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Evaluation of tenrec population viability and potential sustainable management under hunting pressure in northeastern Madagascar

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Abstract

Across the Global South, wildlife is an important source of nutrition and income, particularly for rural communities. While wildlife consumption provides a valuable source of nutrition, high levels of hunting can endanger wildlife species. In the Makira region of north-eastern Madagascar, human health is threatened by food insecurity and malnutrition, and spiny tenrecs are a crucial source of subsistence bushmeat with 91% of households consuming tenrecs at least once per year. Moreover, Makira's human populations are increasing, resulting in forest decline and degradation. In order to inform conservation and public health efforts, we investigated the influence of hunting, habitat loss and forest degradation on spiny tenrec population dynamics in the Makira region. We collected data on tenrec population densities as well as hunting and consumption by humans in 51 communities. We used these data to conduct a population viability analysis for the two most commonly hunted spiny tenrecs (*Tenrec ecaudatus* and *Setifer setosus*). We found that current harvest rates for these species are generally sustainable in the Makira region, largely due to tenrecs' extraordinary fecundity. However, even assuming no change in current hunting rates, tenrec populations could become threatened if fecundity were to decline or background mortality to increase, both possible scenarios under future trajectories of habitat loss and degradation. We find that any future increase in hunting-induced mortality rates for tenrecs are similarly unsustainable – and likely to occur as human populations expand and hunting areas decline. We conclude that there is a vanishing window of opportunity to sustainably manage tenrec hunting in northeastern Madagascar in order to avoid negative conservation and human health outcomes.

Introduction

Across the Global South, wildlife is an important source of nutrition and income, particularly for rural communities. Approximately ~150 million households worldwide rely on wildlife harvest for income and consumption (Nielsen *et al*., 2018). While wildlife consumption can provide necessary nutrition to vulnerable communities, it threatens >300 mammal species with extinction (Ripple *et al*., 2016). Many hunted species face compounding effects from habitat loss and degradation, and unsustainable hunting hastens local extirpations or extinction (Ingram *et al*., in press). Hunting, habitat loss and environmental degradation are especially concerning in Madagascar, where native terrestrial non-volant mammals are entirely endemic (Goodman, Raherilalao and Wohlauser, 2018), wildlife consumption is critical to human health (Golden *et al*., 2014), and forest cover declined 40% between 1953 and the 2000s (Harper *et al*., 2007; Vieilledent *et al*., 2018). Collectively, these factors have resulted in tensions between human health and the conservation of intact natural forests that harbor Madagascar's imperiled biodiversity.

Nearly 50% of Malagasy children under age 5 are classified as stunted (impaired growth due to chronic malnutrition), highlighting the societal impact of chronic food insecurity (Rakotomanana *et al*., 2017). Dietary records from communities in north-eastern Madagascar demonstrate widespread deficiencies in protein, vitamin A, vitamin B12, zinc and fat (Golden *et al*., 2019). These are critical nutrients found in animal-sourced foods, further emphasizing the importance of wildlife consumption in maintaining health among communities in the region (Golden *et al*., 2014). While meat from domesticated animals is more accessible to wealthier households, wild meats can support the nutrition of those with lower socioeconomic status (Golden *et al*., 2019).

The conflict between human health and forest conservation is particularly pronounced in the Makira region of north-eastern Madagascar, where human communities experience high rates of food insecurity and malnutrition while living adjacent to nationally protected lowland and littoral rainforest (Golden *et al*., 2019). In the Makira region, several native wildlife species are hunted, including lemurs, bats, birds, carnivores (fosa, fanaloka, vontsira among others (Farris *et al*., 2015)) and spiny tenrecs: 95% of households report consuming at least one of these wild meats over the course of a year (Golden, 2009). Past research has demonstrated the heavy dependence of the local population on wildlife consumption, valuing the replacement cost of wildlife with domesticated meats at 57% of annual household income (Golden *et al*., 2014). Specifically, 91% of human households in the Makira region report hunting at least one of two species of spiny tenrec, *Tenrec ecaudatus* or *Setifer setosus* (family Tenrecidae, subfamily Tenrecinae), which comprise approximately 75% of wildlife biomass consumed annually in the region (Golden *et al*., 2014). The tenrec species *Hemicentetes semispinosus* is also found in this region, though it is rarely hunted and was not included in our study (Goodman *et al*., 2018). Therefore, the sustainability of tenrec hunting has considerable implications for the health of local populations, especially children (Golden *et al*., 2011).

The literature on tenrec population dynamics and the impacts from hunting is limited. Previous studies largely focused on tenrecs in captivity (Stephenson, 2007; Harrison and Harrison, 2017), or on tenrec natural history or ecophysiology in the wild (Petter and Petter-Rousseaux, 1963; Levesque *et al*., 2012, 2013). Tenrecine hunting rates are known to be highly variable, with 12% of hunters reported to hunt *T. ecaudatus* in the forests of Kianjavato in southeastern Madagascar, compared with 74% in the Lac Alaotra wetland region of central-eastern Madagascar (Borgerson, Johnson, *et al*., 2018; Borgerson, Vonona, *et al*., 2018). The Makira forest of north-eastern Madagascar has the highest known hunting rates, with 91% of households reported to hunt *T. ecaudatus* or *S. setosus* (Golden *et al*., 2014). In Makira, spiny tenrecs are hunted nearly exclusively with dogs at night, though hunting via snares and opportunistic capture also occurs.

