A nutrient-rich traditional insect for improving food security and reducing biodiversity loss in Madagascar and sub-Saharan Africa

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Abstract

Forests, and the vertebrate species within them, are irreplaceable sources of food and nutrition for millions of people living in areas of high biodiversity. Unfortunately, many of these forests are being cleared for agriculture, and many animals are threatened with extinction from unsustainable hunting. Forest clearing and the hunting of threatened species are untenable solutions to long-term food insecurity and adequate nutrition, jeopardizing these species' survival, the healthy functioning of ecosystems, and the cultural identities of local people. Working with communities to develop culturally appropriate ways for people to obtain sustainable and legal sources of food from forests outside of protected areas is a key component of improving both conservation and food security. We tested the feasibility, suitability, and viability of farming an abundant and traditionally eaten forest insect, Zanna tenebrosa (locally known as sakondry), in rural communities whose food security relies heavily on the hunting of threatened vertebrates. We found that the insect is high in macro- and micronutrients, and can be cheaply, easily, and sustainably cultivated to sustainably diversify forest food systems without increasing habitat loss. Given the range of Z. tenebrosa, which covers a broad swath of central Africa, increasing production of this native insect may support multipronged agroecological
approaches to promoting food security, adequate nutrition, and wildlife conservation.

**KEYWORDS**
Bushmeat, Entomophagy, forests, Fulgoridae, habitat, hunting, nutrition, sakondry, traditional foods, wild foods, Zanna, Zanna tenebrosa

**1 | INTRODUCTION**

Food security and biodiversity conservation are two of the greatest challenges facing the world today. People living in areas of high biodiversity often hunt forest vertebrates for essential macro- and micronutrients (Asprilla-Perea & Díaz-Puente, 2019; Gergel et al., 2020; Tata, Ickowitz, Powell, & Colecraft, 2019). Unsustainable hunting threatens many of these animals with extinction (Rowland, Ickowitz, Powell, Nasi, & Sunderland, 2016). The hunting of threatened species is an untenable solution to long-term food insecurity, jeopardizing these species’ survival, the healthy functioning of ecosystems, and the cultural identity of local people (Gardner, Bicknell, Baldwin-Cantello, Struieb, & Davies, 2019; Sunderland & Vasquez, 2020; Wilkie et al., 2016).

The interconnectedness between food security and biodiversity means that the tactics we use to tackle one will inevitably affect the other (Food and Agriculture Organization, 2013; Ickowitz, Powell, Salim, & Sunderland, 2014; Myers et al., 2017; Rowland et al., 2016). While many forecasts assume that forests must be cleared, wildlife must be hunted, or croplands must be expanded to increase food production to meet the needs of a growing global population, recent research shows that food needs can be met without biodiversity loss (Bahar et al., 2020). Strategies that embrace synergies along the agroecological continuum can improve both biodiversity and food security, and may surpass efforts to address either problem alone (Food and Agriculture Organization, 2013; Ickowitz et al., 2014; Myers et al., 2017).

Madagascar is one of the most biodiverse nations on Earth. It is home to nearly 25% of the world’s primate species and the entire diversity of extant lemur species, nearly a third of which are critically endangered because of unsustainable hunting and habitat loss (Estradal et al., 2018; IUCN, 2020). Madagascar is also one of the least food secure nations, with nearly 70% of its population living under the global poverty line, half of whom are undernourished (EIU, 2019). Within Madagascar, lemur hunting is highest in biodiverse northeastern Madagascar (Borgerson et al., 2021), where food insecurity, malnutrition, and hunting are common (Borgerson, McKean, Sutherland, & Godfrey, 2016; Borgerson, Razafindrapaoly, Rajoana, Rasolofonaina, & Golden, 2019; Golden, Fernald, Brashares, Rasolofonaina, & Kremen, 2011). The diet here is severely deficient in both calories and fat, and 40% of meat eaten by pregnant or lactating women comes from wildlife (Golden et al., 2019). Increasing the affordability, accessibility, and stability of nutrient-rich meat in such forest-dependent communities, without increasing habitat loss, is paramount for improving both human livelihoods and conservation in Madagascar.

