MOTHS & LEGENDS

THE CONTRIBUTION OF CHITOUMOU, THE EDIBLE CATERPILLAR *CIRINA BUTYROSPERMI*, TO FOOD SECURITY, AGRICULTURE AND BIODIVERSITY IN A LOW-INTENSITY AGROFORESTRY SYSTEM

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This thesis is submitted for the degree of Doctor of Philosophy

May 2019

Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text. I further declare that it is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University of similar institution except as declared in the Preface and specified in the text.

This thesis does not exceed 60,000 words (excluding appendices and references).

Signed:

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May 2019

Summary

Moths & Legends

The contribution of chitoumou, the edible caterpillar *Cirina butyrospermi*, to food security, agriculture and biodiversity in a low-intensity agroforestry system

Charlotte L. R. Payne

The global food system is essential for sustaining human life, yet in its current form it does so at a great cost to both human and environmental health. Food insecurity and diet-related disease are responsible for 70% of deaths worldwide, and the global extinction rate is ~1000 times estimated background rates due to the widespread destruction of wild habitat for agriculture. The production of livestock for animal protein is a key driver of both trends. This thesis considers the potential of edible insects in existing agricultural systems to mitigate these problems, with a focus on the role of chitoumou (*Cirina butyrospermi*), the commonly consumed shea caterpillar harvested from agroforestry systems in Burkina Faso, West Africa.
I begin this thesis with a review of the role of edible insects in agricultural systems worldwide. Though certain insects are currently touted for commercial scale production, many popular edible insects are already harvested from existing systems, in which they prey on plant crops. These insects often cause damage to crop yields, but also provide vital provisioning, regulating, maintaining and cultural ecosystem services. Yet, few data are available to enable farmers and policymakers to weigh up the costs and benefits of edible insects in agricultural systems. Therefore, I examine the contributions of chitoumou – a popular edible insect in a region with acute food insecurity and environmental degradation – to food security, crop yields and biodiversity.

Firstly, I evaluate the contribution of shea caterpillars to food security. I show that animal protein consumption and food security are higher during caterpillar season, and that higher food security is associated with caterpillar collection, sale and consumption. Shea caterpillars contribute positively to food security, but this effect is seasonal.

Secondly, I investigate the relationship between defoliation by shea caterpillars and crop yields. Observational data show that defoliation does not have a negative association with yields of either shea (*Vitellaria paradoxa*) or maize (*Zea mays*). This challenges assumptions held by some stakeholders that it is necessary to take measures to eradicate these insects.

Thirdly, I look at the relationship of caterpillars to biodiversity, using defoliation as a proxy for caterpillar abundance and bird abundance as a proxy for biodiversity. I find no significant relationship, suggesting that defoliation by caterpillars is not a significant threat to biodiversity in this region.

Consequently, policymakers and smallholder farmers alike should recognize that shea caterpillars are not pests, and that the retention of shea trees will promote food security. However, policymakers in particular should be aware that the contribution of shea caterpillars to food security is seasonally limited. For this reason, assessments of food insecurity and strategies to mitigate food insecurity in this region are best conducted out of caterpillar season. Future research that aims to tackle acute global problems of human and environmental health using edible insects should consider the role of insects in existing agricultural systems, and quantify how such insects affect regions where these problems are most severe.

Notes on collaboration

The data and analyses presented in this thesis are the outcomes of collaborative projects that I initiated and coordinated. I am immensely grateful to all collaborators. The contributions of collaborators to each chapter, and to the Appendices, are explicitly stated below. I am the first author on all papers detailed here (except that summarised in Appendix B).

Chapter 2: [This chapter is published in *Insects* [Payne, C., & Van Itterbeeck, J. (2017). Ecosystem services from edible insects in agricultural systems: a review. *Insects*, 8(1):24. https://www.mdpi.com/2075-4450/8/1/24].] I am first author of this manuscript. I designed the conceptual framework and review process and led on the writing; this work was carried out in collaboration with Joost Van Itterbeeck.

Chapter 3: [This chapter is in review in *Food Security*.] I am first author of this manuscript. I designed the study, collected the data (together with other co-authors), analysed the data and led on the writing; this work was carried out in collaboration with Athanase Badolo, Darja Dobermann, Sioned Cox, Charlotte Milbank, Pete Scarborough, Bakary Sagnon, Antoine Sanon and Fernand Bationo.

Chapter 4: [This chapter is published in *Agroforestry Systems* [Payne, C., Badolo, A., Sagnon, B., Cox, S., Pearson, S., Sanon, A., Bationo, F. and Balmford, A., (2019). Effects of defoliation by the edible caterpillar "chitoumou" (*Cirina butyrospermi*) on harvests of shea (*Vitellaria paradoxa*) and growth of maize (*Zea mays*). *Agroforestry Systems*, 1-10. https://link.springer.com/article/10.1007%2Fs10457-019-00385-5].] I am first author of this manuscript. I designed the study, collected the data (together with other co-authors), analysed the data and led on the writing; this work was carried out in collaboration with Athanase Badolo, Sioned Cox, Bakary Sagnon, Antoine Sanon and Fernand Bationo.

Chapter 5: [This chapter is in review in *Bird Study*] I am first author of this manuscript. I designed the study, collected the data (together with other co-authors), analysed the data and led on the writing; this work was carried out in collaboration with Athanase Badolo, Tom Finch, Mohamed Moulma, Bakary Sagnon, Antoine Sanon and Fernand Bationo.

Appendix B: I am second author of this manuscript. I supervised the study, which was an undergraduate dissertation project led by Sioned Cox. I led on adapting the full dissertation thesis into a manuscript for publication. This work was carried out in collaboration with Sioned Cox, Athanase Badolo, Robert Attenborough and Charlotte Milbank.

Appendix C: I am first author of this manuscript. I co-designed the study, collected the data (together with other co-authors), analysed the data and led on the writing; this work was carried out in collaboration with Athanase Badolo, Bakary Sagnon, Antoine Sanon and Fernand Bationo.

Acknowledgements

I would like to thank my main supervisor, Andrew Balmford – thank you for believing in me throughout, and thank you for your wisdom and your patience every time I came to you for guidance, even from the other side of the world. I'd like to thank my second supervisor, Pete Scarborough, for insight and direction at times when I needed it most, and for your extreme generosity in appraising my karaoke performances. I'm indebted to my advisors, David Aldridge and Chris Sandbrook – thank you for helping me to keep my feet on the ground as I tried to tread the tricky path of interdisciplinarity.

Thank you to my co-authors. Your contributions to the content and direction of this thesis have been invaluable. Athanase Badolo, Joost Van Itterbeeck, Darja Dobermann, Antoine Sanon, Fernand Bationo, Tom Finch, Sioned Cox, Charlotte Milbank, Bakary Sagnon, Sally Pearson – thank you, it's been an honour to work with you and I hope to do so again. Thank you to all members of the Conservation Science Group; thank you for your advice, support and ideas throughout. Thank you for inviting me to be part of other exciting projects, and thank you for the inspiration I gained from every lab lunch. Thank you to my fellow academics for sharing your thoughts on my work, particularly Mike Rayner (to whom I am also grateful for everything from encouraging my interest in biology to giving me career and life advice), Kenichi Nonaka (いつもいつも楽しくて面白くて大感謝しております), Alan Yen, Josh Evans, Brian Fisher, Chris Kaplonski, Bhaskar Vira, Rene Cerritos. To Chris and Sioned, an additional thank you for our daily exchange of three good things, which have made me smile before sunrise nearly every day of writing up.

I have been extremely lucky to receive financial support for all of the work detailed in this thesis, from funding bodies and also from the public. To all who donated to our crowdfunding campaign on Experiment.com, to the Natural Environment Research Council of the UK (NERC), to the Barilla Center for Food and Nutrition (BCFN), to the Japanese Society for the Promotion of Science, to King's College, Cambridge, and to the Department of Zoology at the University of Cambridge – thank you.

I could not have done any of my field data collection were it not for the insights and generosity of Baly Ouattara. Thank you, Baly, for supporting me in so many ways during my time in Burkina. Kahit Hien, without you none of this would have been possible; thank you for all that you do and I very much hope that we continue to work together. Poda Nambepierre, I don't even know where to start. Your fierce kindness, your heartfelt laughter, and your sharp intelligence, kept me going through some extremely difficult times. Remembering such times, I wish to list the attributes of everyone who helped me during fieldwork, but to do so would take me another day. Nevertheless, I'd like to use a few lines for this, because you are all people who have changed my life. Moumouni Ouattara, thank you for being constantly uplifting and positive, and thank you for all of your hard work. Sita (Sanou Asfietta), thank you for your wisdom and understanding, and for the days we spent together doing interviews and focus groups until our bodies told us to rest. Bertine Some, thank you for your camaraderie and your frank perceptiveness, both during the working day and later, in each and every cabaret. Madou Ouattara, thank you for being someone I could trust to solve all manner of problems. Baya Ouattara, thank you for welcoming me to Soumosso, for working with me in the fields, and for always looking out for me. Sagnon Asonsi and your wonderful family, thank you also for making me feel welcome and cared for every time I came to Sitiena. The families and children of Soumosso, Koba, Larama and Sitiena – thank you for all of the joy and the insights that you shared with me, each and every day of my time living with you. Thank you for being incredible neighbours, whom I always felt I could trust and depend on. Argita and Alimatou, you rescued me. Antoinette and Albertine, I can't thank you enough for your love and kutoku.

For the past year, I've been living in a place which is in many ways very different from Burkina Faso, but is happily very similar in the most important ways. I feel lucky every day to wake up surrounded by people and animals whom I feel great love and affection for, and to know that I'm in good company no matter what the day will bring. In room order: Kyle, Helen, Lucy, Nina, Jess, Dorje, Bev, Tal, Nick, Alexander, James (I would have been lost without the male voice of reason, and I mean that with 99% sincerity – thank you). Peppe, thank you for your wry humour and gentle pawing. Apricot ducks, chocolate ducks, chickens, thank you for all of your quacks and quirks at each and every sunrise. Thank you Geoffrey Roughton, for your benevolently anarchical and infinite kindness. Thank you, to all at 9 Adams Rd, for your unwavering solidarity and support, for the music and the laughter, for the meditation and the dancing, for the cleaning and the gardening; in all times of plenty and in all times of want.

Finally, to my mother and father – thank you for everything, always. And to Dani – thank you for our life together, and for a happiness I never thought possible.

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List of acronyms

AICc	Akaike Information Criterion, corrected for small sample size
ANOVA	Analysis of variance
BCFN	Barilla Center for Food and Nutrition
bn	Billion
CFA	The West African CFA franc (currency code XOF according to the International Standard Organisation standard ISO 4217)
FAO	Food and Agriculture Organisation of the United Nations
FIP	Forest Investment Program
g	grams
GDA	Guideline Daily Amount
GLAD	Global Land Analysis and Discovery
GPS	Global Positioning System
ha	Hectares
HFIAS	Household Food Insecurity Access Scale
ICP-OES	Optima Inductively Coupled Plasma – Optical Emission Spectrometer
INFOODS	International Network of Food Data Systems
IOM	Institute of Medicine
IPIFF	International Platform of Insects for Food and Feed
IPM	Integrated Pest Management
IQR	Interquartile range
IUCN	International Union for Conservation of Nature
Kcal	Kilocalories
kg	Kilograms
km	Kilometres
mg	Milligrams
mins	Minutes
ml	Millilitres
NACIA	North American Coalition for Insect Agriculture
NCDs	Non-communicable diseases
NERC	Natural Environment Research Council, United Kingdom

NGO	Non-government organisation
NS	Not significant
QGIS	An open source geographic information system application
R	A programming language supported by the R Foundation for Statistical Computing
RCT	Randomised controlled trial
RDA	Recommended Daily Amount
RISD	Rhode Island School of Design
RNI	Reference Nutrient Intake
RRD	Red ring disease
SI	Sustainable Intensification
ton	United States ton (2000lbs)
tonne	Metric tonne (1000kg)
UK	United Kingdom
UNHCR	United Nations High Commissioner for Refugees
UNICEF	United Nations Children’s Fund
US	United States
USD	United States dollar
VIF	Variance Inflation Factor
WFP	World Food Programme
WHO	World Health Organisation of the United Nations
wk	Week
yrs	Years

This sustenance
Will not sustain, unless -
Consider insects.

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Chapter 1. Introduction

1.1 THE GLOBAL FOOD SYSTEM IN CRISIS

The global food system sustains human life worldwide, yet also threatens the health and economic security of billions of people, and the existence of thousands of wild species. Diet-related health problems are prolific and varied. Thirty-two percent of children under 5 in low- and middle-income countries are stunted due to undernutrition (Tzioumis et al. 2016), whilst 500 million adults worldwide are clinically obese (Seidell and Halberstadt 2015). Diet-related non-communicable disease was responsible for 70% of deaths globally in 2013 (Benzinger et al. 2013), and 54% of children under 5 worldwide suffer from anaemia, the most prevalent micronutrient deficiency (Perez-Escamilla et al. 2018). Environmental problems associated with the global food system are also intensifying. In the past century, natural forests, wetlands and grasslands have been steadily cleared to make way for cropland and pasture for food production (Ramankutty et al. 2018), and species extinction rates are estimated at approximately 1000 times higher than estimated background rates (De Vos et al. 2015). Current growth suggests that the environmental impacts of the food system will rise by 50-90% by 2050, significantly accelerating biodiversity loss (Springmann et al. 2018).

While the prevalence of undernutrition is declining (Tzioumis et al. 2016), overnutrition is increasing worldwide (Seidell and Halberstadt 2015). Both overnutrition and undernutrition are associated with micronutrient deficiency (Zhao et al. 2015; Christian et al. 2018). Dramatic increases in crop yield now produce enough calories to feed the global population, yet despite this billions of people still live in perpetual nutritional or caloric insecurity (Ramankutty et al. 2018).). Nutritional insecurity – whereby diets contain sufficient calories but lack adequate nutrients for health – most commonly involves a lack of adequate protein or iron. Protein inadequacy affects 0.7-35% of children by continent worldwide (Ghosh et al. 2012), and iron-deficiency anemia affects 32% of children (Stoltzfus 2003) worldwide. These are manifestations of food insecurity that, in addition to caloric inadequacy, have serious consequences for health and child development. Smallholder farmers, who produce over half of the world's food calories, are disproportionately likely to be food insecure (Sibhatu et al. 2017). Therefore, while novel technologies that increase yields from existing cropland may be part of the solution, evidence suggests that this alone will not necessarily increase food security nor public health (DeFries et al. 2015). Dietary diversity, sanitation, clean water and women's education are key drivers of increased food security, all equally or more important than caloric intake (Ramankutty et al. 2018). High food insecurity is commonly associated with undernutrition (Weigel et al. 2016) and micronutrient deficiency (Ghose et al. 2016), but may in some regions be associated with high prevalence of overnutrition due to the relatively low cost of energy-dense snack foods (Gubert et al. 2016).