Given limited past study of tenrecine population dynamics, the key role that their consumption plays in human health and nutrition, and the high hunting pressure faced by extant populations, we aimed to quantify the impact of hunting on spiny tenrec survivorship and population viability to inform conservation and management strategies. Because human populations are increasing in the Makira region, in conjunction with declining and degrading forests (Harper *et al*., 2007; INSTAT Madagascar, 2019; Vieilledent *et al*., 2018), we additionally sought to assess if future conditions would change tenrec hunting sustainability. Our results can inform conservation and nutrition efforts in Madagascar, and globally in regions where nutritional needs are in conflict with hunting practices that threaten population viability.

Materials and methods

Approach

We collected data on tenrec population density, consumption and hunt areas via live-trapping, household dietary recall interviews and hunter interviews. We used these data, along with natural annual mortality rates from the literature, to simulate distributions of potential population sizes and mortality rates for spiny tenrecs across Makira. Then, we performed a population viability analysis (PVA) based on different hunting conditions. We used the Lefkovitch matrix method (Lefkovitch, 1965), a modification of the Leslie matrix method (Leslie, 1945, 1948) that relies on life stage (rather than annual) survival rates, in our PVA to analyze the sustainability of spiny tenrec hunting under various life history conditions (such as declining reproductive rate and increasing natural mortality rates) and increasing hunting scenarios.

Study site

We studied 51 human communities surrounding the Makira Natural and Masoala National Parks in north-eastern Madagascar (Fig. S1). These parks are among the largest contiguous blocks of rainforest remaining in Madagascar and contain substantial biodiversity and diverse human populations (Golden *et al*., 2014; Text S1).

Study species

The family Tenrecidae is endemic to Madagascar and includes 31 described extant species and several more awaiting formal description (Everson *et al*., 2016; Goodman *et al*. (2018)). Here, we focused on the two tenrec species most heavily consumed by humans in the Makira region: the spiny tenrecs, *Tenrec ecaudatus* and *Setifer setosus* of the subfamily Tenrecinae (Text S2).

Local tenrec population density estimates

Trapping

We conducted live trapping in intact and degraded forest to estimate spiny tenrec densities in different habitats in the Makira region (Text S3). Briefly, we established six pitfall trapping transects in one focal study community. Across all transects, there were 99 pitfall traps and 126 Tomahawk traps (Fig S2). On average, individuals were captured 1.34 times, and only a single animal (of 106 individuals) showed trap happy behavior with >4 captures.

Mark-recapture models for local population density

We conducted a spatial capture–recapture (SCR) analysis to estimate the density of tenrecines using the secr package in R (Efford, 2021). First, we used live trapping data to produce capture histories for traps and individuals. The transects covered a small portion of the total study area (<5%) and the total number of captures was small (n = 139), so it was not possible to include habitat or survey period as covariates in the SCR analysis. Though we noted each animal's sex and weight upon capture, we were unable to confidently assess age class.

Results from the SCR analysis were used to derive a density estimate for *S. setosus*. By comparison, low recapture numbers and potential biases in pitfall trapping of *T. ecaudatus* (which is large enough to occasionally escape pitfalls) undermined our confidence in estimates for this species. As a result, we elected to explore a range of possible densities for *T. ecaudatus*, rather than deriving density from the trapping data. To this end, we first explored a scenario in which we assumed consumption rates to be proportional to population density for both tenrec species, such that we estimated the ratio of *T. ecaudatus* to *S. setosus* density as equivalent to the ratio of consumption of these animals in each of the 51 communities. Because *T. ecaudatus* was always consumed at higher rates than *S. setosus* (resulting in higher densities), we also considered lower densities, assuming *T. ecaudatus* density to be equal to one or one-half the density of *S. setosus* (Text S4).

In all cases, we incorporated substantial uncertainty associated with estimation of density into downstream analyses, such that our conclusions were not contingent upon the precision of these estimates. The SCR analysis provided a mean and standard error of density for *S. setosus*; we converted this standard error estimate to a standard deviation estimate to define a normal distribution of possible *S. setosus* densities, which we truncated between zero and five standard deviations above the mean to avoid negative density values. We then drew density estimates used in downstream stochastic simulations from this distribution at random. For *T. ecaudatus*, we defined an additional normal distribution around the scaling factor of *S. setosus* to *T. ecaudatus* density. For the sensitivity analyses at one or one-half the density of *S. setosus* (Text S4), we randomly drew this scaling term from a normal distribution with a mean of, respectively, one or one-half, and a standard deviation of, respectively 0.1 or 0.05, for each successive simulation. For analyses included in the main text, in which we assumed tenrec densities to be proportional to local consumption rates, we calculated the average and standard deviation of the *S. setosus to T. ecaudatus* consumption ratio across all 51 Makira communities, and used these estimates to define a normal distribution of a *S. setosus to T. ecaudatus* density scaling term. Then, for each downstream simulation, we drew both a density estimate for *S. setosus* and a scaling ratio for *T. ecaudatus* from the respective distributions to randomly assign a density for *T. ecaudatus*. In this manner, we explored a wide range of potential densities for each species, such that all major conclusions were robust to uncertainty surrounding these estimates.

Tenrec annual and seasonal consumption estimates

Household interviews of wild meat consumption

We obtained data on spiny tenrec consumption from a longitudinal dataset collected by Madagascar Health and Environmental Research (MAHERY) (Golden *et al*., 2017). This dataset describes annual bushmeat consumption in 52 communities in the Makira Natural Park and Masoala National Park, via interviews of 1155 households conducted annually between 2005 and 2013 (Golden *et al*., 2014). We used tenrecine consumption data from 51 communities for which we possessed data on the total number of households present to estimate total community-level consumption. When available, the total number of households was derived from the INSTAT 2009 survey (INSTAT/DDSS., 2009); otherwise these numbers were obtained from a local community census conducted by the MAHERY team (unpublished data).