Insects are an important source of food for two billion people; 2,100 species are eaten in 130 countries worldwide, including Madagascar (Dürr, Andriamazaoro, Nischalke, et al., 2019; Jongema, 2017; Randrianandrasana & Berenbaum, 2015; Van Itterbeeck et al., 2019). One traditionally eaten and preferred species of forest insect, Zanna tenebrosa (Fabricius, 1775; Fulgoridae, Hemiptera; locally known in Madagascar as sakondry), is a particularly intriguing candidate for farming. We find that, unlike other farmed insects (e.g., crickets; Halloran et al., 2016), Z. tenebrosa does not require high-quality feed, can be open-air reared on easily grown bean plants, and does not colonize or feed from any other agricultural crops. In this study, we worked with primary forest adjacent communities in northeastern Madagascar to co-develop methods for Z. tenebrosa ‘farming.’ We examined Z. tenebrosa farming’s: (a) feasibility and success, through a pilot community rearing program; (b) viability, through human perceptions of the insect and its farming; (c) the insect’s nutritional, microbial, and antimicrobial properties, and potential effects on current malnutrition and food insecurity; (d) effects on the production of host plants, to determine if both beans and insects can be grown simultaneously; (e) effects on forest clearing, to ensure such efforts are capable of improving nutrition and food production without requiring additional land and increasing habitat loss; and (f) potential nutritional and conservation impacts on a broader global scale.

**2 | MATERIALS AND METHODS**

We applied the following multidisciplinary methods, from January 2019 through December 2020, to examine the potential of dedicated Z. tenebrosa (locally known as sakondry) rearing to improve food security and nutrition, while increasing the sustainability of wildlife hunting on...
the Masoala Peninsula of Madagascar. To maximize project impact, we invited five communities (two control and three test), comprised of 312 households, whose food security relied most on forests to collaborate in our research (identified from Borgerson et al., 2019). All participants provided verbal free and informed verbal consent and/or assent prior to the start of the project. This research was approved by Human Subjects Institutional Review Boards (#IRB-FY18-19-1349 Montclair State University), the Republic of Madagascar, and Madagascar National Parks (#104/19/MESSupRes/SG/DGRP/PBZT/DIR).

2.1 Feasibility and success of Z. tenebrosa farming

We identified host plants grown in the region to use for rearing Z. tenebrosa, including Phaseolus lunatus, Phaseolus vulgaris, numerous domestic and wild species of the genus Vinga, including V. umbellata, V. unguiculata, and V. marina, and Psophocarpus scandens. In 2019 and 2020, community members received seed stock for seven varietals of P. lunatus and V. umbellata, as well as training on Z. tenebrosa cultivation. Most (93%) households planted nitrogen-fixing beans in their own unused or underused horticultural, agricultural, fallow, communal, and/or backyard lands to improve food production without clearing. During Year 1 of production, 81% of households raised plants to maturity, with a slight decrease to 75% of households in Year 2. Over 4,414 plants reached maturity during the first two years of project (more than three times this many reached seedling size [13,372], as plant survival rates were low [33%]) and supported sakondry at the three test sites. No Zanna adults, nymphs or eggs were moved to the plants; wild Zanna arrived on their own to these plants, reproduced, and quickly established manageable populations. We monitored each host plant’s growth, Zanna population size and structure, and bean and insect harvest on a biweekly basis. Finally, we surveyed all households (312) in five communities (three test, two control) about their investments, profits, and losses from various types of livestock farming, as well as their perceptions of the program’s success.

2.2 Viability of Z. tenebrosa farming

If people consider Z. tenebrosa a highly valued food item, then a program to increase access to them would be more likely to succeed. When beginning Z. tenebrosa farming, we used 107 consumer taste-tests, with 100 g samples of whole, dry pan-roasted Z. tenebrosa and powdered baked crickets (Gryllus madagascariensis), to measure opinions and sensory perceptions of taste, cleanliness, texture, smell, and appearance in Likert-scaled and open-ended qualitative surveys. While G. madagascariensis is not eaten in the region, it was included in the consumer test tastes, as crickets are the insect most often recommended for food production programs. Taste test participants ranged from age 7 to 84 (95 adults age 30–55, 9 young adults age 18–29, 13 children). We also held 12 focus groups, with 6–10 participants each, to identify, rank, and sort photographs of Z. tenebrosa, threatened hunted lemurs, and 100 other commonly eaten farmed, purchased, and wild foods based on their taste and perceived identity (i.e., an children’s/adult, male/female gendered, meal/snack, national/foreign, healthy/unhealthy, tasty/not tasty, and clean/unclean food).

