservation of Nature (IUCN-SOS 2018A-117), and Forschungskredit of University of Zurich (FK-21-128). Institutional Animal Care and Use and Human Subjects Institutional Review Boards (No. 10-0010,0595 University of Massachusetts Amherst; 12–0028,13-1862,15-0002,2230 Harvard University; 18-19-1349,19-055,22-077 Montclair State University) approved all research.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The anonymized datasets generated and/or analyzed during the current study are available in supplementary materials and at https://osf.io/3amqy/.

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How to cite this article: Borgerson, C., Bankoff, R. J., Golden, C. D., Razafindrapaoly, B. N., Rasolofoniaina, B. J. R., Rajaona, D., Pascal, E., De Angelo, P., & Martin, D. A. (2023). Drivers and sustainability of bird hunting in Madagascar. *Conservation Letters*, e12960. https://doi.org/10.1111/conl.12960