Generalized linear models of consumption

We used consumption data from the MAHERY interviews to inform predictive models of household spiny tenrec consumption. We used the *R Cran glmmtmb* package to fit generalized linear mixed effects regression models with a Poisson distribution to our collected data on monthly and annual household level consumption (Brooks *et al*., 2017). We constructed GLM models of both annual and monthly household spiny tenrec consumption (Text S5). These models were used to predict tenrec consumption across all communities.

Tenrec hunting-induced mortality rate estimates

To estimate hunting-induced mortality rates, we calculated the proportion of the total tenrec population consumed by communities in the region each year as predicted by the generalized linear models (rather than raw offtake). We assumed spiny tenrec consumption rates to be equivalent to hunting rates because only 2% of wild meat consumed in this region is estimated to be sourced by sale (Golden *et al*., 2014). This assumption allowed us to consider all mortality from consumption to be hunting-induced.

We first stochastically simulated a distribution of population sizes for spiny tenrecs in the region, based on estimates of density and hunting area surrounding the communities (Text S6). For each hunting area, we considered scenarios in which 25%, 50%, 75% or 100% was habitable by tenrecs, to

Table 1 Literature-derived life history parameters used for population viability analysis

	Interbirth interval (Months)	Age at First reproduction (Months)	Litter size (number of infant spiny tenrecs per litter)	Background mortality (%)
Minimum *S. setosus*	12.0	6.0	1.0	15.0
Midpoint *S. setosus*	12.0	6.0	3.0	17.5
Maximum *S. setosus*	12.0	6.0	5.0	20.0
Minimum *T. ecaudatus*	12.0	6.0	1.0	15.0
Midpoint *T. ecaudatus*	12.0	6.0	16.5	17.5
Maximum *T. ecaudatus*	12.0	6.0	32.0	20.0
Sources	(Hayssen *et al.*, 1993; Jones *et al.*, 2009)	(Hayssen *et al.*, 1993)	(Jones *et al.*, 2009; Olson, 2013; Stephenson *et al.*, 2007)	(Künzle, 1998)

account for terrain such as rivers and high elevation where neither tenrec species can live.

Then we estimated the average annual household consumption for each tenrec species, by taking the mean of tenrec consumption (per species) across households and years for each community, based on the results of the annual generalized linear model. We then multiplied this average annual household consumption by the number of households in each community to estimate an approximate total annual consumption for each species in each of 51 communities.

Finally, we defined a distribution of possible annual mortality rates by dividing the total consumption estimates plus the mean background mortality estimates by the mean of the distribution of tenrec population sizes at each percentage of habitable area. Mortality rates greater than 1 were possible, indicating that all tenrecs in the population were killed, plus additional tenrecs (due to migration into the habitable area or hunting outside the hunting area). We maintained these values to avoid artificially truncating the distribution.

Population viability analysis

Derivation of life history parameters

We obtained life history parameters of litter size, age at first reproduction, interbirth interval and background mortality from the literature for both tenrec species, using the minimum, maximum and midpoint for each parameter (Table 1, Text S7). Importantly, since mortality data were not available for the study species, we adopted background mortality rates reported in the literature for another tenrec species in captivity, *Echinops telfiari*, in all simulations (Text S7).

Construction of Lefkovitch matrices and zero-growth isoclines

We used these life history parameters to construct Lefkovitch matrices for both tenrec species (*Text S8*), from which we determined theoretical zero-growth isoclines assuming minimum, maximum and mean fecundities (Lefkovitch, 1965; Lyles and Dobson, 1988; Dobson and Lyles, 1989; Brook *et al.*, 2018). We also conducted an elasticity analysis for the effect of the parameters on the dominant eigenvalue of each matrix; this value defines the population trajectory (i.e. increasing at values > 1 vs. declining at values < 1) for the modeled species (Caswell and Trevisan, 1994; Caswell, 2006).

Estimating total mortality rate

We used the distributions of hunting-induced mortality described above to calculate a standard deviation, from which we generated a 95% confidence interval on annual hunting-induced mortality. We added this to the literature-derived range of background mortality of 15% to 20% (Künzle, 1998) to determine a 95% confidence interval for total annual mortality.

Evaluating viability of estimated mortality rates

Finally, we compared zero-growth isoclines to annual total mortality rates estimated for each species in each community to determine the sustainability of spiny tenrec hunting in the Makira region. Because considerable estimation was involved in the calculation of both background and hunting mortality, we conducted sensitivity analyses to investigate the influence of variation in parameters on our conclusions of sustainability, including (1) exploring the effect of mean, and upper and lower 95% confidence interval bounds of total adult annual mortality, and recalculating results assuming (2) 25%, 50%, 75% and 100% of hunt area to be habitable by spiny tenrecs, (3) infant mortality levels equal to 1.3, 1.5 and 1.7 times the total adult annual mortality, and (4) fecundity rates based on minimum, midpoint and maximum litter sizes. Additionally, we calculated the theoretical maximum number of households that could consume a specified number of *S. setosus* and *T. ecaudatus*, while remaining within sustainable limits as defined by the zero-growth isoclines.