2.3 Human impacts of Z. tenebrosa farming

2.3.1 Preliminary nutritional, microbial, and antimicrobial analyses

We collected 500 g of Z. tenebrosa from farmed plots to determine their nutritional and microbial content, as well as their antimicrobial properties. The life cycle stages collected are representative of what is eaten—primarily last instar stage insects supplemented by adults of both sexes. We dry pan-roasted the insects with salt in the traditional manner and brought them to the Laboratoire de Microbiologie et Nutrition at the Centre National de Recherches sur l’Environnement in Antananarivo, Madagascar, for analysis one week after collection. Individual methods to determine the physiochemical and microbiological composition of the samples are presented in Supplementary Materials (Table S1). Antimicrobial analysis was completed using the techniques in Tekwu, Pieme, and Beng (2012) with a 6 mm disk, a cellular concentration of 106 cells/ml, and an extract concentration of 2,000 μg. An extract was considered active if the diameter of the inhibition halo was greater than or equal to 10 mm.

2.3.2 Food security, dietary diversity, and malnutrition

We used weekly, monthly, and annual surveys of 1,118 individual members of 312 households, asking each a total of 3,024 questions about their food security and the quantity, origin, cost, production, hunting, and/or acquisition of 175 different wild and cultivated foods eaten during the prior 24 hr, the past week, and the past year,
during a 1–2 hr interview. We surveyed individuals from five communities (three test and two control, matched for their ecological and sociological similarities). We surveyed all households in small communities. In communities with greater than 75 households (one of the five communities), we randomly selected 50 study households by using a grid system, assigning a number to each household in each grid, and selecting a subset of households in all quadrants using a random number array. We estimated the value of non-purchased animals by using the mean sale/purchase price for age-class/unit of each item, determined from household recalls of livestock sales and meat consumption during the prior 24 hr and week. We analyzed dietary diversity using the Minimum-Dietary-Diversity-for-Women scale (Food and Agriculture Organization and FHI 360, 2016) and food insecurity using weighted Coping-Strategies-Indices (CSI; CARE, 2008). We defined food insecure households as those which lacked adequate food to feed their family ≥1 day during the prior week. We used weekly surveys on insect consumption to calculate the nutritional value provided by Zanna. During interviews, we collected indicators of health and malnutrition from 1,118 individuals aged 12 days to 93 years old (all available members of the 312 interviewed households). We measured individual height, weight, and mid-upper arm circumference (MUAC), and used WHO guidelines to determine whether individuals were malnourished, stunted, underweight, wasted, or had severely low BMIs (WHO, 2006). We converted all household members into their adult male equivalent (AME) score using FAO guidelines (Weisell & Dop, 2012).

2.4 Effects of Z. tenebrosa on host plants

One of the appealing aspects of farming Z. tenebrosa is its ability to be reared on bean plants. To quantify impacts on bean production, we designed a separate controlled experiment using 40 P. lunatus plants, each grown within a netted structure 12 m×2. Twenty were enclosed with, and twenty exclosed from, Z. tenebrosa. We added 50 late-instar nymphs and adult Z. tenebrosa to each enclosure, allowing the insects to reproduce freely. We measured the number of ripe bean pods and the dry weight of beans daily. To examine differences between plants grown with and without bugs, we first used Shapiro–Wilk’s test of normality and Levene’s test of equality of variances (Rv.3.5.1), using a two-sample t test when both assumptions were met, and an independent two-group Mann–Whitney U test when normality was violated.

2.5 Effects of Z. tenebrosa on forest clearing

We analyzed differences in tree clearing within 50 forest plots in communities where we farmed Z. tenebrosa (test) and where no action was taken (control). We established 2 transects, each 2 km in length, at each site, and GPS marked 10 habitat plots in 200 m increments, 20 m from the transect line. Each 20 m diameter plot was composed of three concentric circles. In the first circle (1 m radius), we identified and counted (or estimated the percentage of ground cover of) all small plants, that is, woody seedlings and herbaceous ground cover with a diameter at breast height (DBH) <2.5 cm. In the second circle (3 m radius) we identified, counted, and measured the DBH and height of woody stems of medium-sized plants, that is, shrubs, saplings, and woody and herbaceous climbers (vines and lianas) between 2.5 and 10 cm in DBH. In the third circle (10 m radius), we identified each tree with a DBH greater than 10 cm, and recorded its geographic location, vernacular name, DBH, and height.