One possible solution involves increasing the production and consumption of meat from livestock. Meat is high in protein and iron, and higher meat intakes are associated with better health outcomes in low-income countries (Jackson et al. 2016). However, high meat consumption also predicts incidence of some diet-related non-communicable diseases (NCDs) in wealthier countries (Godfray et al. 2018). Most crucially, though, the environmental impacts of meat and dairy products from livestock exceed the impacts of plant-based foods (Clark and Tilman 2017). This is in part because mammals and poultry occupy a higher trophic level than plants. Since energy is lost at each stage of the food chain, the yield per unit area is lower than that of plant-based food. In the case of ruminants, methane emissions are also a significant part of their environmental footprint (Johnson and Johnson 1995). Without major technological or systemic change, the global livestock sector alone will exceed estimates of 'safe' limits to human impacts on the environment by 2050 (Pelletier and Piedmers 2010).

Our food system is reaching crisis point, yet the global population – currently 7.2 billion – is forecast to grow to 9.6 billion in the next three decades (Gerland et al. 2014). This will only exacerbate problems that are already severe; we must find new ways to approach food production worldwide, particularly in the case of animal protein.

1.2 Proposed solutions

This is not the first time that humans have been concerned about the need to feed a growing population. However, the problems described above are occurring on a far greater scale than ever before. In response, a great deal of research and investment is being directed towards finding effective solutions. One broadly advocated concept is sustainable intensification (SI). SI states that the key targets that must be met in ensuring food security are increases in both production and yield per m^2 of land, and that methods used to achieve this must be environmentally sustainable (Garnett et al. 2013). This approach has gained a great deal of attention and support, but has also been criticised for being ill-defined, since it is not characterised by any single technology and even experts in the field disagree on its operational definition (Peterson and Snapp 2015). Alternatively, a mixed strategy that combines land spared for wild nature with both high and low intensity farming may be the best solution within a given landscape (Finch et al. 2019). Another is the production and promotion of less land-intensive sources of protein, which could have a major impact on improving food system sustainability given the environmentally destructive nature of the current global livestock sector (Clark and Tilman 2017). Research into alternatives to livestock-derived protein has yielded several possibilities, including artificial meat (Bhat et al. 2015), microbial protein (Matassa 2016) and insects (Van Huis and Oonincx 2017). Although these protein sources may be nutritionally adequate meat alternatives that could significantly reduce the environmental impacts of the food system, all require further research and development. Ultimately, there will be no single panacea to solve all of the problems within the global food system, and as such, all approaches warrant thorough consideration.

1.3 EDIBLE INSECTS AS AN ALTERNATIVE SOURCE OF PROTEIN

Of these alternative sources of protein, edible insects have been the first to become more widely available to consumers. The promotion of insects as an environmentally preferable alternative to conventional livestock was suggested by scientists in the 1970s (DeFoliart 1975, Meyer-Rochow 1976), but was first initiated on a larger scale by the Food and Agriculture Organisation of the United Nations (FAO) via reports published in 2010 (Durst et al. 2010) and 2013 (Van Huis et al. 2013a). Insects can potentially be grown using less water, energy and lower quality feed than conventional livestock, and therefore can be produced with a significantly lower environmental footprint (van Huis and Oonincx 2017). The same holds true for microbial protein and artificial meat, but insects have a distinct advantage: they are already consumed by an estimated 2 billion people worldwide (van Huis et al. 2013a), and they have been farmed on a commercial scale for several decades, largely due to their use in traditional medicine, scientific research, the production of silk and honey and the pet food industry (Zhang et al. 2008). Perhaps due to these advantages, the commercialisation of novel insect foods is now on the rise: there has been a significant increase in companies selling edible insects (Dunkel and Payne 2016), and many of these companies are now members of coalitions that aim to influence regulatory policy concerning insect foods, such as the International Platform for Insects for Food and Feed (IPIFF) in Europe and the North American Coalition for Insect Agriculture (NACIA) in North America). Insects are now sold as food by supermarket chains in parts of Europe and North America, and the global edible insect industry is estimated to be worth approximately US$69 million by 2024 (Ahuja and Deb 2018). Insects are rapidly becoming a part of the global food system.

Yet, the cultivation of insects for human food is not a twentieth century innovation. Edible insects have been semi-cultivated by humans for millennia, via environmental manipulation (van Itterbeeck and van Huis 2012). That is, humans have modified the environment in ways that, intentionally or not, support larger populations of insects that are then harvested for food. The most obvious example of this is the cultivation of plant crops, which are a large and predictable supply of feed biomass for many insects. Insects that eat plant crops are generally considered to be pests by growers, but some species are also converted into a source of food. Farmers who harvest edible insects from their cropland are almost exclusively smallholders, who make a crucial contribution to the global food system yet are often subject to nutritional insecurity (Sibhatu et al. 2017). However, little is known about the impact of insect harvesting practices on crops, human nutrition, food security and biodiversity in such systems. The overriding aim of this thesis is to address this knowledge gap.

1.4 Methods and approach

In this thesis, I first consider the role of edible insects in agricultural systems worldwide via a framework that considers ecosystem services and disservices (Chapter 2) and is thus relevant to multiple stakeholders (Millennium Ecosystem Assessment 2005; Perrings et al. 2010). This is an extremely broad topic, yet few publications look explicitly at edible insects in agricultural systems and even fewer quantify services and disservices. For this reason, I opted to conduct a non-systematic literature review. My co-author and I then combined this knowledge with communication from other researchers in the field of edible insects, and data from previous fieldwork. We wrote a narrative review structured by the four categories of ecosystem services: provisioning, regulating, supporting and cultural services (Potkin and Haines-Young 2016).

I then aimed to investigate the impacts of insect harvesting in a field setting. I selected as my field sites two rural regions of southwestern Burkina Faso, West Africa; the next section describes this study system and my overall methodological approach.

1.5 THE STUDY SYSTEM

I chose to work in Burkina Faso because this is a region in which many of the problems facing the global food system are particularly acute: 85% of the population are dependent on agriculture for their main source of income (FIP 2012), and 85% of land has been cleared for agriculture and has no form of protection (Beal et al. 2015). Food insecurity is high in rural areas, affecting an estimated 45% of households (Chagomoka et al. 2017). Malnutrition is also rampant: according to national survey data an estimated 33%, 11% and 24% of children across the country are stunted, wasted and underweight, respectively (Beal et al. 2015). Moreover, 37.6% of women and 72.1% of children living in rural areas are anemic (Martin-Prevel et al. 2016). Wild foods, including both edible wild plants and animals, are still an essential part of the diet for many people and contribute key micronutrients (Hama-Ba et al. 2017). Yet harvesting practices may be unsustainable, as overall biodiversity is severely threatened: many animal species are now nationally extinct as a result of land clearance and hunting, including chimpanzees (Kühl et al. 2017) and three major large carnivores (Brugière et al. 2015).

Burkina Faso is one of many countries in sub-Saharan Africa in which edible insects are culturally and nutritionally important, and are harvested from agricultural land (Anvo et al. 2016, Rémy et al. 2018). The most widely eaten edible insect in southwestern Burkina Faso is the final instar larva of the Saturniid moth *Cirina butyrospermi,* known as *chitoumou* in the Dioula, Mossi and Bobo languages. *C.butyrospermi* is morphologically indistinguishable from *Cirina forda,* but differs in its feeding and ranging habits: *C.forda* is a generalist feeder while *C.butyrospermi* has only one host plant (see below); *C.forda* specimens with publicly available genome sequence data have been collected in nine countries across sub-Saharan and southern Africa, while *C.butyrospermi* specimens with sequence data have only been collected in Guinea and Burkina Faso (Ratnasingham & Herbet 2007). *C.butyrospermi* (hereafter shea caterpillar) larvae are harvested from shea-dominant agroforestry systems.

They are seasonally abundant in such systems because the host plant of the shea caterpillar is the shea tree (*Vitellaria paradoxa*), known as *karité* in French or *shiyiri* in Dioula – a species of high economic and nutritional importance in the region which is retained at high densities in agricultural fields (Elias 2013). Shea trees are owned by the individuals who own the land in this system – that is, either the farmer or village chief. The farmer of the field has rights to the nuts that fall from the trees, but the caterpillars are considered common property for all (I was told repeatedly during fieldwork that the caterpillars are "*pour toute la monde!").* Previous studies have referred to *Cirina spp* as pests (Odebiyi et al. 2003, Dwomoh et al. 2004) and have suggested that insecticides should be used to reduce caterpillar abundance (Dwomoh et al. 2003). However, to do so could endanger those who eat them via food contamination with chemical insecticides (Belluco et al. 2013), and could also cause serious harm to the sustainability of caterpillar populations (Yen 2009, Yen 2015a). Systematic research is crucial to better understand the dynamics between this species, their host plant, and the humans who eat them.

Currently, both scientists and industry players are taking action to extend the availability of caterpillars throughout the year. A group based in Bobo-Dioulasso has developed a method of breaking the diapause of the species (Bama et al 2018), and FasoPro, a company based in Ouagadougou, has been preserving the caterpillars in sealed packets with flavouring to extend their shelf life. However, no rearing system has yet been fully successful, and sealed packets are not affordable nor available to individuals local to this region.

I selected as my field sites the villages of Soumosso, Koba and Larama, in Hauts-Bassins province (hereafter referred to as the Soumosso-Koba-Larama area), and the village of Sitiena, in Comoe province (**Figure 1**). Both sites are within the shea belt, a region stretching across sub-Saharan Africa in which shea trees occur throughout the landscape (Maranz and Wiesman 2003). The landscape is dominated by shea parklands, and maize (*Zea mays*) is the most common and staple crop. To my knowledge, no shea cooperatives exist in this region. Households are reliant on agriculture for their livelihoods: all are smallholder farmers who consume their own produce and sell surplus at local markets. The most common ethnicity in the Soumosso-Koba-Larama area are Dioula and Mossi; the most common ethnicities in Sitiena are Gban and Karaboro. The most commonly observed religions in both are Muslim, Christian and different types of traditional Animism. While some ethnic groups and religious practices are more widely represented in each village, there are people of multiple ethnicities living in all villages, and many marriages are mixed by both ethnicity and religion. This is in part due to the predominant practice of exogamy – women leave their natal village to live with their husband – but also to migration from northern regions. The climate is Sudano-sahelian; the mean monthly temperature ranges from highs of 29.1-36.5°C to lows of 18.7-24.8°C throughout the year, and average humidity from 25-82%; there is a short rainy season in June-July each year. Further detail on sites and sampling methods are given in the Methods sections in Chapters 3, 4 and 5.

Figure 1. Map showing locations of main study areas in Burkina Faso Sitiena (10°36'19.5", -004°49'03.3"), and the Soumosso-Koba-Larama area, which is comprised of the three adjacent villages Soumosso (11°00'44.2", -004°02'45.8"), Koba (11°00'52.1", -003°59'42.2) and Larama (11°03'02", -004°00'02.3")

1.6 THE BIOLOGY OF THE SHEA TREE AND SHEA CATERPILLAR

The shea tree is a long-living (>200yrs) savannah species that is both perennial and deciduous, and is found in 21 countries across sub Saharan Africa in a region referred to as the 'shea belt' (Naughton et al. 2015). While the shea tree does occur naturally in uncultivated landscapes, it is also commonly retained in agricultural fields referred to as shea parklands. In the study region that is the focus of this thesis, shea tree density in the parklands ranged from 1.6-36 trees per ha with a median of 13 (Chapter 5), and long term farmer selection of favourable trees has resulted in a population that has notably ‘large fruits, sweet pulp, and high kernel fat’, as these are the traits deemed important by local communities who eat the fruits and use the kernels to make shea butter (Boffa 2015). The trees produce fruit every year between July and October. They are pollinated by honeybees, but may have other pollinators that have not yet been studied (Boffa 2015). The trees can reach up to 20m in height, and they reproduce in both managed and unmanaged land, with gene flow between the two (Allaye Kelly et al 2004). IUCN listed the shea tree as Vulnerable after its most recent assessment in 1998, and identified the key threats to this species to be overexploitation for wood use, agricultural encroachment, and human population pressure (IUCN 2019).

The shea caterpillars are the larvae of the silkmoth *C.butyrospermi.* The moth emerges from its pupal state every year in June, after the first rains. As an adult it is at risk of predation by *Tockus erythrorhyncus,* and red ants during egg-laying (Moussa 1993). The moth lives for 24 hours, during which time it mates and lays eggs at night on nearby trees, with an mean of 483 eggs per cluster; after a mean of 30 days incubation period, a mean of 84% of these eggs hatch, into first instar larvae (Rémy et al 2018). The eggs are preyed upon by three species of parasitic microhymenopteran, the most significant of which is *Mesocomys vuilleti* (Moussa 1993). The surviving larvae grow through five instars over a period of 33 days (Rémy et al 2018). During this time they consume only the leaves of the shea tree. Their natural predators include insectivorous birds and several entomophagous insect species, including *Stenocallida nigriventis* (Coleoptera) and *Glypsus erubescens* (Hemiptera) (Moussa 1993). In natural conditions, their survival level at each stage is presently unknown. They are gregarious until their third instar, at which point they start to forage independently. They disperse over the ground, moving to new trees when one tree has been entirely defoliated. We do not know the distance that they disperse. Once they have reached their final instar, the pupae burrow into the soil below the shea trees and pupate. They remain in diapause for 286 days (Rémy et al 2018).

1.7 Caterpillar collection, preparation and consumption

In the study region, caterpillar collection happens for the most part between 2am and 6am, during July and/or August. Men, women and children who wish to collect caterpillars leave their house in darkness, taking a torch and a bucket. They walk from shea tree to shea tree, across all fields regardless of land ownership, shining a torch on the trunk and the ground below to find caterpillars. When they find caterpillars, they pick them up by hand to transfer them to the bucket. When the bucket is full they return home and often use another bucket to continue collecting until the sun rises. Shortly after sunrise, collectors return home to wash and prepare the caterpillars. They wash them at least three times and then cook them over fire with some potassium and salt to help preserve them. Once this process is complete, the caterpillars are ready to sell, or to cook fresh, or to sun-dry. If the caterpillars are to be sold, they are taken to main roads and busy junctions, where women come from trading posts and nearby towns (usually Bobo-Dioulasso and Banfora, in Soumosso-Koba-Larama and Sitiena respectively) to buy caterpillars in bulk, using a large empty can as a measuring vessel. If the caterpillars are to be eaten fresh by the family, they are usually cooked within 24h, with oil, onions, tomatoes and seasoning. If they are to be sun-dried, they are spread out on a tarpaulin sheet during the day for three consecutive days until they are deemed dry enough. They are then either sold, or they are rehydrated, cooked and consumed, within a few months.