Results

Local tenrec population density estimate

Across both years of trapping, the MAHERY team captured 99 *S. setosus* (73 individuals: 40 females and 33 males, 26 recaptures) and 40 T. *ecaudatus* (33 individuals: 9 females and 24 males, 7 recaptures). Low capture rates prevented density analyses in the first year. In the second year – the lower capture and recapture rates for *T. ecaudatus* (17 captures for

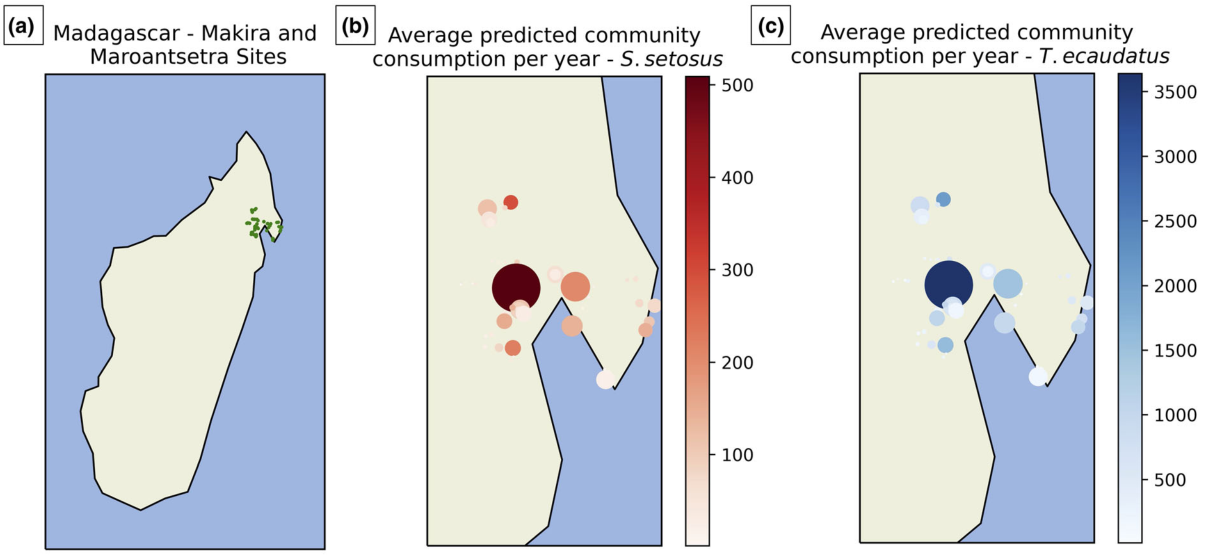

Figure 1 Maps showing the location of study sites in Madagascar (a), and the estimated average consumption per year for *S. setosus* (b) and *T. ecaudatus* (c). The average annual consumption is signified by the intensity of marker color, and the size of the community is proportional to the marker size. Maps made in Cartopy (Met Office, 2010)

T. ecaudatus vs. 59 for *S. setosus*) were insufficient to accurately estimate detectability and density. We derived a robust density estimate from the SCR model for *S. setosus* in the second year of 211.5 (SE = 61.38) *S. setosus*/km^2.

Tenrec consumption estimates

Spiny tenrec consumption was highly variable across communities. *T. ecaudatus* was always consumed at much higher levels than *S. setosus*, and community consumption of both species was correlated. We depict total predicted annual community consumption (Fig 1), as it is total consumption, not per household consumption, that determines hunting-induced mortality rates at the population level.

To understand seasonality in hunting-induced mortality, we quantified the average predicted household monthly consumption across all communities for each month. We show the average number of tenrecs consumed each month by households across the 51 communities (Fig 2). There is clear seasonality in consumption, with maximum levels occurring in February and minimal levels from July to October when tenrecs are in torpor (Treat et. al., 2018).

Tenrec mortality rate estimates

Assuming that tenrec consumption is proportional to population densities, our stochastic distributions of tenrecine population densities demonstrate that *T. ecaudatus* has a mean population density some 7.1 times larger than *S. setosus* in the Makira region (Fig S3a; though see Text S4, Fig. S4a, Fig S5a for sensitivity analyses assuming lower *T. ecaudatus* densities). The majority of simulated hunted areas were found to be less than 50 km^2 (Fig S3b). Under assumptions of density proportional to consumption, population sizes were correspondingly also larger for *T. ecaudatus* than *S. setosus* populations (Fig S3c, d), though under more conservative scaling factors assuming *T. ecaudatus* density to be equal to or half that of *S. setosus*, corresponding population sizes were reduced (Fig S4b, Fig S5b).

The distributions of total annual mortality rate (the sum of natural background mortality and hunting) were similar for *T. ecaudatus* (min = 17.5%, max = 69.9%) and *S. setosus* (min = 17.5%, max = 69.4%) (Fig S6). Estimated annual mortality rates represent hunting-induced mortality (based on the mean of the stochastically constructed distributions for each study species population size) plus background mortality (17.5%, the center of the 15–20% range quoted in Künzle (1998)) under scenarios where 25%, 50%, 75% or 100% of hunt area was modeled as habitable. Under assumptions by which *T. ecaudatus* density was modeled as proportional to consumption, the higher *T. ecaudatus* population size was counterbalanced by the higher harvest rates, such that the overall mortality rate remained similar to that for *S. setosus*. In sensitivity analyses assuming *T. ecaudatus* density equal to or less than *S. setosus*, this resulted (predictably) in more dramatic overall mortality rates (Fig S4c, Fig S5c). Mortality rates higher than 100% indicate scenarios in which all tenrecs in the defined population were hunted in our simulations. This could occur if hunters hunted outside the defined habitable area or tenrecs from external populations entered the habitable area. Additionally, in all cases where habitable area was modeled as a lower percentage of hunting area, hunting-induced mortality rates were necessarily higher.