2.6 Potential global impact of Z. tenebrosa farming

Z. tenebrosa farming methods can benefit forests and people beyond Madagascar. To measure potential broader impacts of Z. tenebrosa farming and its suitability for sustainably improving food security in areas of high biodiversity on a greater geographic scale, we estimated the potential range of Z. tenebrosa by compiling published data on insect species presence (Lallemand, 1959; Metcalf, 1947) and museum specimens with known collection localities (GBIF Secretariat, 2020; Table 1), and examined the overlap of this range with both food insecurity and regions of high forest biodiversity. People who are currently undernourished in areas of high biodiversity are likely to rely on forests to meet their food needs. We used the Global Food Security Index (GFSI; Economist Intelligence Unit, 2019) and National Biodiversity Index (NBI; SCBD 2020) to estimate national risk of natural resource use exploitation (Molotoks, Kuhnert, Dawson, Smith, & Molotoks, 2017). GFSI is a composite measure of food affordability, availability, and quality, ranking 113 countries from most (1) to least (113) secure. The NBI measure is based on estimates of a country’s species richness and endemism in four terrestrial vertebrate classes as well as vascular plants, and ranks vertebrates and plants equally. Index values range between 0.0 and 1.0, with 1.0 being the highest.
One hundred and sixty-one nations were assessed for NBI in the database at the time of access, and we ranked them and determined their global percentiles to allow for comparisons. We then overlaid country-level GFSI and NBI percentiles with *Z. tenebrosa*’s range with to identify countries where insect farming would have the greatest impact on natural resource conservation (Table 1).

### 3 | RESULTS

#### 3.1 | Feasibility and success of *Z. tenebrosa* farming

Wild *Z. tenebrosa* of various instars and sexes arrived on plants after they reached 29 cm in length/height; 12.0% of first arrivals on plants were adult females, 32.0% were adult males, 20.0% were last instars, 20.0% were fourth instars, 4.0% were third instars, and 12.0% were first or second instars. However, the first appreciable colonies of >15 insects occurred once plants reached 1.4 m. The smallest plant to support a female who laid an egg case was also 1.4 m tall (although females were often observed to lay on dead growth and other dead plants nearby as well as on small plant cuttings and other dead wood).

During the first year of production (2019) alone, these plants (n = 1,534) supported a colony of 89,542 harvestable insects, demonstrating the responsiveness of the system and expected capacities of a program within its first year of establishment. To date, at least 91,507 *sakondry* have been eaten in addition to this maintained population. Given that planting in our study was voluntary and planting dates were variable throughout the year, potential production is likely much higher.

*Z. tenebrosa* are harvested during their fifth instar, especially during the final days before their last shed, when the insects put on a large amount of fat. This stage is preferred over earlier instars (when insects are small) or adults (which have less fat and a different texture due to increased chitin). We discouraged the harvest of adult females in case they had not yet reproduced. Of the live insects on each plant after collection, 34.94 were instars too small for harvest (10.80 ± SD15.56 fourth instar, 12.00 ± SD16.73 third instar, and 12.09 ± SD17.13 first and second instars); 26.14 were of harvestable size (22.68 ± SD123.54 fifth instar, 1.73 ± SD2.79 adult males, and 1.73 ± SD2.60 adult females); and an additional mean of 5.48 ± SD10.01 insects were harvested.

Production exceeded harvest; people collected 60.9–75.7% of fifth instar, or 44,736 insects, and 107.97 kg of

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**Table 1** Percentiles of global biodiversity and food insecurity within countries where *Zanna tenebrosa* has been reported