1.8 PARTICIPATORY APPROACH AND PILOT STUDY

I opted to use a participatory research approach to this work, aiming to include from the very beginning the opinions and concerns of stakeholders and particularly smallholder farmers (Reed 2008). To this end, I visited my intended field sites and conducted a short pilot study in April 2016. I conducted semi-structured interviews with male and female heads of household about their livelihoods, and also about their concerns regarding shea caterpillars. During my short stays in both Sitiena and the Soumosso-Koba-Larama area I initiated informal discussions about the role of caterpillars in peoples' lives, and following these I recorded any folk wisdom discussed. I found that people in these villages did not regard the caterpillars as pests and did not feel that they had a negative impact on harvests of shea nuts, contrary to pre-existing literature (e.g. Odebiyi et al. 2003, Dwomoh et al. 2004, Dwomoh et al. 2003). People in the village were interested in increasing yields of shea caterpillars through enclosed rearing systems, but many were sceptical about the likelihood of this ever being successful. They were emphatic about the importance of caterpillars for their own livelihoods. I sought to contact commercial, higher intensity farmers and farming companies. However, while I did identify one landowner in the Soumosso-Koba-Larama area who uses organic farming techniques in order to support biodiversity and sells products commercially, I otherwise found that currently, there is no land used for commercial-scale high intensity agriculture in either the Soumosso-Koba-Larama area or in Sitiena. I spoke to a prominent conservation-oriented non-government organization (NGO), Naturama, who voiced a desire to know more about the interaction of caterpillars with livelihoods and biodiversity. I spoke to a representative working for the FAO (Food and Agriculture Organisation of the United Nations) in Ouagadougou who felt that research on shea agroforestry was necessary, but was unsure of the importance of the caterpillars, perhaps due to his cultural background: he had grown up in a northern region of Burkina Faso where caterpillars are not used as food. I interviewed scientists at the University of Ouagadougou who were interested in the ecology of the caterpillars and potential breeding methods. Following this pilot study I used information gathered from all stakeholders to develop research questions to guide my field study, and a plan for collaboration with local scientists and farmers. My key questions are therefore:

1. What is the contribution of caterpillars to food security?
2. Is there any association between caterpillar abundance and yields of plant crops?
3. Is there any association between caterpillar abundance and biodiversity?

1.7 CHAPTER OVERVIEW

Following the literature review in Chapter 2, in Chapters 3, 4 and 5 I present the main empirical results of my fieldwork; In Appendices I and II I detail secondary studies undertaken in the same time frame. Chapters 3-5 were prepared as papers for publication, and each can be read as a stand-alone study. When all are read consecutively, there may be some minor repetition in the Methods sections of each.

In Chapter 3 I ask if and how shea caterpillars contribute to household protein consumption, income and food security; these are questions of high relevance to policymakers and NGOs working to combat poverty and malnutrition in this region. In Chapter 4 I ask if and how the prevalence of shea caterpillars varies with yields of the main plant crops in the region, shea and maize: are shea or maize yields lower in the presence of many caterpillars, for example These are important questions to smallholder farmers living in the shea belt. In Chapter 5 I ask how bird abundance and diversity vary with shea caterpillar abundance; these questions are important for conservationists working in parts of West Africa where caterpillars are used as food. Finally, in Chapter 6 I discuss the significance of my key findings for policymakers and farmers, I consider actions that may be taken to ensure the future sustainability of this farming system, and I suggest directions for further research.

A harvest,

With six-legged forerunners

Enriched.

収穫期は

六本足のやつに

豊富させ

Chapter 2. Ecosystem services from edible insects in agricultural systems: a review

ABSTRACT

Many of the most nutritionally and economically important edible insects are those that are harvested from existing agricultural systems. Current strategies of agricultural intensification focus predominantly on increasing crop yields, with no or little consideration of the repercussions this may have for the additional harvest and ecology of accompanying food insects. Yet such insects provide many valuable ecosystem services, and their sustainable management could be crucial to ensuring future food security. This review considers the multiple ecosystem services provided by edible insects in existing agricultural systems worldwide. Directly and indirectly, edible insects contribute to all four categories of ecosystem services as outlined by the Millennium Ecosystem Services definition: provisioning, regulating, maintaining, and cultural services. They are also responsible for ecosystem disservices, most notably significant crop damage. We argue that it is crucial for decision-makers to account for edible insects and to evaluate the costs and benefits of their presence in agricultural systems. We recommend that a key priority for further research is the quantification of the economic and environmental contribution of services and disservices from edible insects in agricultural systems.

2.1 INTRODUCTION

There is growing concern about our ability to feed our rising population. Population trends suggest that there will be 9.6 billion people on the planet by 2050 (Gerland et al. 2014), with food demand growing by 60% and meat consumption rising from 39kg per capita in 2005/7 to 49kg per capita (Alexandratos and Bruinsma 2012). Thus, a concerted effort is underway to seek new ways of increasing food production (Godfray et al. 2010). Clearing more land for agriculture is considered an untenable solution, since land clearance has been linked to major biodiversity loss and climatic change (Foley et al. 2005), and latitudes with high agricultural potential are also home to high levels of biodiversity. Agricultural intensification is often portrayed as the only other option open to us, as it can facilitate increased food production while also sparing land for wildlife and carbon sequestration (Tilman et al. 2011).

2.1.1 Ecosystem services and agricultural systems

Measurement of the efficacy of agricultural intensification tends to focus on the quantity of commodity crops produced, without consideration of several other key dependent variables (Tomlinson 2013). These often-overlooked variables include: (1) The abundance and nutrient content of additional crops essential for health such as fruit and vegetables; (2) The abundance of edible and non-edible byproducts of lower-intensity farming systems; (3) How (or whether) agricultural intensification improves the health of those suffering from nutritional deficiencies; (4) Who reaps the economic benefits of agricultural intensification. Edible insects harvested from agricultural land are a significant example of the second of these variables—an edible byproduct of lower intensity systems—and their presence or absence is likely to have an impact on all of the others. For example, edible insects tend to be high in essential micronutrients (variable 1), and are likely to be used as both a protein source (variable 3) and a source of income (variable 4) by smallholder farmers who gather them. They are often a highly valued food source in such regions, unhindered by the cultural aversion to insect foods often emphasised in a Western context (Looy et al. 2014) and enjoyed primarily for their sensory properties (Tan et al. 2015).

An ecosystem services approach is one way of identifying these and other impacts, which would not be identified through measuring plant crop yields alone. Ecosystem services have been defined as ‘the benefits ecosystems provide to people’ (Reid et al. 2003), and this is still the most common definition used today (Potschin et al. 2016). Ecosystem services are usually divided into four (or three) categories: provisioning, regulating, maintaining or supporting (sometimes subsumed into the ‘regulating’ category), and cultural services. Recognizing the value of these services is crucial for identifying the agricultural strategy that is most appropriate in any given context (Costanza et al. 1997).

2.1.2 Edible insects in agricultural systems

Edible insects are one of the many byproducts of low-intensity agriculture, and are usually a seasonal and protein-rich food. Their collection and processing requires low energy expenditure, and they are consumed locally and/or sold at profit. Agricultural intensification, when it comprises mechanization, tree clearance, and pesticide use, threatens the existence of many edible insects. This is particularly true for edible insects that are sold and consumed in significant quantities, and are therefore those most crucial to ensuring food security.

At least 108 countries have a tradition of consuming edible insects, and the number of native species consumed within each country ranges from only one (e.g., France) to as many as 450 (Mexico) (Jongema 2015). However, even in regions where a large number of species are eaten, it is often the case that a very small proportion of these seem to account for the majority of insect consumption. Since insect consumption per person has not yet been satisfactorily quantified in any context, our most reliable indicator of consumption comes from market trends, using commercial availability as a proxy for consumption. This also indicates that these few species account for a large proportion of the economic profit made from trade in edible insects. **Table 2.i** lists the key examples that are reported in current literature:

Species (Colloquial Name, *Scientific Name*)	**Region(s)/ Countries**	**Ecosystem Services**	**Details**	**Ecosystem Disservices**	**Farming System(s)**	**Ref(s)**
Chapulines, *Sphenarium purpurascens*	Mexico	Provisioning, Cultural, Supporting	Source of income and nutrition; part of regional identity; herbivory assists nutrient cycle	Herbivory with influence on yield	Smallholder grain crops (primarily maize, alfalfa)	(a)
Agave worms, *Comadia redtenbacheri* (red) *Aegiale hesperiaris* (white)	Mexico	Provisioning, Supporting	Source of income and nutrition; aids decomposition	Herbivory with influence on yield	Agave plantations (primarily for pulque and mescal production)	(b)
Palm weevil larvae (*Rhynchophorus* spp.)	Papua New Guinea, Asia, Central Africa, West Africa, South America	Provisioning, Supporting	Source of income and nutrition; aids decomposition	Disease vector (*Bursaphelenchus cocophilus.* red ring disease nematode)	Sago palm groves, oil palm plantations, coconut palm plantations, date palm plantations	(c)
Wasp brood (*Vespula* spp.)	Japan, South Korea, China, New Zealand, Papua New Guinea	Provisioning, Regulating, Cultural	Source of income and nutrition; consumes crop pests and regulates forest animal community; source of education and part of regional identity	Can be harmful to humans	Small-scale vegetable gardens	(d)
Locust (*Locusta migratoria)*	Middle East, Central Africa, East Africa	Provisioning, Supporting	Source of income and nutrition; herbivory assists nutrient cycle	Herbivory with influence on yield	Grain crops	(e)

Cricket (*Acheta* spp., *Gryllus* spp.)	Asia	Provisioning, Supporting	Source of income and nutrition; herbivory assists nutrient cycle	Herbivory with possible influence on yield	Small-scale vegetable gardens, rice paddy fields	(f)
Grasshopper (*Oxya* spp.)	Asia–China, South Korea, Japan	Provisioning, Supporting	Source of income and nutrition; herbivory assists nutrient cycle	Herbivory with influence on yield	Rice paddy fields	(g)
Dragonfly larvae (species unknown), water beetles (*Cybister* spp. and *Hydrophilus* spp.) and other aquatic taxa	Southeast Asia–Thailand, Laos	Provisioning, Regulating	Source of income and nutrition; regulate the aquatic faunal community through predation		Flooded rice paddy fields	(h)
Termite (*Macrotermes* spp.)	Southern Africa, Central Africa, East Africa, Southeast Asia	Provisioning, Supporting	Source of income and nutrition; soil manipulation aids water infiltration and herbivory assists nutrient cycle	Herbivory with possible influence on yield	Mixed smallholder crops, palm plantations	(i)
Shea caterpillar (*Cirina butyrospermi*)	West Africa	Provisioning, Supporting	Source of income and nutrition; herbivory assists nutrient cycle	Herbivory with possible influence on yield	Mixed agroforestry systems (Maize, millet, cotton, etc)	(j)
Weaver ant (*Oecophylla smaragdina*)	Asia	Provisioning, Regulating, Supporting	Source of income and nutrition; consumes crop pests and regulates herbivory, fruit damage and pollination; herbivory assists nutrient cycle	Negative effect on host tree productivity and pollinator abundance	Tropical plantations (e.g., mango, citrus, cashew)	(k)
Leafcutter ant (*Atta* spp.)	South America	Provisioning, Supporting	Source of income and nutrition; herbivory assists nutrient cycle	Herbivory with influence on yield	Tropical tree plantations (e.g., citrus, cocoa)	(l)

Table 2.i. Summary of commercially available edible insect species closely associated with agricultural systems, and the ecosystem services and disservices they provide. References are as follows: a. Cerritos and Cano-Santana (2008); b. Ramos-Elorduy (2006); c. Choo et al. (2009); d. Nonaka (2010); e. Mohamed (2016); f. Hanboonsong and Durst (2014); g. Pemberton (1994); h. Choulamany (2005); Nonaka (2008); i. Sileshi et al. (2009); j. Badanaro et al. (2014); k. Van Mele (2008); l. Holldobler and Wilson (2010)

2.1.3 The economic and nutritional contributions of insects in agricultural systems

Insects are an integral part of agricultural systems worldwide, and are recognized as being of considerable economic importance. Losey and Vaughan (2006), for example, estimated in 2009 that wild insects were worth $57 billion per year in the US. They define wild insects as those that are not domesticated or mass-bred in enclosed systems, therefore encompassing both those insects that are found in non-cultivated landscapes, and those that range freely in existing agricultural systems.

Losey and Vaughan (2006), in their review of ecosystem services provided by wild insects, focused on dung burial (a regulating/supporting service), pest control (a regulating/supporting service), pollination (a regulating/supporting service), and wildlife nutrition (a provisioning service). All of these concern insects within agricultural systems. Here, we offer a global perspective, with a focus on insects that already provide provisioning services to human communities through their role of food. Our review is necessarily skewed by the nature of data that is available in English language peer-reviewed publications, and we have selected for inclusion in this article those examples that are best represented in the literature. We consider the role of these insects in offering provisioning, regulating, maintaining, and cultural services. This is important because insect eating habits and land use patterns are changing, and we risk losing many of the valuable ecosystem services provided by edible insects as a result. A dietary shift towards a more westernized diet, accompanied by a population shift to urban areas, has in many countries led to a decline in the consumption of traditional foods in regions with a long history of insect consumption (Raschke and Cheema 2008, Van Huis 2013a), although an exception to this is found in parts of Southeast Asia (Yhoung-Aree et al. 2005). Meanwhile, the clearance of wild land and the adoption of agrochemical use by traditional farmers threaten the habitats in which many edible insects are found, jeopardizing both their safety as a food source and their future availability (Van Huis 2013b, Yen 2015b). In 2013, an influential report by the Food and Agriculture Organization of the United Nations (FAO) highlighted the potential of insects as food (Van Huis et al. 2013a). The report included a section on insects as a natural resource, and mentioned the importance of ecosystem services provided by edible insects, including those in existing agricultural systems. Yet the main focus of the report, and indeed its main impact to date, has been to stimulate growth in the farming of edible insects in high density, enclosed systems (Müller et al. 2016). With this review we hope to reopen the discussion about the importance of proactive management for conserving edible insects in existing agricultural systems, in order to ensure that future generations also benefit from the ecosystem services that they provide.

2.2 METHODS AND APPROACH

Due to the broad scope of the topic, we chose to conduct this review as a narrative overview of the literature, combining data from published literature with knowledge gained from our own field experience and consultation with fellow researchers in this field (Green et al. 2006). In particular, we relied on several key texts to lead us to further literature via their extensive and relevant reference lists. These key texts included: Van Itterbeeck and Van Huis (2012), Van Huis et al. (2013a), Ramos-Elorduy (2006), Hanboonsong and Durst (2014), Mitsuhashi (2016), DeFoliart (2002).