Population viability analysis

To determine if hunting offtake was within sustainable levels, we compared the zero-growth isoclines computed

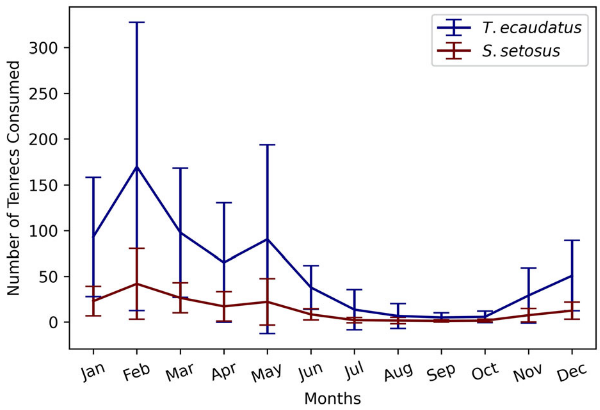

Figure 2 Predicted average consumption per month for *T. ecaudatus* and *S. setosus*, in a prototypical community of 100 households. Error bars represent +/-1 SD from the average predicted monthly standard deviation, and the trend lines connect each month's estimate to show the seasonal pattern

from literature-derived natural history parameters to our estimated tenrecine mortality rates. After superimposing the confidence interval for total adult annual mortality across all communities on each tenrec species' zero-growth isoclines, we found that present mortality rates fall largely within sustainable levels, except in cases when infant mortality was modeled as high (Fig 3). In simulations assuming a lower percentage of spiny tenrec habitable area or lower litter sizes, adult mortality rates were also more frequently unsustainable, and estimated hunting mortality comprised a larger share of total mortality.

When assuming *T. ecaudatus* densities to be proportional to consumption rates, our estimates indicate that at least 50 of 51 and 47 of 51 communities in Makira are currently carrying out sustainable hunting practices, for *T. ecaudatus* and *S. setosus*, respectively, except under simulated assumptions of low fecundity (Fig 4). When fecundity is modeled as low, fewer communities are estimated to hunt sustainably, and the number is further decreased (to 31 of 51 communities for both species) under simulations assuming particularly high adult and infant mortality and low per cent tenrec habitable area (Fig 4). These are realistic scenarios given ongoing human population growth and habitat loss and degradation in the region, which may reduce tenrec fecundity and survivorship in the near future. Indeed, under future projections in which both tenrec species' adult mortality is modeled at a mean value (indicating no change to current hunting practices), but habitable area is assumed to be 25% of hunt area, while fecundity is modeled at a minimum and infant mortality at a maximum, the resulting analyses indicate that only 38 of 51 communities will practice sustainable hunting if maintained at current rates. Under conditions in which adult mortality is increased to its maximum, this number falls to 31. By contrast, under scenarios maintaining the same habitat, fecundity and infant mortality assumptions, but modeling adult mortality at a minimum (corresponding to a decrease in current hunting rates), our projections suggest that as many as 41 out of 51 communities could continue to practice sustainable hunting. Under more optimistic scenarios in which both adult mortality and, critically, tenrec fecundity, are modeled at their current mean values, even assuming only 25% habitable area and maximum juvenile mortality, our estimates of the number of Makira communities practicing sustainable hunting increases dramatically, to 50 and 48 for *T. ecaudatus* and *S. setosus* respectively. Elasticity analyses suggest that the sustainability of tenrec consumption for each community is most tightly dependent on fecundity (Fig S7; Caswell and Trevisan, 1994; Caswell, 2006). Because average lifespans for tenrecs are short but reproductive gains are massive, juvenile survival to the first annual reproductive event has the most wide-ranging impact of any parameter on population viability as a whole (Fig S7).

Additionally, in sensitivity analyses assuming *T. ecaudatus* density to be equal to or smaller than that of *S. setosus* (rather than larger, in proportion to consumption rates), all projections of population viability for this species were correspondingly jeopardized (Text S4, Fig S4d, Fig S5d). Indeed, under the worst-case density conditions, assuming *T. ecaudatus* density to be one-half that of *S. setosus*, but with mean adult mortality and fecundity, midpoint juvenile mortality (1.5 times adult mortality), and 50% habitable area, only 28 out of 51 communities were currently estimated to practice sustainable hunting, in contrast to all 51 when *T. ecaudatus* density is proportional to consumption. This number falls to 2 of 51 communities for the highest adult and infant mortality, and lowest fecundity and habitable area.

Collectively, we observe that the number of households in Makira that we estimate to be hunting tenrecs sustainably trades off with the per household consumption rate (Fig 5, Fig S8). At present, assuming 50% of hunting areas around our study communities consist of suitable spiny tenrec habitat and mean life history parameters for both tenrec species, the average household consumption per year, for the average number of households in our Makira study appears to be sustainable. However, under future scenarios in which human populations are projected to increase, or per cent spiny tenrec habitable area decreases this finding may change (Fig 5, Fig S8).

Discussion

We assessed population viability of tenrec species under a range of hunting and natural demographic threats, a first for this ecologically and nutritionally important taxonomic group. Using mean parameter estimates drawn from literature and population densities and consumption rates calculated from our own field data, we show that most current spiny tenrec hunting rates are sustainable in the communities studied in north-eastern Madagascar. However, we identified considerable uncertainty in all scenarios explored, and highlighted how assumptions of higher adult or infant mortality, lower fecundity or density, or reduced habitat rapidly undermine these outcomes, resulting in distinctly unsustainable hunting practices. We predicate these more pessimistic