| Country b | Biodiversity Percentile (%) c | Food Insecurity Percentile (%) d | *Zanna tenebrosa* Presence Reported In |
|-----------|-------------------------------|----------------------------------|---------------------------------------|
| Angola    | 70.8                          | 88.5                             | Lallemand 1959                        |
| Benin     | 66.5                          | 75.2                             | Lallemand 1959                        |
| Congo, Democratic Republic of | 75.2                          | 97.3                             | Metcalf 1947, Lallemand 1959           |
| Congo, Republic of | 74.5                          | -                               | GBIF 2020                             |
| Gabon     | 70.8                          | -                                | Metcalf 1947, Lallemand 1959           |
| Guinea    | 62.1                          | 85.8                             | Fabricius 1775, Metcalf 1947           |
| Liberia   | 52.8                          | NA                               | Lallemand 1959                        |
| Madagascar | 93.2                          | 95.6                             | Metcalf 1947, GBIF 2020                |
| Malawi    | 67.7                          | 92.0                             | Metcalf 1947                          |
| Mozambique | 43.5                          | 92.9                             | Metcalf 1947, GBIF 2020                |
| Nigeria   | 49.7                          | 83.2                             | Metcalf 1947, Lallemand 1959           |
| Senegal   | 41.0                          | 71.7                             | Metcalf 1947, Lallemand 1959           |
| Sierra Leone | 75.8                          | 93.8                             | Metcalf 1947, Lallemand 1959           |
| South Africa | 87.0                          | 42.5                             | Metcalf 1947, GBIF 2020                |
| Tanzania, United Republic of | 80.1                          | 85.0                             | Metcalf 1947, GBIF 2020                |
| Togo      | 85.1                          | 90.3                             | Metcalf 1947                          |
| Uganda    | 77.0                          | 86.7                             | GBIF 2020                             |
| Zambia    | 47.2                          | 89.4                             | GBIF 2020                             |

Abbreviations: GFSI, Global Food Security Index; NBI, National Biodiversity Index.

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bSpecimen location is based on geographic locality, and specimens were alternatively listed as present within Belgian Congo; Congo belge: Matadi, Stanleyville, Cabinda; Congo français, Libreville; Tanganyika and Zanzibar; Nigérie du sud; Natal, Cape of Good Hope; and Nyasaland.
cCalculated from the NBI (SCBD, 2020).
dCalculated from the GFSI (EIU, 2019).
eMuseum specimens.
beans during the first year of establishment. On any given day, each bean plant supported a mean 64.52 live *Z. tenebrosa* (SD 137.53, median = 33) and 1.27 egg cases (SD 2.03, median = 0). During 2 years of production, each household ate 2,014.64 g in dry weight (SD 3,064.73) and produced an additional 5,496 g (SD 5,429.54) (1,097 g during Year 1 and 3,044 g during Year 2) of sakhondry. Deviation in production among households was high. The maximum number of insects produced by a single household in one year was 24,552. In contrast, households within our control communities ate a mean 5.49 wild *Z. tenebrosa* (SD 25.62) during the same period.

All households reported a net profit in food or income from *Z. tenebrosa* production. Households sold one *kapoaka* (a standard local measurement using a heaped empty condensed milk tin), for 5,000–10,000 MGA (Malagasy Ariary; median market price = 7,000 MGA, or $2.80). Households harvested 3,011,351 MGA (Year 1) and 5,369,100 MGA (Year 2) in insects at a mean household annual investment of 0.20 days labor (SD 2.32) and < 100 MGA ($ <0.01) after seed stock distribution (SD 386 MGA or $0.10; Table S2). Perceived volatility of production and human-wildlife conflicts over production were both low compared to poultry, and the value of insects held per household surpassed that held in ducks and achieved 60% of chickens within the first year of production (Table S2).

### 3.2 Viability of *Z. tenebrosa* farming

Participants consistently ranked *Z. tenebrosa* over both traditionally eaten (e.g., beetle larva) and potentially farmed (i.e., crickets) insects during both consumer taste tests (Table S3) and focus groups. All respondents (100.0%) reported positive language to describe sakhondry. Nearly two-thirds (59.7%) of participants described the insect as rich (“*matavy*”) and/or delicious (“*fy*”), 52.2% as a good food they liked (“*tsara*” or “*tiako*”), 3.0% as healthy (“*manaboaka fahasalamana*” or “*vitamin feno*”), and 6.0% described it as superior to any other food because it was “filling, tasty, and you did not need oil to cook it.” When asked, “Would you be ashamed to serve a meal with _____ if a guest were eating at your house?” only 7.7% reported they would be ashamed if it included *Z. tenebrosa* (because “even though we really like them, we don’t know how accustomed people from other regions are to them”). In contrast, while most (72.5%) people also described crickets using at least one favorable word, and the flavor of the powdered insect was compared with commonly eaten small dried fresh-water shrimp, 15.0% of respondents described it as having a poor texture (“*mafakofako*”), 15.0% as bad or inedible (“*ratsy*” “*tsy tsara*” “*tsy dia sakofo loatra*”), and 12.5% as okay (“*antony*” “*tsaratsara*” “*tsy dia tsara*”). One-third (30.0%) reported they would be ashamed to serve a meal which included crickets.