We use a theory-driven thematic analysis (Dixon-Woods et al. 2005), and structure our review according to categories of ecosystem services, and disservices, promoted by the Millenium Ecosystem Services Assessment and reinforced in consequent literature. We chose this theory driven structure to help minimise selection bias. The resulting paper highlights important areas commonly overlooked by publications focusing on either ecosystem services or edible insects. We deemed this approach to be more appropriate than a systematic review. This is firstly because we cover a range of issues too broad for the focused approach required by a systematic review, and secondly because there is a dearth of high quality quantitative data on this topic, precluding current opportunities for meta-analysis. We hope that this review alerts others to some of the gaps and opportunities in this field.

We limited the scope of this review to include only ecosystem services provided by insects within existing agricultural systems. **Figure 2** illustrates some of these systems. We exclude those edible insect species of high nutritional and economic importance that are collected only from wild ecosystems, and those that are reared in enclosed systems, although these too no doubt provide multiple ecosystem services. We do include the *Bombyx mori* silkworm, which is bred primarily for silk production and its cultivation requires that large areas of land are devoted to mulberry plantations, therefore the resulting edible product is part of an existing agricultural system. Overall, the species and systems we discuss are necessarily constrained by the literature available to us; for example, we found very little published research on the role of edible aquatic insects in agricultural systems.

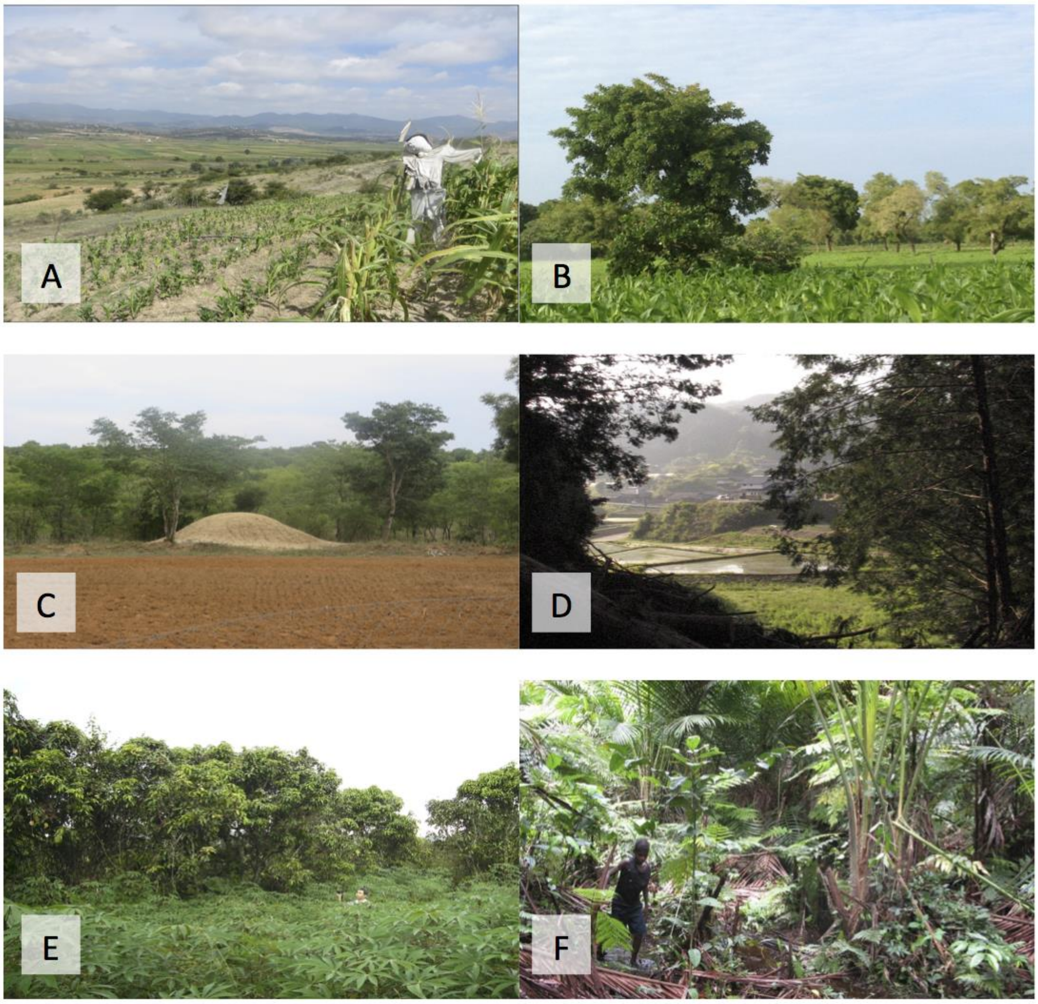


Figure 2. Examples of agricultural systems with edible insects (A) Maize fields in Oaxaca, Mexico, where edible grasshoppers (*Sphenarium purpurascens*) are harvested; (B) Agroforestry (mixed maize *Zea mays* and shea *Vitellaria paradoxa*) fields in western Burkina Faso, where edible caterpillars (*Cirina butyrospermi*) are harvested; (C) A freshly ploughed field with a termite mound in northeastern Zimbabwe, where termites (*Macrotermes* spp.) are harvested; (D) A 'satoyama' (mixed paddyfield and forest) landscape in Japan, where edible wasps (*Vespula* spp.), hornets (*Vespa mandarinia japonica*) and grasshoppers (*Oxya* spp.) are harvested; (E) A mango and papaya plantation in Thailand where weaver ants (*Oecophylla smaragdina*) are harvested; (F) A palm plantation in Papua New Guinea where palm weevil larvae (*Rhynchophorus* spp.) are harvested. (Photos A–D by Charlotte Payne, photo E by Joost Van Itterbeeck, photo F by Kenichi Nonaka).

2.3 Provisioning Services

Provisioning services are those that provide goods for direct human use, and which are often part of the economy (Reid et al. 2003). Edible insects in agricultural systems provide food and income.

2.3.1. Food

All edible insects are a potential source of food for humans. The most recent list counts 2,141 different species (Mitsuhashi 2016), but given uncertain identification, the neglect of research into the dietary repertoire of many ethnic groups and the possible inclusion of synonyms among others, the actual number of species may differ significantly from this value. Hard data, and reliable data, on consumption levels and actual nutritional contribution are scarce. The lack of this type of data is a severe impediment to understanding the true significance of insects as a food source in peoples' current diets.

As a food, insects are consumed in various ways. They can be served alongside regional staples as the main source of protein in a complete meal. This is commonly the case with the shea caterpillar *Cirina* spp. in West Africa (usually served in a tomato sauce with rice or maize meal, or as a sandwich filling) and the grasshopper *Sphenarium purpurascens* ('*chapulines*') in Mexico (usually served with maize tortillas). In Thailand, insects are mainly eaten as snacks, including deep-fried grasshoppers (various species), water beetles (various species), and bamboo caterpillars (*Omphisa fuscidentalis*) (Hanboonsong 2010). In Laos, a paste is made of crickets (*Brachytrupes portentosus*), stinkbugs (*Tessaratoma quadrata*), and giant water bugs (*Lethocerus indicus*), amongst others, with other condiments mixed in (Nonaka 2009; Nonaka et al. 2008). This is used as a dip which makes the dry glutinous rice more palatable. Also in Laos, the larvae and pupae of the weaver ant *Oecophylla smaragdina* are added to fish soup and as a supplement they provide extra flavour and texture. A few adult ants, which have a sour flavour, are added as a condiment in similar fashion to using lemon on fish (Van Itterbeeck et al. 2014).

However, little is known about the nutritional composition and health implications of these different preparations, nor about their frequency of consumption in the societies that eat them. A review of the nutritional content of insects used as food worldwide revealed that while some are a protein-rich food source, others are extremely high in fat (Raubenheimer and Rothman 2013). An analysis of the nutritional value of edible insects in different health scenarios suggests that insects have the potential to be conducive to better nutrition, but that some could also be detrimental in certain dietary scenarios due to their high saturated fat content (Payne et al. 2016). This, however, is speculative, as there is currently little data available about the place of insects in contemporary diets. Some figures have been published estimating the frequency of traditional insect consumption, however. For example, among the Tukanoan Indians in the northwest Amazon, Dufour (1987) found that 12% (for men) and 26% (for women) of animal protein in the diet was provided by edible insects.

The extent to which insects are consumed in any given part of the world is largely constrained by availability, which in turn is increasingly constrained by human influence. Heavy pesticide use is causing a continuing decline in insect populations worldwide, with 67% of invertebrate populations showing a 45% mean decline (Dirzo et al. 2014). Yet pesticide use is not ubiquitous, and some species are highly abundant when in season, and can thus be eaten in large quantities (e.g., various caterpillars in sub-Saharan Africa, Illgner and Nel 2000), while others are a rare treat (e.g., *Vespula* wasps in Japan, Payne and Evans 2017). The overwhelming majority of edible insects are highly seasonal, and in many parts of the world at least one species of edible insect is available at any one time in the year (see e.g., Table 2.2 in Illgner and Nel 2000).

Yet this does not preclude year-round consumption of a single species: For many insects found in large quantities, preservation techniques such as smoking and drying are used to conserve them beyond their season and there is ample potential for improving these techniques for longer preservation (Illgner and Nel 2000). Use of insects as food is also complementary to the use of more well-known food sources. For example, when fish and game availability is low, insect consumption is high, and, when fish and game availability is high, insect consumption is low (Dufour 1987). Insects may thus be consumed out of need, opportunism, and personal preference, and these reasons vary with the season and by species.

Importantly, edible insects also provide indirect contributions that meet human nutritional needs. Honey is major example of this, and the calories supplied by honey bees are widely recognised to be a significant source of nutrition, particularly among forager groups (Crittenden 2011). In Southern Africa, the kaolin-rich soil generated by termite mound construction is a major source of edible clay, which is particularly important for pregnant women in this region (Hunter 1993).

2.3.2. Income

Insects regularly fetch high prices when sold at markets, higher than the crops from which they were collected and often higher than conventional fish and meat (e.g., chicken, pork, and beef) (Munthali and Mughogho 1992, Chidumayo and Mbata 2002). Weaver ant larvae and pupae sell for about US$12 per kg in Laos and their sale can account for up to 30% of annual household income in rural Thailand (Sribandit et al. 2008). Grasshoppers in Mexico sell for US$13 per kg, and wasp nests, a rare treat, sell for US$100 per kg in Japan (Payne 2015). Trading in edible insects harvested from agricultural systems can be a lucrative business, sometimes even to the extent that the insect becomes the primary product, while the status of the plant crop is reduced to that of a feed crop or by-product. This is the case for some farmers in Thailand with Patanga grasshoppers (*Patanga succincta*) that feed on maize (Hanboonsong 2010), and similarly for some farmers in Mexico who choose to grow alfalfa in order to harvest edible grasshoppers (*Sphenarium purpurascens*) from their fields (Cerritos 2015).

Conventional silkworm farming (with *Bombyx mori*), which requires large areas of land to be set aside for mulberry trees, is a notable example in which the insects have remained a by-product of the system for millennia. Yet the additional income provided by these edible insect is far from insignificant. The trade was worth about US$50.8 million in 2004, generated among about 137,000 households (Sirimungkararat et al. 2010). Such figures have triggered a commercial interest in Madagascar where edible wild silkworm pupae are now being promoted as additional income to silk production (Conservation through Poverty Allevation International). Edible insects collected from agricultural systems thus often serve as a livelihood diversification strategy providing multiple income-generating opportunities (Illgner and Nel 2000), which even have the potential to exceed the profits generated by the crops themselves. Thus the collection of edible insects from agricultural systems can enable farmers to develop a multi-production system, which is known to be a more resilient strategy for the smallholder farmers who produce the majority of the world’s food (Altieri et al. 2012).

2.4. Regulating Services

Regulating services are those that regulate the surrounding ecological community, thus maintaining an ecosystem that is well-equipped to consistently deliver marketable services

(Reid et al. 2003). Edible insects in agricultural systems do this through pollination, and through the control of crop pests.

2.4.1. Pollination

Global agriculture relies to a great extent on insects for pollination and this pollination service is of significant economic value (Potts et al. 2010). The most significant edible insect pollinators are the Apidae family of bees, which are one of the most geographically widespread edible insect groups (Illgner and Nel 2000). Both the adults and brood (i.e., larvae and pupae) of bees are used as food in Asia, North and South America, Oceania, and recently Europe (Chen et al. 1998, O'Dea et al. 1991, Posey 1987, Evans et al. 2016). Bees and bee brood collected for food may come from the wild and may be kept in hives (O'Dea et al. 1991), which have been used by humans for millennia to keep bees. Honey bees (*Apis* spp.) in particular are now found worldwide in high quantities (Crane 2013). Honey bees are also known to increase yields of 96% of agricultural crops (Klein et al. 2007), and bee pollination in the US alone has been valued at US$3.07 bn (Losey and Vaughan 2006). Although bee colonies show signs of decline of up to 30% causing alarm worldwide (Pettis and Delaplane 2010), the consumption of bee brood does not necessarily threaten bee numbers. This is because many beekeepers routinely remove a proportion of bee brood in order to protect colonies against the destructive varroa mite (*Varroa destructor*), a sustainable management strategy that can help guard against colony collapse (Evans et al. 2016).

Butterflies and moths are other important edible pollinators of agricultural crops. The widely distributed sweet potato horn worm *Agrius convolvuli*, a hawk moth, is reported to be an important pollinator of papaya in Kenya (Martins and Johnson 2013). This importance may very well also be the case in Southeast Asia where *A. convolvuli* also occurs and papaya is an important crop (Plantwise Knowledge Bank). In Africa, the caterpillars of *A. convolvuli* are eaten (Nonaka 1996). They are found on crops including sweet potato, groundnut, taro, morning glory, lima bean, cowpea, and sunflower, where they may become a pest problem (Plantwise Knowledge Bank). In Asia, adults may be eaten fried. However, since hawk moths are excellent flyers and difficult to catch, hawk moth consumption is rare. Although edible butterflies and moths are not being actively managed in agricultural production systems, the adults do provide important pollination services while the caterpillars may be a pest. The outcome of this interplay between food, pest, and pollination has not been investigated for edible Lepidoptera.