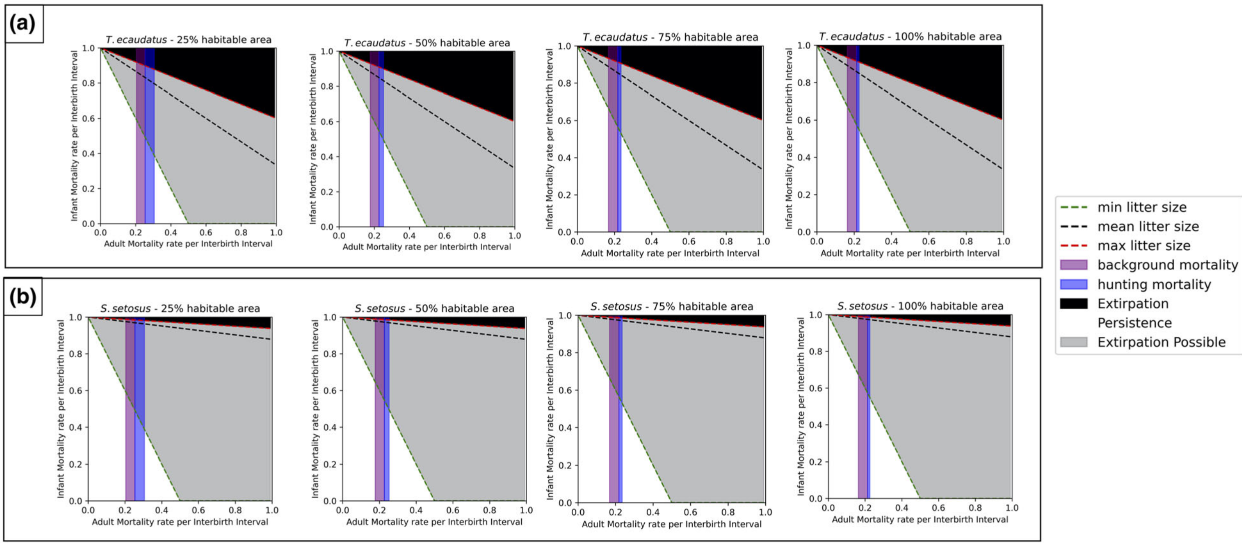

Figure 3 Population growth isoclines for *Setifer setosus* and *Tenrec ecaudatus* based on reported life history parameters in the literature, with total predicted mortality overlaid based on assumed habitable area. The black dotted line represents the zero-growth isocline for the mean reported litter size, while the red and green dotted lines represent where the zero-growth isocline shifts when calculated for the minimum and maximum reported litter sizes, respectively. Points in the area above the isocline (black) indicate population extirpation; points below the line indicate population persistence (white), points between the minimum and maximum litter size isoclines (grey) are more indeterminate, and points on the isocline indicate zero-growth. The colored band represents the 95% confidence interval for total adult mortality (background + hunting-induced). The purple portion of the band represents the range of background mortality as derived from the literature (15–20% per year), and the blue band represents the 95% confidence interval on hunting-induced mortality added to this background

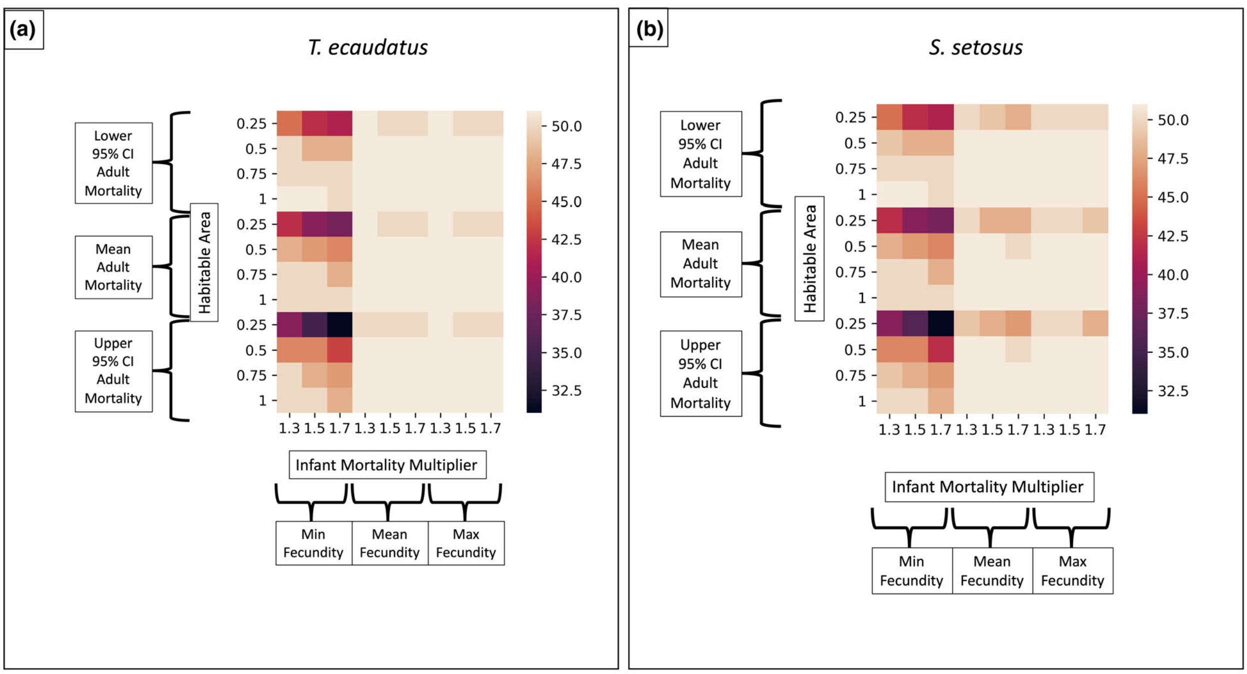

Figure 4 Number of communities (of 51) with sustainable spiny tenrec mortality under various parameter estimates. The x and y axes correspond to different combinations of parameter estimates (as labelled), while the color (as denoted by the scale bar) corresponds to the number of communities with sustainable hunting rates for the given parameter estimates. Darker colors indicate fewer communities with sustainable hunting