Respondents reported that native, traditionally eaten foods like insects and lemurs, were foods associated with Malagasy identity (*sakafo gasy*), whereas poultry and other livestock were considered “foreign” (*sakafo vazaha*); 90.1% of focus groups identified lemur-meat, 100% *Z. tenebrosa*, and 90.1% other local insects as “national”, and 81.2% classified poultry and other livestock as “foreign.” *Z. tenebrosa* were seen as tasty, appropriate for all ages and genders, and clean because they live above the ground and are thus distanced from potential waste.

After one year of *Z. tenebrosa* farming, 82.8% of test households were “very happy” with the project, 17.2% “pretty happy,” and 0% “unhappy” or “unsure.” Most control households (99.6%) wished to eat the insect more regularly and 95.9% wished to be included in project expansion. Only 0.7–2.4% of people did not eat the insect because of inherited familial proscriptions (a food taboo or *fady*, common across Madagascar). The primary reported barrier to farming expansion and participation, from those who wished to farm the insect in both test and control households, was insufficient high-quality seed stock and low seedling survival.

### 3.3 Human impacts of *Z. tenebrosa* farming

#### 3.3.1 Nutritional, microbial, and antimicrobial analyses

*Z. tenebrosa* are a high protein, low carbohydrate food that is rich in essential lipids and many essential micronutrients (Table 2, Figure 1): 100 g of *Z. tenebrosa* yields 471.45 kcal, 7.91 mg zinc, 4.69 mg iron, and is comprised of 34.7% protein and 34.9% lipids. When stored, the cooked Zanna samples did not contain harmful microorganisms including coliform bacteria, *Escherichia coli*, salmonella, *Staphylococcus aureus*, *Bacillus cereus*, *Clostridium perfringens*, intestinal enterococci, or *Vibrio* (Table 3). This confirms our experience that, unlike other meats, cooked *Z. tenebrosa* preserve extremely well at ambient temperatures (i.e., >2 months in a rainforest environment, with occasional reheating). In fact, stored insects showed significant antimicrobial activity against *Streptococcus pneumoniae* (Table 4).

#### 3.3.2 Food security and nutrition

Food insecurity, malnutrition, and hunting were prevalent in the surveyed communities. Most households
(72.8%) were food insecure (CSI mean = $2.29 \pm 2.43$; median = 2.00) and dietary diversity was low (mean score $3.44 \pm SD1.13$; $3.06 \pm SD0.88$ control and $4.60 \pm SD0.86$ test). Half (50.8%) of children under age 5 ($n = 120$) were stunted (Table S4) and the MUAC of children under age five ($n = 86$) indicated that 45.3% were severely malnourished, 11.6% were moderately malnourished, 27.9% were at risk of malnourishment, and 15.1% had values within the ‘normal’ range.

Half of weekly household expenditures were used to buy food (mean 49.8 ± 30.0%; median 60.5%); a third of this (mean 36.5 ± 35.9%; median 18.7%) was used to buy a meat or vegetable, which is typically eaten on top of rice. While 76.0% of households ate at least one animal product (wild or domestic) during the prior week, 84.6% worried that they did not eat enough meat. A mean of $4.22 \pm 17.22\%$ of all meat eaten during the prior 24 hours came from forests (range 0–100%) and nearly all households (93.1%) ate at least one forest mammal or bird during the prior year (mean of 9.58 forest mammals and 9.82 birds per household), including a mean 0.84 threatened lemurs (a total of 1,677 mammals [including 142 lemurs] and 1,660 birds for all surveyed households).

Following the introduction of Z. tenebrosa farming, 20.3% of households were able to move from low to

### Table 2

| Parameter               | Composition |
|-------------------------|-------------|
| **Macronutrient**       | %           |
| Protein                 | 34.68       |
| Carbohydrates           | 4.68        |
| Total Lipids            | 34.89       |
| Moisture                | 15.22       |
| Ash                     | 10.53       |
| Energy (kcal/100g)      | 471.45      |
| **Micronutrient**       | mg/100g     |
| Calcium (Ca)            | 20.96       |
| Chromium (Cr)           | 0.20        |
| Copper (Cu)             | 0.83        |
| Iron (Fe)               | 4.69        |
| Potassium (K)           | 476.89      |
| Magnesium (Mg)          | 50.85       |
| Manganese (Mn)          | 1.36        |
| Sodium (Na)             | 3.59        |
| Phosphorus (P)          | 321.74      |
| Nickel (Ni)             | 0.13        |
| Zinc (Zn)               | 7.91        |
| **Heavy metals**        | mg/100g     |
| Cadmium                 | 0.10        |
| Lead                    | 0.21        |