2.4.2. Biological control and animal community regulation

Biological control of pests by insects provides significant economic and environmental benefits (Losey and Vaughan 2006), and many edible insects consume insect pests. A key example of this is the weaver ant (*Oecophylla* spp.), which is a highly abundant and territorially dominant generalist predator that plays an important role in animal community regulation and pest control in a variety of valuable tree crops including mango, citrus, and cashew (Crozier et al. 2009). Weaver ants are found in Southeast Asia and northern Australia (*O. smaragdina*) and sub-Saharan Africa (*O. longinoda*) (Crozier 2009). Though rarely or not eaten in Africa (DeFoliart 2002), the Asian weaver ant (*O. smaragdina*) is one of the most common insect foods in Thailand and Laos (Hanboonsong 2010). The large-sized larvae and pupae, destined to become new queens, are favoured while the sour tasting adult ants are used as a condiment (Van Itterbeeck et al. 2014). Offenberg (Offenberg 2015) advocates the use of weaver ants as food and as pest control. For example, both in Thai pomelo and Vietnamese mixed citrus (pomelo and orange) the presence of weaver ants increased crop yields in comparison to absence of ants. Yields were, however, equal between ant control and chemical control of pest insects; yet this is not always the case and the use of chemicals do often give higher yields than the use of weaver ants. However, because ants are a much cheaper control method than chemicals, the end result is a profit gain of up to 47% for the Thai and Vietnamese farmers (Offenberg 2015). This does not include profit gains from trade in weaver ants for food. Key issues herein are that (1) using the larvae and pupae as human food does not impede the biological control capacity of the adult workers that are harvested in very minor quantities and (2) the egg-laying queen remains untouched (Van Itterbeeck et al. 2014). Many plantation owners welcome the establishment of colonies in their crop trees and benefit from this multi-production system, notably in economic terms.

Edible wasps are also important predators of crop pests. The edible wasp *Vespula* spp.—which is found in mixed rice paddy and vegetable farming systems throughout Asia, Oceania, North America, and Europe—is a generalist predator and consumes many common crop pests (Donovan 2003). The wasp larvae are harvested as food after the crop harvest, thus not affecting their efficacy as pest control agents. Estimates of the economic value of wasps to agriculture are unknown, but likely to be high given the quantities of insects they consume: *Vespula* spp. have been known to consume 1.4–8.1 kg/ha/year of prey in temperate climates, and 26.6–99.0 kg/ha/year where hibernation is not practiced (Donovan 2003). In the US, where wasps are a major predator of crop pests, Losey and Vaughan (2006) estimate the control of pests by carnivorous insects at US$13.6 bn. Unfortunately, farmers in Japan are finding that wasp nests, which were once common on the edges of rice fields, are now located increasingly far into the forests, a change that is believed to be a consequence of widespread pesticide use (Payne and Evans 2017).

2.5. SUPPORTING SERVICES

Supporting services are those that ensure other ecosystem services can function (Reid et al. 2003). Edible insects in agricultural systems enhance water infiltration, encourage soil formation, and maintain the nutrient cycle. These interconnected processes support the primary productivity of agricultural crops. Several studies have shown that the removal of insects such as ants and termites results in an overall yield decrease of 27%–50% (Gras et al. 2016, Wielgoss et al. 2014). Importantly, these studies consider not the removal of a single species of insect but instead a suite of insects that provide supporting services. A single edible species may contribute to supporting services only in the context of a broad and diverse suite of insect species, some of which will not be edible. The evidence that follows should be considered with this in mind.

2.5.1. Water infiltration and water retention

Leafcutter ants (*Atta* spp.) are a delicacy in several countries in South America; termites (*Macrotermes* spp.) are consumed as food throughout Southern Africa and Southeast Asia (DeFoliart 2002). These insects are found within agricultural landscapes, and in the case of termites, smallholder farmers in many countries welcome the presence of termite mounds in their fields. Soil dwelling ants and termites enhance water infiltration. In arid tropical agricultural systems, water infiltration and retention is particularly problematic. A controlled experiment has suggested that due to improved water infiltration, the presence of ants and termites in such climates can significantly improve crop yields (Evans et al. 2011).

2.5.2. Soil formation and nutrient cycling

Healthy soils that contain mineral elements needed to maintain life are the essential for regulating all other ecosystem services (Alcamo and Bennet 2003); therefore the formation of soil and cycling of nutrients back into the soil are crucial regulating services that some edible insects perform.

Termites and ants are important soil engineers. They are surface foragers yet they dwell in the soil (or in the case of some ants, arboreally), and therefore they transport large quantities of nutrient-rich vegetable and animal matter from above ground. Their actions create accumulations of organic matter, which increase and concentrate soil nutrients that are important for maintaining soil fertility. While ants do this by spreading naturally occurring patches of unevenly fertile soil, termites create new fertile soil by decomposing organic matter. Therefore, this is another way in which the presence of termite and ant communities in agricultural landscapes can support and enhance agricultural productivity (Evans et al. 2001, Whitford 1996). This is recognized by farmers in parts of Africa and Asia who regularly harvest parts of termite mounds in order to spread the soil across their fields as fertilizer.

In addition to termites and ants, several other edible insect species living in agricultural systems are herbivorous and live above ground. These include Orthopteran and Lepidopteran insects such as grasshoppers (*Oxya* spp., *Sphenarium purpurascens*), locusts (*Locusta migratoria*), and shea caterpillars (*Cirina* spp.), all of which occur in large quantities in certain agricultural landscapes, as indicated in **Table 2.i**. The caterpillars consume the leaf matter of trees in agroforestry systems, while Orthopteran herbivores consume both crops and weeds in agricultural fields. Grasshopper and locust presence in fields is known to negatively affect yield (Cerritos and Cano-Santana 2008, Musuna et al. 1988). The shea caterpillar is also thought to have a detrimental impact on shea nut productivity, though this relationship is yet to be confirmed (Dwomoh et al. 2004). However, in non-agricultural tropical ecosystems, invertebrate herbivores are known to assist in nutrient cycling, and liberating nitrogen and phosphorus from tree species (Metcalfe et al. 2014). Since both of these minerals are common fertiliser ingredients, tropical herbivory by edible locusts, grasshoppers and caterpillars in agricultural systems may act, through nutrient cycling, as a natural fertiliser. The benefits of this are likely to be minor relative to crop losses incurred by Orthopteran pests, but in agroforestry systems, herbivory, through the addition of fecal matter to the soil, may contribute to soil fertility.

Another important example is the palm weevil, which is found in palm plantations and used as food in South America (*Rhynchophorus palmaraum*, *Rhinostomus barbirostris*), Africa (*Rhynchophorus phoenicis*, *Rhynchophorus bilineatus*), and Southeast Asia (*Rhynchophorus ferrugineus*) (van Itterbeeck and van Huis 2012). Fallen trees and unworked portions of trees cut to harvest starch are used by weevils that deposit their eggs either directly on the inner tissue or on the trunk. The larvae burrow through and feed on the inner tissue thus accelerating decomposition and aiding nutrient cycling and soil formation (Choo et al. 2009).

2.5.3. Primary and secondary production

In the course of their life cycles, all edible insects accumulate and concentrate energy and nutrients. Some individuals die and decompose, feeding these nutrients back into the soil in a more concentrated form. Others are consumed by insectivorous animals, including humans. All insects therefore contribute to primary and secondary production. Though this is something they share with all other organisms, insects are particularly notable due to their high food-biomass conversion ratio. When insects consume and digest animal or vegetable matter, they store a significantly higher proportion of the energy provided by their food compared to mammals. For example, controlled experiments have suggested that the food conversion ratio is 12-fold more efficient for crickets than for cattle (van Huis 2013a). There are two important reasons for this. The first is that mammals—nearly all of which are homeothermic—must use a large amount of energy to maintain a stable internal body temperature, while poikilothermic insects have an internal temperature that varies with external influence and does not require energy to maintain. The second reason is that insects have extremely fast and short life cycles, and high rates of reproduction per individual, compared to longer-lived mammals, which invest a far greater proportion of energy in reproduction. Insects therefore generate biomass at a far higher rate. Therefore, the accumulation and concentration of energy by edible insects is a particularly significant contribution to both primary and secondary production.

2.6. Cultural Services

Cultural ecosystem services are those that provide ‘recreational, aesthetic, and spiritual benefits’(Reid et al. 2003). Edible insects in agricultural systems are a rich source of such benefits, notably in their contributions to cultural identity, artistic endeavour, folklore and education.

2.6.1. Cultural identity

In many parts of the world, edible insects are celebrated as an integral part of local identity. An important example of this is the edible grasshopper *Sphenarium purpurascens.* These grasshoppers are eaten in many states in Mexico, but the state of Oaxaca has claimed them as emblematic of Oaxacan culture. At tourist sites in Oaxaca, souvenirs depicting the grasshopper are sold alongside the insects themselves. In other parts of the world, events celebrating edible insects highlight their importance as part of regional cultural identity. For example, in Burkina Faso, the Bobo region is known for its shea caterpillars, and an annual shea caterpillar festival highlights the importance of this edible insect to the communities that eat it. The same is observed in Japan, where several towns and villages throughout the central region hold annual wasp festivals. Significantly, these festivals often use very localized colloquial terms for the wasps themselves, highlighting their importance for community identity formation even on the village level (Payne and Evans 2017).

2.6.2. Art and folklore

Celebration of edible insects has also found expression in art and folklore worldwide. Two examples of this that involve edible insects found in agricultural systems include the appearance of the rice grasshopper (*Oxya* spp.) in Asian art and poetry, and the role of the termite in African folklore. Asian art often expresses seasonality, and as such the seasonally available grasshopper, which is traditionally collected from agricultural fields in September, is a recognized symbol of the end of summer and beginning of autumn (**Figure 3**).

Figure 3. Grasshopper and bee, Things creeping under hand Woodblock print by Mori Shunkei, 1820.(Reproduced with kind permission from the RISD Museum, RI, USA. www.risdmuseum.org)

The poet Kobayashi Issa in several of his well-known haiku—a form of poetry that always includes a seasonal reference—also uses the grasshopper to indicate this time of year:

A cool breeze

The grasshopper singing

With all his might

Good friend grasshopper
Will you play
The caretaker
For my little grave?
Giddy grasshopper
Take care…Do not
Leap and crush
These pearls of dewdrop

The grasshopper is a positive, playful presence in Issa's poetry. Similarly, termites play a positive and helpful role in African folklore. In parts of West Africa, the presence of a mound can prompt the recounting of traditional tales (Motte-Florac and Thomas 2003). One such tale is the Dogon origin myth, which is the story of a God with two wives, one of whom is a termite. The termite controls the flow of water in the creation of the world, and is named 'the water drawer of God', in an echo of the known function of termites in influencing water infiltration. Termite mounds are also given spiritual significance in parts of Kenya and Tanzania, where the mounds represent a transformative spirit world, or sexuality and the power of procreation (Sileshi et al. 2009).

2.6.3. Education and recreation

The practice of collecting edible insects is often done by women and children, and in the process, young children are given an insight into the nature of the ecosystems in which they live. For the majority of cultures in which this occurs, such education is not explicit. However, in Japan where collectors do not rely on edible insects for their income, the educational benefits of insect collection are more formally recognized, albeit on a small scale due partly to diminishing numbers of available insects (Payne 2015). Until the late 1980s, it was common for children in rural schools to be taken by their teachers to collect grasshoppers in neighboring fields as a class activity on a late summer day. Similarly, in parts of central Japan, educational wasp hunting trips are offered as family activities for both local children and visiting urban tourists. For adults in Japan, wasp hunting is now often practiced as an enjoyable hobby, comparable to fishing or hunting that enhances practitioners' understanding of, and connection to, the natural environment (Payne 2015). Recently, as edible insects have received increased attention in mainstream media, many science outreach events have educated the public about edible insects and their place in ecosystems worldwide. Examples include, but are by no means limited to, a series of Wellcome Trust-funded events run as part of London's Pestival in 2013 (Wellcome press release 2013), wine tasting with edible insects at the Natural History Museum in London in 2015 (Natural History Museum 2015), and bug banquets held annually at Montana State University since 1988 (Montana State University 2017).

2.6.4. Edible insects as educators

We can, and do, learn a great deal from the behaviour of edible insects. One example of this is their role as bioindicators of environmental change, which facilitates appropriate management of other ecosystem services. Their high sensitivity to biochemical change means that insects can alert human communities to atmospheric and climatic variation in its early stages (Schowalter 2013). For example, the collection and consumption of aquatic larvae in central Japan has informed awareness of eutrophication and pollution in nearby lakes (Murakami and Yamagushi 2009). Another example of insects as educators is the major role played by social insects in informing efficient design in architecture (Hensel et al. 2013) and engineering (Brambilla et al. 2013). In Zimbabwe, the ventilation system in mounds built by Macrotermes colonies has been mimicked in the design of buildings in Harare, Melbourne, and London, which consequently use less than 10% of the energy of similarly-sized conventional buildings (French and Ahmed 2010). Similarly, an algorithm developed from observing weaver ants known as Ant Colony Optimisation has been used for diverse purposes including the design of efficient waste (Bovwe et al. 2016) and irrigation (Nyugen et al. 2016) systems. It is perhaps no coincidence that the insect species occurring in large enough quantities to be exploited as food are often successful social and ecological engineers.

2.7. ECOSYSTEM DISSERVICES

The harmful or costly impacts of ecosystems on humans are often referred to as 'ecosystem disservices', and they are crucial to understanding the overall impacts of ecosystem services (Dunn 2010). Edible insects in agricultural systems are capable of multiple disservices, including crop consumption, threatening human health, and spreading disease. Crop consumption in particular may be so severe that it entirely negates any ecosystem services provided by edible insects. However, to our knowledge there is not a single study that quantifies both the services and disservices contributed by edible insects, and without this it is impossible to know whether or not their presence has a net cost or benefit, nor the extent to which using insects as food may reduce the costs of their disservices to agriculture.

2.7.1. Crop consumption leading to yield loss

The majority of edible insects in agricultural systems are crop pests, and are there precisely because agriculture creates large areas of concentrated food sources. Of the known edible insects, Orthopteran pests are the most widespread and most destructive. The edible grasshopper *Sphenarium purpurascens* is one of the most important crop pests in Mexico and consumes a wide range of crops (Potschin and Haines-Young 2016). The desert locust *Schistocerca gregaria* is estimated to destroy crops to the value of US$2.5 bn and hundreds of thousands of tons of grain (Cerritos Flores et al. 2014). It seems likely that the extent of these yield losses and the devastating effect they can have on farmers' livelihoods far outweigh any supporting services contributed by Orthopteran pests. However, the income that harvested Orthopteran pests represent is unknown, and likely to change with fluctuations in demand for edible insects. The time and equipment cost of harvesting and processing these insects may also reduce their value in providing provisioning services. Overall, although it has been suggested that harvesting crop pests could negate their costs to agriculture (Cerritos Flores et al. 2014), this has never been satisfactorily quantified within a single agricultural system.

The Lepidopteran shea caterpillar (*Cirina* spp.) is another example of a herbivorous edible insect, but it feeds only on the leaves of the shea tree. Shea trees are common throughout West African agroforestry systems, and shea caterpillars can defoliate entire trees during their short period of abundance in July/August. One study suggested that shea nut production was significantly lower for trees that had been defoliated in the preceding year (Owusu-Manu and Kuma 1990), but this result was not replicated in a larger study, which found that caterpillar defoliation showed no association with shea nut abundance in the following year.