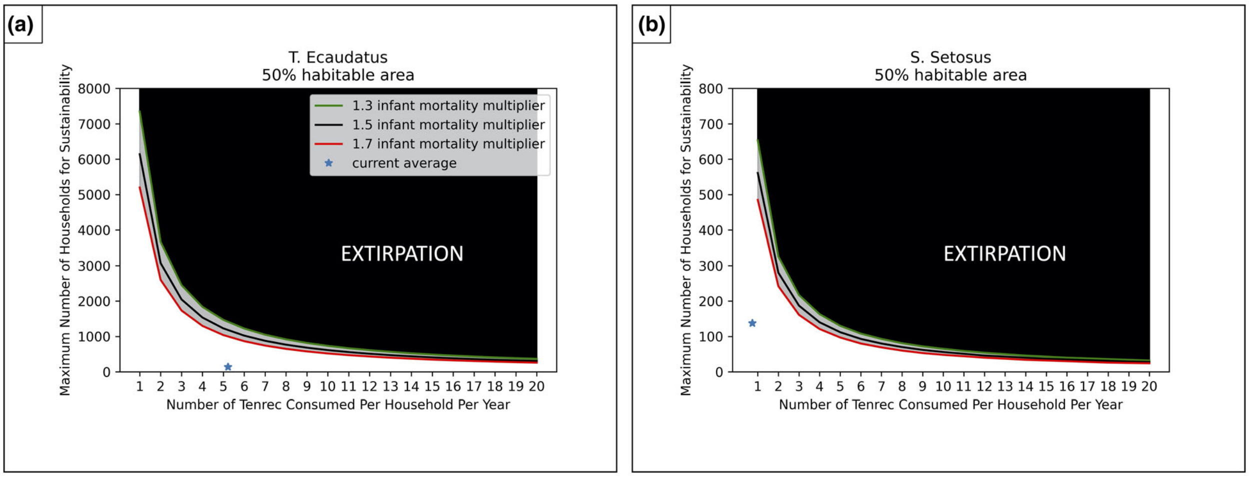

Figure 5 Predicted maximum number of households for sustainable hunting of *T. ecaudatus* (a) and *S. setosus* (b): Under assumptions of mean tenrec population size, fecundity and background mortality, and 50% tenrec habitable area, the maximum number of households that can consume tenrec in the given quantity is shown. The blue star indicates the current average consumption and number of households. The green, black and red lines indicate the maximum number of households when infant mortality is set at 1.3, 1.5 and 1.7 of adult mortality, respectively. The black area corresponds to unsustainability, the white to sustainability and the grey to indeterminate sustainability

scenarios on the assumption that increasing human population growth and accelerated deforestation and habitat degradation in the Makira region are likely to affect key parameters in our analyses, including mortality rates and tenrec habitable area. Given these impending demographic and environmental changes, there is a rapidly closing window of opportunity to sustainably manage tenrec hunting in north-eastern Madagascar and avoid negative conservation and human health outcomes.

Several direct and indirect factors will likely push tenrec hunting toward less sustainable levels in the coming decade. First, current tenrec hunting rates may increase as human population sizes grow, increasing the demand for animal protein. The annual growth rate of the Malagasy population between 1993 and 2018 was 2.63% for the Analanjirofo region, which includes Makira (INSTAT Madagascar, 2019). The human population structure is largely young, with nearly 60% of the population concentrated in individuals under the age of 25 (Central Intelligence Agency, 2020). Between 2015 and 2018, the average fertility rate was 4.6 children per woman (UNICEF Madagascar, 2018). In our study area, where malnutrition is prevalent, future population growth will likely exacerbate pressures associated with food insecurity and elevate hunting rates for wildlife – with the potential to negatively impact spiny tenrec population trajectories.

Second, human population growth is also likely to accelerate deforestation in the region, thus reducing habitable area for spiny tenrecs. There is rapid deforestation (Vieilledent *et al*., 2018) across Madagascar, and forest coverage has substantially declined in Makira between 1995 and 2011 (Zaehringer *et al*., 2015). This habitat loss threatens tenrec populations (Stephenson *et al*., 2019). Moreover, habitat fragmentation, which occurs as deforestation progresses, can threaten mammalian population trajectories. In the event of intensive forest fragmentation, commonly hunted species, such as spiny tenrecs, will face dual threats from both increased hunting rates and habitat decline, in addition to other factors including climate change, invasive predators and disease.

Third, as human population growth combines with habitat loss, population declines of other targeted species may lead to increased demand for spiny tenrecs, which could, again, result in unsustainable harvest rates. Our results fit within a body of literature evaluating the population viability of other mammalian species subject to hunting pressure in Madagascar. A study of two species of hunted Malagasy fruit bats found that populations of both are subject to hunting pressures: one species, *Eidolon dupreanum*, appears resilient to these hunting threats as a result of high intrinsic survival and fecundity rates, while the other species, *Pteropus rufus*, is undergoing severe population declines, despite comparable demographics (Brook *et al*., 2019). The difference in these two species' population trajectories appears to result largely from differences in the intensity of human hunting (Brook *et al*., 2019). In contrast, other population viability analyses have shown that hunting rates are largely unsustainable for large-bodied lemurs in the same Makira region in which our study was conducted but that small-bodied lemurs with high fecundity rates (*Microcebus* and *Cheirogaleus* spp.) appear resilient to hunting pressures (Brook *et al*., 2018). In the case of lemurs, species-specific demographics appear to modulate outcomes for population viability under largely comparable hunting pressure (Brook *et al*., 2018). The sustainability of small-bodied lemur hunting echoes our findings that current rates of spiny tenrec hunting in Makira are presently sustainable. Like *Microcebus* and *Cheirogaleus* spp., both *T. ecaudatus* and *S. setosus* are small-bodied and fecund. However, these species are all subject to increased hunting pressures and background mortality caused by human population growth, deforestation and habitat loss.