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**Figure 1** Comparison of nutritional content of dry-roasted Zanna tenebrosa, beef, and chicken. The nutritional data for beef (boiled, 15–20% fat) and chicken (dark meat, boiled, with skin) comes from Stadlmayr et al. (2012). Cooking methods were selected based on how the meat is most commonly eaten at the site and were not adjusted for dry matter content (Z. tenebrosa = 15.2%, beef = 49.1%, chicken = 58.6%)
medium dietary diversity. Farmed *Z. tenebrosa* provided each AME (adult-male equivalent) an additional annual maximum of 1,935 insects per person, or 9,816 kcal, 722 g protein, 726 g fat, 165 mg zinc, and 98 mg iron, and an annual mean of 378.28 ± 360.47 insects per person, or 1,918 kcal, 141 g protein, 142 g fat, 32 mg zinc, and 19 mg iron. This equates to a per-plant mean of 305 kcal, 23 g protein, 23 g fat, 5 mg zinc, and 3 mg iron in insects. Given that these plants also produced edible beans, the nutritional benefits from each plant were even higher.

### 3.4 Effects of *Z. tenebrosa* on host plants

*Z. tenebrosa* had minor effects on host plant production. The number of ripe bean-pods at any given timepoint was not significantly different between plants which were exclosed from, or enclosed with, *Z. tenebrosa* (mean 10.72 ± SD10.76 vs. 8.77 ± SD8.78 ripe bean-pods; *W* = 3,652.5, *p* = .1071; Figure 2). The weight of dried beans was on average 43 mg, or 10%, lighter on plans enclosed with *Z. tenebrosa*, likely a biologically insignificant, if statistically significant, difference (*T* = 2.5123, *p* = .013; Figure 2). Further, even after farming was well established, *Z. tenebrosa* did not feed or colonize any other agricultural crops (including rice, maize, and cassava), even when in close proximity to the host plant.

### 3.5 Effects of *Z. tenebrosa* farming on forest clearing

Before *Z. tenebrosa* farming began, the test sites had a mean of 93.9 plants of any size, and 6.8 large trees per forest plot, with a mean large-tree height of 17.0 m and DBH of 21.55 cm. The control sites had a mean of 43.15 plants of any size, and 5.1 large (DBH ≥ 10 cm) trees per forest plot, with a mean large-tree height of 13.6 m and DBH of 18.24 cm. Tree loss in habitat plots was similar between test...
and control sites ($T(29.64) = 0.80, p = .43$); plots at test sites lost a mean of $2.13 \pm SD4.73$ large trees, whereas control sites lost $3.6 \pm SD7.28$.

### 3.6 Potential global impact of Z. tenebrosa farming

Z. tenebrosa are documented in 18 countries (Figure 3, Table 1), all but two of which are within the quartile of the world’s least food secure nations (EIU, 2019). Further, seven rank within the quartile of the world’s most biodiverse nations, with Madagascar eleventh globally, and number one within Africa (SCBD 2020; Figure 3). However, no data on the traditional consumption and perceptions of the insect outside of Madagascar exists, and is a priority for future research.

### 4 DISCUSSION

Farmed Z. tenebrosa can provide traditional sources of macro- and micronutrients in regions of low food security and high biodiversity without the need to increase agricultural land or reduce forest biodiversity. In Madagascar, native Z. tenebrosa: (a) can be easily, rapidly, and cheaply cultivated in remote communities with limited connection and infrastructure; (b) are a traditionally eaten food perceived as wild, ‘natural,’ clean, flavorful, rich, cheap, available during seasons of low food security, and tied to local identity; (c) are high in essential micro- and macronutrients; (d) can be raised on agricultural bean host plants without greatly affecting bean production; (e) can be farmed without increasing agricultural lands or forest clearing; and (f) have a wide native range that overlaps with areas of low food security and high biodiversity, making the project potentially replicable across all of Madagascar and much of sub-Saharan Africa.

Z. tenebrosa are a nutritious and sustainable food. Like beef, chicken, pork, and other edible insects (Nowak, Persijn, Rittenschober, & Charrondiere, 2016; Rumpold & Schlüter, 2013), Z. tenebrosa offer valuable sources of macro- and micronutrients which are both essential to proper human physiological functioning and are deficient across its range. When prepared in the
traditional manner, *Z. tenebrosa* are superior to both chicken and beef in their energy, protein, potassium, calcium, iron, and zinc content (Figure 1).