2.7.2. Harm to humans

The majority of edible insects in agricultural systems are not directly harmful to humans. However, a notable exception to this are Hymenoptera such as ants, hornets, wasps, and bees, which are capable of inflic ting pain and can—in rare cases of a venom allergy—result in death. Hornets, wasps, and bees do this through venom injection, while weaver ants bite the skin and spray acid into the wound. There is a scale used to measure Hymenopteran stings that ranges from “no pain” to “traumatically painful” (Starr 1986). Although allergic reactions are rare, affecting only 2.2% (Kalyoncu et al. 1997) to 3% (Golden 1989) of studied populations, incidence of death from Hymenoptera stings is high compared to deaths caused by other wild animals.

2.7.3. Disease vectors

Insects may be vectors of diseases. Among the edible insects discussed in this article, the only disease vector of which we are aware is the palm weevil, *Rhynchophorus* spp., which is a vector of the destructive red ring disease (RRD), *Bursaphelenchus cocophilus*. RRD causes palms to yellow and eventually die, or to produce stunted leaves, and it is major threat to yields in oil and coconut palm plantations. The palm weevil is its only known vector, and targeting the weevil itself is widely considered the only way to combat RRD (Oehlschlager et al. 2002).

2.8. Discussion

In this paper we have given an overview of some of the ecosystem services and disservices provided by orders of insects that are found in agricultural systems and that include edible insects. We have used examples to illustrate the ways in which some edible insects within these orders contribute to these services.

It is no coincidence that so many of the world’s commercially available insects are those found in existing agricultural systems: The spread of agriculture has also enabled many of the edible insects that accompany it to occur at higher densities than in wild landscapes. Perhaps it is thus also no coincidence that humans worldwide find these insects so palatable. Many of them do, after all, consume parts of the food plants that we have cultivated for our own consumption over millennia. Perhaps our relationship with our crops and the edible insects that live among them could best be described as symbiosis, a mutualistic interaction with an ancient history. In addition, as collecting insects for food may involve opportunism and as insects available in aggregations and large quantities are targeted, for matters of energetic efficiency, agricultural fields are excellent edible insect resources.

Yet current management practices are focused on the destruction of most of insects that co-occur with agriculture. Integrated Pest Management (IPM) strategies are a notable exception to this, and within IPM the maintenance of edible insects in agriculture has been advocated as a possible novel management direction [(Soloneski 2014). For this to be realized, a more in-depth understanding and quantification of the ecosystem services and disservices obtainable from edible insects will certainly be necessary. For example, in Mexico an experimental study found that alfalfa plots where grasshoppers were collected for food had fewer oothecae (egg cases) when compared with control plots, presumably leading to less severe consequent outbreaks (Cerritos and Cano-Santana 2008). Plots where insecticide was used had even lower oothecae densities. While this study shows the potential efficacy of insect collection for pest control, it lacks systematically collected data on yield or income that would allow a comparison between the financial returns from grasshoppers with the loss of alfalfa yield, vs. the costs of pesticide use (Cerritos 2015). This is crucial, since even trials of pesticides used against non-edible insects have found mixed results in terms of the overall costs and benefits of pesticide use (Felland et al. 1990). A later study modeled the potential biomass available from the harvest of Mexican grasshoppers, if pesticides were abandoned (Cerritos Flores et al. 2014). This study found that 350,000 tonnes of grasshoppers could be obtained, potentially supplying nine million people with a year's supply of necessary dietary protein and US$350,000 of income, as well as reducing health problems from pesticide use. However, no estimates were offered with regard to yield losses nor labour costs to these farmers, because the yield losses and labour costs incurred by a strategy of grasshopper collection instead of pesticide use have not been quantified. Furthermore, the longer term effects of grasshopper collection have not been monitored, and the sustainability of the grasshopper harvest over time could depend heavily on harvesting intensity. Finally, the impact of increased grasshopper supply and reduced alfalfa supply on market prices for these commodities could be significant, and could influence whether or not farmers benefit from harvesting these insects. Overall, it is likely that we could learn a great deal from combining such knowledge with traditional management strategies that support the edible insect populations while also boosting crop production.

Weaver ant (*Oecophylla* spp.) biological control and use as human food is an important example of this. Research suggests that harvesting the larvae and pupae, while very few worker ants are removed, causes the worker ants to increase production of new workers (Offenberg and Wiwatwitaya 2009). This response would benefit the colony and its role in the plantation. After all, queen-destined larvae and pupae are those favoured as food, and new adult queens do not contribute to colony survival but leave the colony to establish a new colony (Offenberg and Wiwatwitaya 2009). Weaver ant management involves, amongst others, feeding sugar water, not harvesting the queen, connecting trees with strings for easier access by worker ants, and creating sticky barriers on tree trunks to avoid attacks by ground nesting antagonistic ants (Offenburg 2015). Further improvements can be made. The above strategies increase the fitness of colonies within plantations, but not the fitness of those outside the plantation. In addition, colonies do not live forever—surrounding vegetation must be preserved so incipient colonies may be established that can come to inhabit the plantation (Van Mele 2008). Furthermore, because the reproductive females are intensively harvested, colony reproduction of plantation colonies is expected to be low or non-existent. Breeding and raising new colonies indoors is one avenue of research to address this (Nielsen et al. 2016).

Another example is that of *Vespula* spp. wasps, which have also been proposed as a candidate for developing novel biological control strategies (Donovan 2003). Perhaps such strategies could be developed in combination with knowledge of wasp rearing developed by farmers in rural Japan, who keep nests near to their homes and vegetable gardens, in some cases even harbouring thousands of hibernating wasps over the cold winter months in the hope of promoting their survival and increasing wasp numbers (Payne and Evans 2017).

An understanding of the ecosystem services and disservices contributed by edible insects is crucial for developing such strategies. One illustration of this is the case of the edible hawk moth, *A. convolvuli*. The moth is a pollinator of papaya, an important ecosystem service, and forest conservation is required to secure this service (Martins and Johnson 2013). Yet the caterpillars are sometimes a pest of crops, an ecosystem disservice. Incorporating trade in hawk moths as food may improve incentives for conservation (Munthali and Mughogho 1992). Can management be developed to reap benefits of this triangle? Can hawk moth caterpillars be grown on one crop and the adults used to pollinate papaya and used as food source?

Similarly, palm weevils, found throughout the tropics, provide valuable ecosystem services that may counteract their role as pests. Indigenous peoples in Venezuela, for example, are highly knowledgeable of weevil biology and, given their preference for *R. palmarum* as food, exercise controlled supply of larvae (Choo et al. 2009). The *R. palmarum* adults are attracted to exposed inner palm tissue, while *R. barbirostris* adults oviposit on the intact surface of the trunk. The former also arrive more quickly than the latter. By intentionally felling trees and making deep cuts in the trunk, thereby exposing more inner tissue, a higher number of *R. palmarum* grubs can be harvested (Choo et al. 2009). Weevils are also reported to oviposit eggs on standing palm trees in which case they are considered a pest, as described above with red ring disease (Illgner and Nel 2000). Choo et al. (Mohamed 2016) suggest building on the knowledge and practice of indigenous peoples to aid in weevil control in palm plantations. Perhaps a management system could be developed to attract the weevils to intentionally felled trunks of lower-quality palms, avoiding the infestation of the standing higher-quality palms (DeFoliart 1993). The resulting grubs provide additional food and income, as do all the insects reviewed here.

2.9. Conclusions

Although the current focus on advancing the use of edible insects as food lies on production in enclosed systems (Illgner and Nel 2000, Dossey et al. 2016), this review highlights the ecological and economic importance of edible insects in existing agricultural systems. This is important because current land management tends to promote the continued expansion of agriculture that relies on agrochemical use and prioritises monocultures (Tilman 1999), thus endangering the existence of these valuable insect species (Cerritos and Cano-Santana 2008, Yen 2015b, Payne 2015, Pettis and Delaplane 2010, Soloneski 2014, DeFoliart 1997). There is considerable evidence to suggest that agricultural intensification can increase crop plant yields, thus enabling food production to meet growing demand while also freeing a greater area of land to be devoted to wild nature, decelerating environmental degradation (Phalan et al. 2011). However, demand for animal protein is a significant element of increasing food demand. If increases in yields of grain used for animal feed come at the expense of destroying protein-rich edible insects that contribute multiple ecosystem services to humans, which is the more economically and environmentally viable strategy?

The answer to this is likely to differ significantly for different systems, particularly given the diversity of crops and insect species that coexist worldwide. We certainly do not argue that all or even any edible insects offer a known net benefit to agriculture via ecosystem services. However, we have discussed several edible insect species that contribute important ecosystem services, suggesting that there may be significant environmental, nutritional, and economic incentives to maintaining edible insects within certain agricultural systems. For example, collecting pest insects as food could reduce both their efficacy as pests and the costs of controlling them. Without clearer comparative data, it is impossible to know whether these benefits outweigh the costs of their ecosystem disservices. Yet another consideration is the changing global climate, which threatens the livelihoods of many of the world's food producers. Particularly smallholder food producers could benefit significantly from the development of resilient multi-production systems that yield both plant and animal foods. In order to achieve this, we argue that edible insects and the ecosystem services they provide should be considered in the development of agricultural intensification strategies, particularly in tropical settings. Similarly to many research areas in the broad field of insects as food, hard data to guide such programs is currently lacking. To determine the relative costs and benefits of agriculture that incorporates food insects, we recommend conducting comparative life cycle analyses that compare the economic, environmental, and nutritional outputs of grain-livestock systems and crop-insect agriculture. To determine the impacts of adopting crop-insect agriculture on farmers' livelihoods, we recommend conducting field trials, using a randomized controlled trial (RCT) framework (Baylis et al. 2015), in tropical farming systems. To develop strategies for maximizing benefits and minimizing costs accrued by edible insects, we advocate combining knowledge from traditional management strategies with recent scientific understanding of insect ecology.

Overall, we hope that this review will stimulate a greater interest in the commercial and environmental potential of edible insects in existing agricultural systems. Recent commercial and research interest in insects as food has rarely appreciated the exceptional opportunities that are offered by these insects. We look forward to future research that will elucidate and quantify the costs and benefits accrued by the presence of edible insects in agricultural systems, and to the development of innovative agricultural strategies that will maximize the ecosystem services provided by such insects.

For now we have

Plenty. Feast, sell, prosper,

For now.

今が

満足。食って売って繁栄し

今に

Chapter 3. The contribution of chitoumou, the edible shea caterpillar *Cirina butyrospermi*, to the food security of smallholder farmers in southwestern Burkina Faso

ABSTRACT

Edible insects have been advocated as a means to combat food insecurity, which is prevalent in West Africa. In this study we look at the contribution of the shea caterpillar *Cirina butyrospermi,* colloquially known as 'chitoumou', to the food security of smallholder households in rural southwestern Burkina Faso. We used a mixed methods approach to understand the relationship between caterpillar collection, consumption, and sale by smallholder households, and their seasonal food security status. We found that caterpillars are an important source of food and income for households, significantly increasing the household consumption of animal protein and, with shea nuts, representing the main income source for the majority of women. We also found that food security is higher during caterpillar season, and that household-level food security during this season can be predicted by the amount of caterpillars collected, consumed and sold. However, this relationship holds only during the caterpillar season, suggesting that the positive impact of caterpillars on food security is temporally limited. We conclude that the shea caterpillar is an example of an edible insect that is crucial for seasonal food security in a widespread agricultural system.

3.1 INTRODUCTION

Food insecurity disproportionately affects those who produce the majority of the world's food: over half of all food calories are produced by rural smallholder farmers, who live in the Global South (Samberg et al. 2016) and are disproportionately likely to be food-insecure (Sibhatu et al. 2017). The reasons behind this are complex. At the FAO World Food Summit in 1996, food security was defined as a situation in which 'all people, at all times, have physical and economic access to sufficient, safe, and nutritious food to meet their dietary needs and food preferences for an active and healthy life'. Several definitions since have also focused on the importance of access, particularly in the context of unpredictable and fluctuating world markets (Porter et al. 2014).

Given the importance of financial markets, perhaps it is no wonder that it is the producers themselves who suffer disproportionately from food insecurity. However, the relationship between economic growth and increased food security is complex and variable, and may depend on the nature of government policies concerning food and development (Timmer 2005). The FAO advocates that economic growth can only promote food security in the context of sustainable livelihood opportunities that are inclusive of the rural poor and augment both income and food production (FAO 2015a). Dietary quality is also a key element of food security, although consensus about what constitutes a nutritionally adequate diet fluctuates (Semba 2015). The emphasis is not on food insecurity being due to a lack of food per se, although this is the case for approximately 815 million people (FAO 2015b). More prevalent today is 'hidden hunger', which affects over 2 billion people globally and refers not to caloric deficiency but to a lack of adequate micronutrients (IFP 2014). Strategies to tackle food insecurity among rural smallholders have included those that are 'food-based', such as supplementation (Burchi et al. 2011), as well as those that focus on improving livelihoods (Garibaldi et al. 2017). Yet ultimately, food insecurity cannot be reduced to either component part. Food sovereignty (Weiler et al. 2014), education (Kaiser et al. 2015) and empowerment of women and minority groups (Conceicao et al. 2016) also play key roles in improving food security. Thus, food security has multiple dimensions that include the social, the cultural and the political.

Edible insects have been highlighted as a means of combating these different aspects of food insecurity: many insects are high in protein and micronutrients, are often collected by women and minority groups, and can improve the livelihoods of rural smallholders able to harvest them (Van Huis et al. 2013a). Many edible insects are harvested from wild land, but others are found within agricultural systems and can be a valuable source of both nutrition and income for farmers (Payne and Van Itterbeeck 2017). Previous studies have shown that insects make a significant contribution to food security (Manditsera et al. 2019, Baiyegunhi et al. 2016), but many unanswered questions remain about whether this is due to their contribution to income or to household meals, and also how much this benefit extends beyond the time when insects are seasonally available.

In West Africa, food insecurity is a significant problem. An estimated 9 millon people are undernourished and 1 in 5 children are underweight (FAO 2015c). There is some evidence to suggest that this may be due to increasing yield deficits due to climatic change, which have been cited as one cause for increased southward migration to escape desertified, unproductive soils (Ritzema et al. 2017). Regardless of the driving forces behind such movement, in many regions population density is increasing as a result, and this rise in population pressure is contributing to environmental degradation (Douxchamps et al. 2016).