Fourth, though hunting rates appear sustainable in present scenarios, there is potential for environmental stochasticity to cause local extirpations. We considered tenrec zero-growth isoclines to be unsustainable if the dominant eigenvalue of each species' Lefkovitch population transition matrix (λ) was less than one. However, at small spiny tenrec population sizes, Allee effects and stochasticity in population densities may enable local extirpations even at $\lambda = 1$ (Dennis, 2002). Therefore, the threshold for sustainable hunting may be more conservative than that presented here. If population density is indeed proportional to consumption rates, then *S. setosus*, with a lower baseline population size, will likely be more vulnerable to Allee effects than *T. ecaudatus*. If, however, *T. ecaudatus* population sizes are lower than assumed in our primary analyses, then this vulnerability, combined with the very high consumption rates observed for this species in the Makira region, will make it particularly susceptible to stochastic extirpations. Current demographic trends highlight the urgency of monitoring and managing spiny tenrec population dynamics to sustain food security in Madagascar, in light of high rates of tenrecine consumption present across our study sites.

Our research has several limitations. Due to uncertainty in the density estimates underlying our estimations of spiny tenrec population sizes, there is corresponding uncertainty in our adult mortality estimates. Furthermore, our main text assumption, by which we estimate *T. ecaudatus* densities in proportion to the ratio of *T. ecaudatus* to *S. setosus* consumption, adds additional uncertainty; the greater consumption of *T. ecaudatus* could be a reflection of taste preferences (Borgerson, Vonona, *et al*., 2018) or comparative ease of hunting due to larger size, rather than an accurate reflection of higher population density. Because of these concerns, we explore conditions under which *T. ecaudatus* densities are assumed to be equal to or less than those of *S. setosus* in our supplementary materials; these analyses emphasize that current hunting rates for *T. ecaudatus* may be considerably more unsustainable than main text estimates suggest.

Our study is further limited by uncertainty surrounding our estimates of background mortality – ideally, allometric approaches could be used to correlate population age structure to background mortality rates for tenrecs (Zullinger *et al*., 1984; Brook *et al*., 2019). However, a lack of sufficient data on spiny tenrec population age structure and up-to-date species-specific growth parameters limited this approach; instead, we relied on an estimate of background mortality in captive *E. telfiari*. Natural mortality rates may, of course, vary between different tenrec species, and it is possible that mortality rates are higher or more variable in the wild than in captivity. Morphological approaches to estimating age from eye-lens weight (Augusteyn, 2014) and molecular approaches to quantifying age from DNA methylation (Stubbs *et al*., 2017) are gaining traction in the wildlife literature. Applications of these techniques to a representative set of spiny tenrec samples would enable construction of age-frequency distributions needed to reliably estimate population-level annual mortality.

These limitations highlight the need for investment in data collection on spiny tenrec populations to guide management. Our findings offer a first attempt at understanding hunting threats to tenrec population dynamics, but their accuracy could be bolstered by more robust data describing wild tenrecine population densities and natural background mortality rates. We also caution that, though tenrecine hunting is widespread throughout Madagascar, generalizing trends from tenrec hunting in Makira to other regions may not be appropriate. As local tenrec species and their densities vary, accurate assessments of local population viability are needed to assess the sustainability of hunting rates in other regions.

It is important to interpret our results conservatively. While we find that current rates of spiny tenrec hunting in north-eastern Madagascar appear to be largely sustainable, these estimates become rapidly unsustainable when environmental conditions (such as habitable area), demographic parameters (such as fecundity and population size), or anthropogenic pressures (such as hunting rates) are altered, as is almost certain to happen in the near future. Ultimately, the results presented here offer an early warning that sustainable management of tenrec hunting must be prioritized. Throughout history, several common species have been driven to extinction through a combination of overhunting and reduced fecundity following habitat loss, including the passenger pigeon and northern cod fish (Halliday, 1980; Rose and Kulka, 1999; Burgess *et al*., 2017). To avoid such an outcome for spiny tenrecs, without compromising human health, a combination of hunting management and nutritional replacement will be necessary. Domesticated meat production, particularly of chickens, is a nascent alternative to compensate for the demand of wild meats in the region (Golden *et al*., 2014; Annapragada *et al*., 2019). Similarly, programs to increase consumption of insects as a protein source have shown early success (Tao and Li, 2018). Replacement of bushmeat consumption with domesticated meats or insect protein may be part of an effective solution that balances food security with conservation, allowing both sustainable hunting and effective nutritional provisioning. By taking steps like this, we can avoid the negative conservation and human health repercussions of unsustainable spiny tenrec hunting in Madagascar.

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Ethics approval

This research was approved by the Madagascar Ministry of Water and Forests (Permit #157/12/MEF/SG/DGF/DCB.SAP/

SCB), UC Berkeley Committee for the Protection of Human Subjects (#2010-01-608) and the Harvard University Institution for Animal Care and Use Committee (#11-30).

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Conflicts of interest

We have no conflicts of interest to declare.

Consent for Publication

All authors give their consent for publication.

Data availability statement

HSPH Office for Human Research Administration IRB 22826-01 prevents us from publicly disclosing hunter harvest data. Citations to publicly available datasets are provided in the text.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.