*Z. tenebrosa*’s long shelf life and lack of microbial activity when stored may be, in part, due to the insect’s significant antimicrobial activity against *S. pneumoniae*. *S. pneumoniae* is responsible for over 10% of deaths in children under age five, and is the leading cause of pediatric sepsis, meningitis, and bacterial pneumonia (O’Brien et al., 2009). Because bacteria are developing resistance to many commonly used antibiotics (Society of Infectious Diseases, 2011), the documentation of such properties in plants and animals, such as this insect, is important.

In contrast to many other agricultural initiatives which require additional land, our efforts embrace the role of forests in food security and improve agricultural output and nutrition without increasing habitat loss. Food insecurity and poverty can create strong incentives to clear and collect biodiversity at high rates to meet subsistence needs (Barrett & Arcese, 1998; Barrett, Travis, & Dasgupta, 2011; Dasgupta & Maler, 2004). Unsustainable use can lead to environmental degradation, and further reduce human welfare, in a cycle of food insecurity, malnutrition, poor health, and biodiversity loss (Ngonghala et al., 2014, 2017). Yet ‘farming’ *Z. tenebrosa* allows communities to increase their reliance on local forest foods, which arrive on their own and reproduce quickly to establish co-cropped populations on fast-growing legumes, while only minimally impacting the simultaneous production of edible beans on host plants. Because host plants can be grown in unused and underused agricultural areas, including on fences, along paths, and between existing crops, they further maximize land use, and reduce rather than increase incentives for forest clearing. The flexibility and responsiveness of this food production system may help prevent or reduce the unsustainable use of forest resources during times of environmental and social stress, while respecting the role those forests play. Further, because *Z. tenebrosa* are found across Madagascar (in all 22 regions) and can be raised on a wide variety of native and cultivated leguminous plants, the expansion of *Z. tenebrosa* farming, and its integration into existing conservation, food security, and reforestry efforts, is relatively straightforward.

Given the sheer number of insect species on earth (Grimaldi & Engel, 2005; Stork, 2018), and increasing recognition of the benefits of insects as food (Nowak et al., 2016), food-production systems have harnessed surprisingly few species of insects. Most commercial insect farming for food has focused on crickets and mealworms (Francuski & Beukeboom, 2020), which are not always traditionally eaten, preferred, or native. Wild, traditionally eaten insects like *Z. tenebrosa*, which can be cultivated within the broader agroecological continuum, can allow forests to continue to meet the needs of a growing global population without requiring significant human or economic capital or biodiversity loss.

The farming of *Z. tenebrosa* alone is unlikely to stop the unsustainable hunting of threatened wildlife, but it can increase food security by providing a legal, safer, and more sustainable source of ‘wildlife’ from forests. Because food insecurity is linked with the hunting of threatened vertebrate species, culturally relevant, ecosystem-based solutions are a key component of addressing unsustainable hunting across central Africa, where logistical challenges can hinder the infrastructure needed to improve animal-based food systems (Coad et al., 2019).

Given the high rates of child malnutrition, food insecurity, and endangered species hunting across *Z. tenebrosa*’s range (Wilkie et al., 2016; Estrada et al., 2018; EIU 2019; SCBD 2020; Borgerson et al., 2021), the farming of this nutrient-rich insect may help support multipronged approaches to improving wildlife conservation.

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**CONFLICT OF INTERESTS**

The authors declare no conflict of interest.

**AUTHOR CONTRIBUTIONS**

Cortni Borgerson, Brian L. Fisher, Be Noel Razafindrapaoly, Joost Van Itterbeeck, and Matthew
L. Aardema: Conceived and designed the study in coordination with local communities and secured the funding support. Cortni Borgerson, Be Noel Razafindrapao, Be Jean Rodolph Rasolofoniana, Jeanne Mathilde Randriamanetsy, Be Lexion Razafindrapao, Delox Rajaona, and Patsy Herrera: Collected the data. Cortni Borgerson, Matthew L. Aardema, and Kenneth M. Martinez: Analyzed and interpreted the data. Cortni Borgerson, Matthew L. Aardema, and Brian L. Fisher: Wrote and edited the manuscript.

DATA AVAILABILITY STATEMENT
The anonymized datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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