Insects are enjoyed as food in many parts of West Africa, where important species include locusts, palm weevil larvae and caterpillars (Anankware et al. 2016, Anvo et al. 2016, Agbidye et al. 2009, Banjo et al. 2006, Tchibozo et al. 2005). Edible caterpillars play an important role in food security throughout Africa as a food that is harvested from forest, savannah and other uncultivated land (Yen 2015a). However, in the shea belt - a cultivated region, spanning 21 countries from Uganda and Sudan in the east to Guinea in the west and dominated by the shea tree *Vitellaria paradoxa* (Naughton et al. 2015) - the shea caterpillar (*Cirina butyrospermi*) is collected in agricultural fields and is a significant part of the wider agricultural system. The caterpillar is colloquially known as ‘chitoumou’, feeds exclusively on the leaves of the shea tree and when in season, is ubiquitous at rural and urban markets and trading posts. Out of caterpillar season, caterpillars are available in dried form. Households that dry caterpillars usually consume them within 1-6 months. Prior research has shown that diets containing shea caterpillars are higher in protein and zinc, two essential nutrients for combatting nutritional deficiencies in this region (Cox et al. 2018).
The aim of this study is to understand the role of the shea caterpillar in relation to food security in the shea belt region of West Africa. We ask how caterpillars compare to other sources of nutrition and income in rural southwestern Burkina Faso, and we investigate the nutritional and financial contribution of caterpillars to households. We use household interview data to ask whether the seasonal abundance of caterpillars has a measurable impact on food security among rural populations in this region, and look at the extent and nature of this impact. Finally, we consider whether ethnicity, location and household wealth predict the quantities of caterpillars consumed and sold.

3.2 MATERIALS AND METHODS

3.2.1. Sampling strategy and study design

We collected data on a random stratified sample of 25 households (stratified by household size) out of 50 in the Soumosso-Koba-Larama area of southwestern Burkina Faso (Fig. 1) which cultivated >1ha of land, cultivated maize, and collected caterpillars. Land in the area is owned by the chief of the village and leased to households, who request permission to cultivate long term and do not pay rent. The head of the household is usually in charge of determining which crops will be cultivated, and in our sample all but one head of household was male. We identified 20 households in the Sitiena area (95 km southwest)) that met the same criteria, but we were not able to take a stratified sample due to time constraints. The female head of household (first wife of the male head of household) in each of the resulting 45 households formed the core sample of women for all structured interviews and Household Food Insecurity Access Score (HFIAS) surveys (Coates et al. 2007). We chose to interview only women because we had found from pilot surveys that they hold the primary responsibility for preparing meals for the household, and for collecting wild foods. We also found that women are responsible for purchasing food for the household, and that they keep the money from the caterpillars that they collect. Looking at the financial benefits of caterpillars to the men and children in households in this region is beyond the scope of this study.

We used a mixed methods approach to give greater voice and agency to research participants, and to recognise the importance of multiple perspectives (Green and Thorogood 2014). We use qualitative data to complement, triangulate and challenge the results generated by quantitative methods (Creswell and Clark 2007). Our quantitative methods of data collection are structured interviews, 24h recall surveys, nutritional analyses and HFIAS surveys; our qualitative methods are focus groups and participant observation.

3.2.2. Structured interviews

We conducted structured interviews with women from our core sample during July-September 2016 and 2017, up to two months after each year's caterpillar season. Questions covered the quantity of caterpillars and shea collected, eaten, sold and given away by the household, the time spent and money gained for each harvest, the money gained from the harvest and sale of shea nuts, and the assets of the household.

To estimate household wealth, we summed the market values of all assets (livestock, forms of transport, and land) for each household, in CFA (West African franc). Market values were as follows: cow 175000CFA, sheep 27500CFA, goat 25000CFA, chicken 2000CFA, guinea fowl 3000CFA, donkey 80000CFA, bike 20000CFA, motorbike 800000, land per ha (hectare) 350000CFA. These values were ascertained from three key informants on separate occasions and we took a mean value in the case of discrepancies.

3.2.3. The caterpillar season

The 'caterpillar season', as used in this study, is a literal translation of the term used locally, chitoumou wakati, in Dioula (chitoumou=shea caterpillar; wakati=time period). is used to refer to the time of year when people are collecting, eating and selling fresh caterpillars. We asked respondents to estimate the number of days that they had collected caterpillars during the past season. Women estimated that they had spent a mean of 15 days (range=5-30, N=44) collecting caterpillars. The estimated season in Sitiena (mean=12 days, N=19) was significantly longer than in the Soumosso-Koba-Larama area (mean=18 days, N=25; Kruskal-Wallis rank sum test, χ^2=10, p<0.005, df=1).

Even within the same village, areas differ as to the exact timing of the caterpillar season. The timing also varies by year. All data on the collection and sale of fresh caterpillars were obtained in July and August.

3.2.4. 24h recall surveys

SC (Sioned Cox) conducted dietary interviews following the 24 hour recall method (Biro et al. 2002) with 16 respondents, who represented a stratified subsample of those women interviewed for the HFIAS surveys (with four respondents from each HFIAS category). SC asked respondents to recall all foods and drinks that they (individually) had consumed during the previous 24 hours, and to estimate portion sizes. Average interview length was 25 minutes, and SC conducted all interviews in the morning to aid recall (Huybregts et al. 2009).

To maximise accuracy of recall SC used the multiple pass method (Wrieden et al. 2003): for the first pass respondents recalled all foods and beverages consumed during the previous twenty-four hours; for the second pass respondents identified when and where foods were consumed; for the third pass SC recalled the report to the respondent to prompt for any forgotten items. Finally SC reviewed, and confirmed with the respondent, all items recorded. Interview questions were conducted in the respondent's first language, with the assistance of trained field assistants. SC used household measures to aid estimates of portion size, and retrospectively converted these to grams using 'FAO/INFOODS Density Database Version 2.0' (Charrondiere et al. 2012a). SC matched food items with energy and nutritional compositional values from the West African Food Composition Table (Charrondiere et al. 2012b). When an exact match was not possible, food items were matched with values available from other published sources available (Anvo et al. 2016, Greffeuille et al. 2010, Nordeide et al. 1996); if these were unavailable SC used the mean of the values for several similar items (in accordance with the 'INFOODS Guidelines for Food Matching' - Stadlmayr et al. 2011). When analysing the data, we found that for N=3 reported dishes the portion reported exceeded 200% of a person's daily Kcal intake; we excluded these dishes from my final analysis.

3.2.5. Nutritional analysis

Wild insects vary widely in their micronutrient composition, depending on the species and their life stage, and also on the habitat and soil composition at their geographical origin (Payne et al. 2015). To determine the average micronutrient content of the caterpillars in this region we collected samples of 3 final-instar individuals from each of 9 fields stratified by distance from the road. We chose to use final-instar caterpillars because this is the life stage at which they are traditionally collected. After weighing the caterpillars we prepared them as they are usually prepared for sale: we boiled them with potassium and dried them in the sun. Micronutrient analyses were carried out at Rothamsted Research, UK. We placed 500mg of each caterpillar sample in 25ml graduated digestion test tubes, with one sample out of every three repeated to check analysis accuracy. Two wheat flour samples were included as a certified standard and two blank control tubes to establish any potential contamination in the solvents. Samples were pre-digested in 5ml of 15:85 nitric:perchloric acid (HNO_3:$HClO_4$) for 5 hours then heated overnight to 175°C to evaporate the acid. 5ml of 25% HNO_3 was added and the tubes heated to 80°C for 60 minutes. Samples were made up to a final volume of 25ml with ultra-pure water, decanted and analysed using an Optima Inductively Coupled Plasma – Optical Emission Spectrometer (ICP-OES) (Zhao, McGrath, & Crosland, 1994). All Nitric acid was Aristar grade.

3.2.6. HFIAS surveys

To measure perceptions of household food security during and outside of caterpillar season, we chose the HFIAS due to its sensitivity to food access, quantity and reported anxiety, its applicability to measuring food security at household level (Jones et al. 2013), and its use in similar settings (Baiyegunhi et al. 2016). We refined the questions for use in the Soumosso-Koba-Larama area with five local bilingual key informants to ensure that translated questions were accurate and contextually appropriate (following Coates et al. 2007). Three of these key informants acted as translators to assist with data collection, with at least one present at every HFIAS interview. We first selected survey respondents from our core sample, and then sought further respondents via snowball sampling (Heckathorn 2011) to expand our sample size. We conducted 59 HFIAS interviews with women outside of caterpillar season (March 2017), and repeated 57 of these during caterpillar season (July 2017). In seven of our 59 cases, it was not possible to repeat the interview with the same woman, due to death (N=2), ill health (N=1) or absence from the village (N=4) but in five of these instances we interviewed another woman in the same household in her place; in the two remaining instances we were not able to identify a meaningful replacement. We calculated all HFIAS metrics reported here from these repeat caterpillar- and dry-season interviews (N=57), following Jones et al. (2013). We calculated the HFIAS score (from 1 to 27) and HFIAS category (from 1 to 4).

3.2.7. Post-HFIAS surveys and focus groups

We also asked HFIAS survey respondents about protein consumption in the past month to further understand the nutritional role of shea caterpillars in relation to other protein sources. Specifically, we asked respondents to estimate the number of times in the past month that they had consumed meat (‘sogo’, which includes poultry, ruminants and wild game), fish (‘jige’) and shea caterpillars (‘chitoumou’). All results reported here reflect the responses of the N=57 women who participated in HFIAS surveys in both seasons.

In order to validate and expand on quantitative data gathered via structured interview and participant observation, we followed a triangulation approach to mixed methods (Creswell and Clark 2007) and conducted 9 focus groups in January 2018, during the dry season. We held focus groups in the Koba (N=6) and Larama (N=9) localities (Fig. 1). Following previous experience conducting focus groups here we limited focus groups to include 2-3 women in each. The first participant for each was selected at random; others were selected according to ethnicity/language (matching the ethnicity/language of the first participant) and/or geographic proximity and availability. In total, 20 women, ranging in age from 18-60yrs (mean age 38.4yrs) and representing three ethnicities (Dioula=8, Mossi=6, Bobo=6), participated in focus groups, which were conducted outside in the village at places chosen by participants, usually next to a homestead.

We recorded all focus group discussions (totaling 217 mins) using detailed notes and a voice recorder for verification. We assigned initial codes to transcripts, used memos to review these codes (following Birks and Chapman 2008) and developed a final set of codes based on emergent themes (Stewart and Shamdasani 2014).

3.2.8. Participant observation

CP spent 13 months living in the Soumosso-Koba-Larama area, and accompanied local women collecting and preparing caterpillars during two caterpillar seasons, in 2016 and 2017. Knowledge and experience gained during this time informed the structure of the study as a whole, and the design and analysis of the focus groups, particularly when writing questions and coding responses.

3.2.9. Ethics

All interview, survey and focus group protocols were developed in accordance with the Research Ethics Review Group, Department of Geography, University of Cambridge, which follows the Policy on the Ethics of Research developed by the University Ethics Committee (University Research Ethics Committee 2016).

3.2.10 Statistical analyses

We conducted a repeated measures two-way ANOVA adjusted for between-subject random error to compare animal protein consumption by type and season. We followed this up with a post-hoc Tukey test to understand the nature of the significant differences that emerged. We conducted a Wilcoxon rank sum test to compare the reported income gained from caterpillars and from shea nuts, per household per year and per person per year, and to understand the relative importance of this income between households with different assets, we also ran the same test for these figures as a percentage of household wealth. We ran a Wilcoxon rank sum test to compare the results of HFIAS surveys during and after caterpillar season, to determine whether perceived food security differed significantly between seasons. After testing for collinearity between the sale and consumption of caterpillars, we ran a multiple linear regression to understand the relationship between caterpillar sale and consumption, and food security during caterpillar season. We ran a second multiple linear regression to understand whether caterpillar sale and consumption predicted food security during the dry season. Finally, we ran a multiple linear regression to determine if the amount of caterpillars consumed or sold was associated with ethnicity, location and household wealth.

All statistical analyses were performed in R (version 3.5.1). Non-normally distributed data (quantity of caterpillars collected, consumed and sold) were $\log_{10}$-transformed before analyses; consumption of dried caterpillars could not be log-transformed because of zero values so was instead analysed as a binary variable (consumed/not consumed). Where means and SDs are reported, these have been back-transformed.

3.3. RESULTS

Caterpillars are collected in large quantities (median =4.26kg per person per season, range=0-39kg, further details given in S1).

3.3.1. Nutritional contribution of caterpillars

Prior to cooking, caterpillars are high in key nutrients: 100g of fresh shea caterpillars exceed half of the recommended daily intake of protein, iron and zinc (150%, 63.7% and 173% respectively) for a woman of reproductive age (**Table A.i**).
When cooked, the reported portion of a caterpillar dish contains a median of 395% (IQR=145), 232% (IQR=42.8) and 456% (IQR=165) of the recommended daily intake for

Protein, Iron and Zinc (**Figure 21**). Portions also contain high amounts of fat (median=209% of recommended daily intake, IQR=102), due to the oil used during the cooking process. During caterpillar season, respondents to HFIAS surveys (N=57) reported eating caterpillars a median of 3 (range= 0-14) times a week, but this fell to a median of 0 (range= 0-2) times a week in the dry season. Animal protein consumption differed significantly by protein type and by season (repeated-measures two-way ANOVA adjusted for between-subject random error, protein: $F_{(2,280)}=9.23, p=0.001$; season: $F_{(1,280)}=41.31, p<0.001$; **Figure 4**. A post-hoc Tukey test showed that while there was no difference in the frequency of fish (p=1) or meat (p=1) consumption between seasons, there was a significant difference in caterpillar consumption (p<0.001) (**Figure 4**). Therefore total animal protein consumption was higher in caterpillar season, due to the consumption of caterpillars (**Figure 4**).

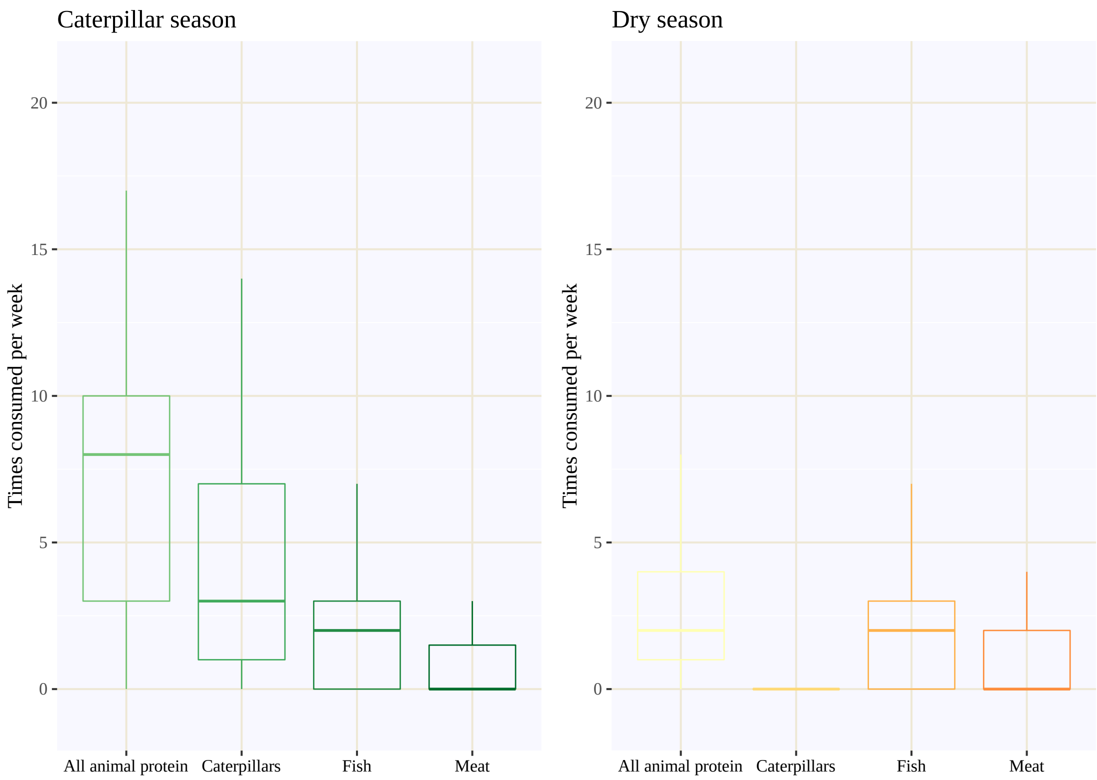


Figure 4. The reported weekly consumption of animal protein sources during the caterpillar season in late July (left) and during the dry season in March (right), according to responses (N=49) to post-HFIAS survey questions.

3.3.2. Financial contribution of caterpillars

Caterpillars are a major source of income: more caterpillars are sold per person per year (median=3.33kg, IQR=4.41kg) than consumed fresh (median = 0.263kg, IQR=0.425kg) or dried (median=0kg, IQR=2.1kg) (**Figure 22**). Reported household and per person income from caterpillars is equivalent to income from shea nuts; the same is true when this is adjusted to represent a proportion of overall household wealth (**Figure 5**). Discussions in focus groups confirmed that women consider caterpillars and shea nuts to be their primary income sources (**Figure 23**).

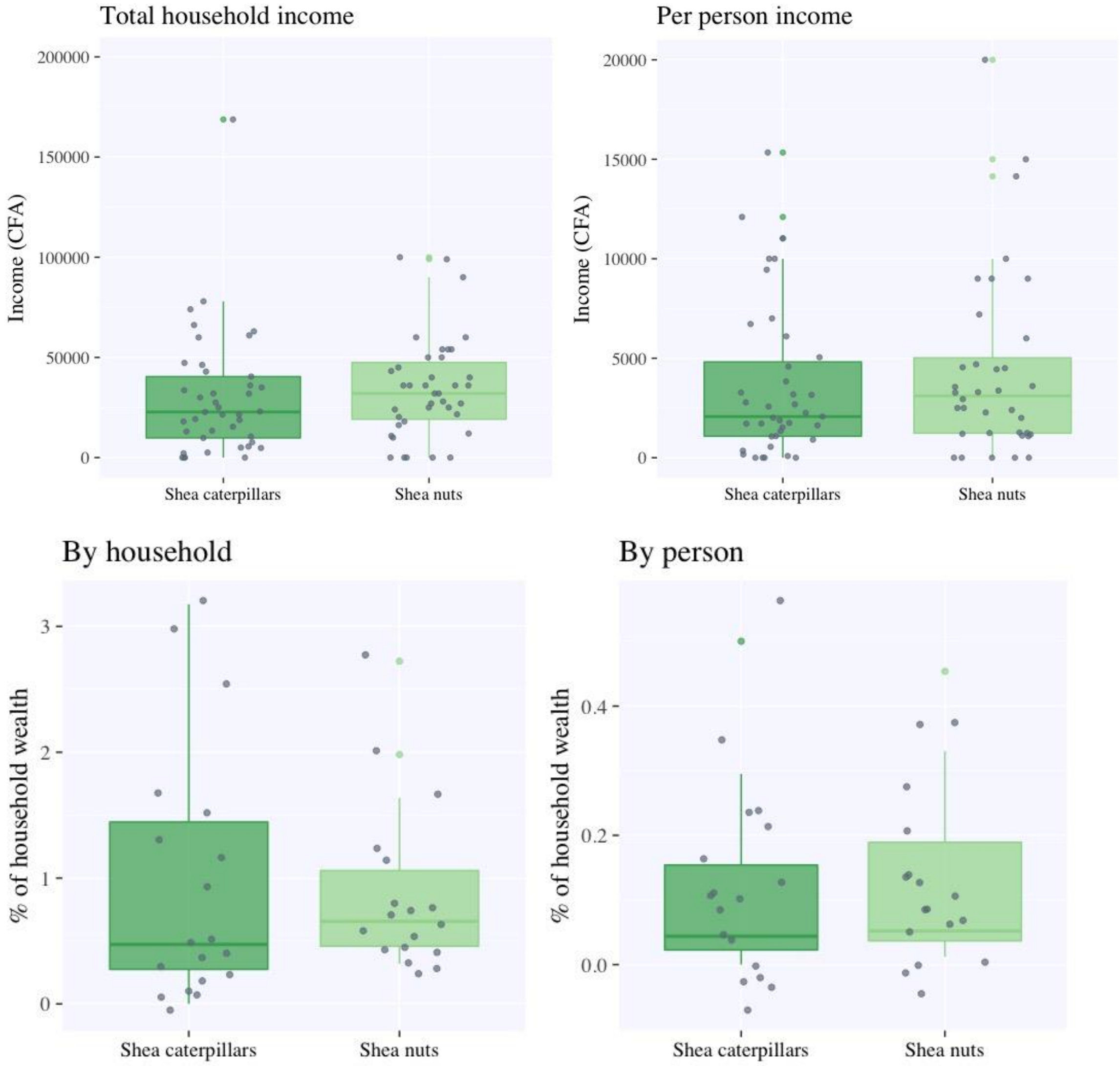


Figure 5. Reported income obtained from shea caterpillars and from shea nuts, per household and per person. Top row: Reported income obtained from shea caterpillars and from shea nuts, per household per year (Wilcoxon signed rank test, V=282, N=36, NS) and per person

per year (V=212, N=36, NS, for income per person). Values are in CFA (African Financial Community), the local currency in Burkina Faso; 1CFA=0.0017USD (as of 15.07.2018). All data represent responses to structured interviews (N=45). Lower row: Reported income obtained from shea caterpillars and from shea nuts, per household (Wilcoxon rank sum test, W=143, N=36, NS) and per person (Wilcoxon rank sum test, W=132, N=36, NS), as a percentage of household wealth estimate. Plots show median and interquartile range; error bars show the largest and smallest values within 1.5 times the interquartile range above and below the 25^{th} and 75^{th} percentiles respectively.

3.3.3. Caterpillars and food security

The majority of households experience some degree of food insecurity during both seasons, but food insecurity is significantly lower during caterpillar season. 28% of households during the dry season, and 52.6% of households during the caterpillar season, are severely food insecure (HFIAS category = 4); HFIAS scores are significantly lower during caterpillar season (paired Wilcoxon signed-rank test, V=384, N=57, $p<0.05$, **Figure 6**).

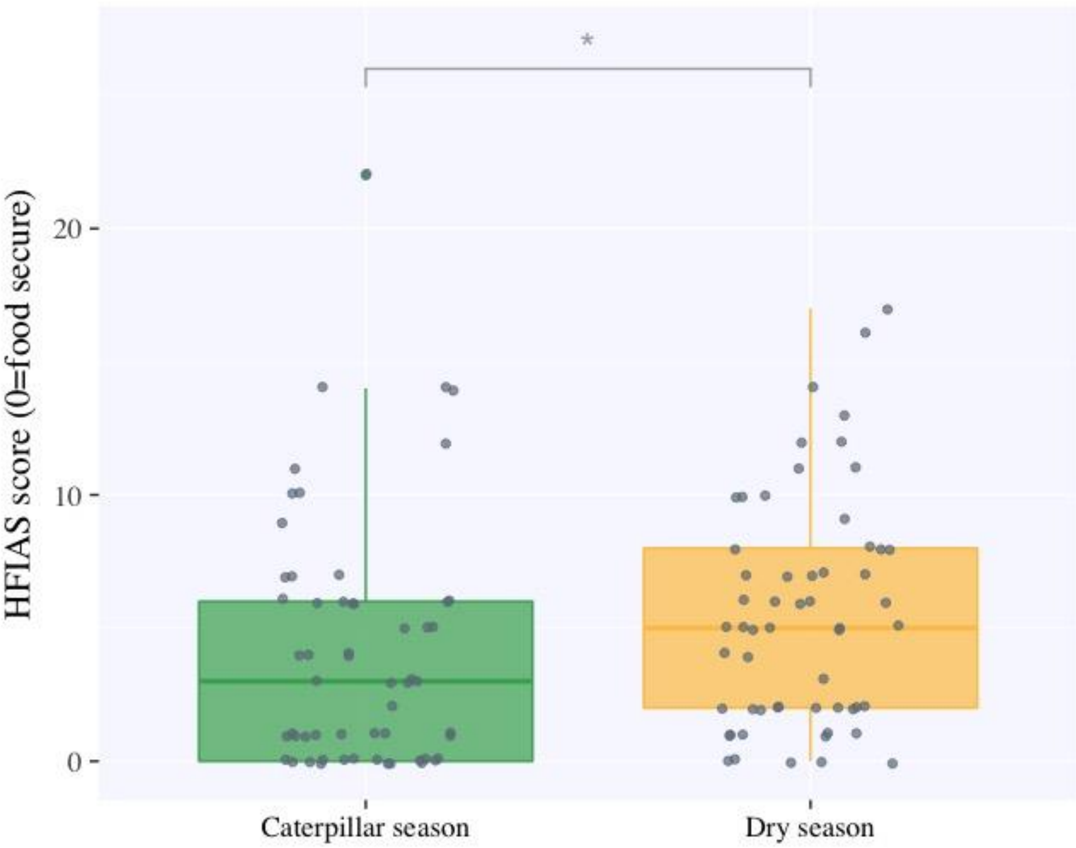


Figure 6. Results of HFIAS surveys during and after caterpillar season. Higher HFIAS scores suggest higher food insecurity. HFIAS scores are significantly lower during caterpillar season

(paired Wilcoxon signed-rank test, V=384, N=57, $p<0.05$). Boxplots show the median and inter-quartile range for each season (median=3 during caterpillar season; 5 during the dry season. IQR=6 during both seasons).

Higher food security during the caterpillar season is predicted by the amount of caterpillars sold and consumed. There is no collinearity between the sale and consumption of caterpillars (Kendall's tau=0.33, z=3.13, following the 0.7 cutoff for collinearity advocated by Dormann et al. 2013), and both predict food security during the caterpillar season (Multiple linear regression, $F_{2,17}=13.21$, $p<0.001$, **Figure 7**): the more caterpillars consumed and sold, the higher the household's food security.

Participants in focus groups all agreed that food security varies seasonally, and that without caterpillars they would be less food-secure overall. There was not a single focus group in which respondents did not discuss poverty and food scarcity, despite a lack of explicit prompting (**Table 3.i**).

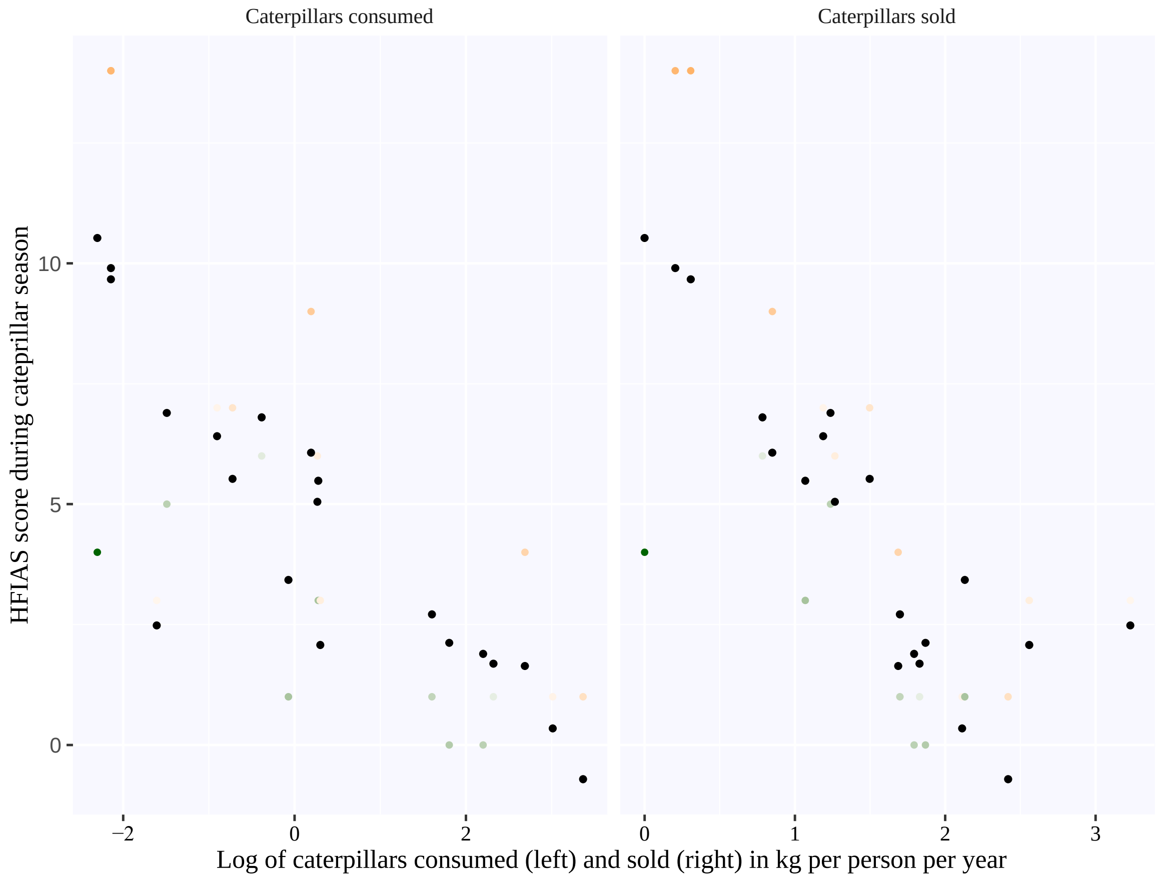


Figure 7. HFIAS scores (actual values are coloured, predicted values are in black) during the caterpillar season and caterpillars consumed (left) and sold (right). Actual values are in orange if higher than predicted values; in green if lower than predicted values. Transparency of actual values reflects residuals: high transparency indicates a low residual value, a more solid colour indicates a high residual value. Caterpillars consumed and sold are kg per person per year, log transformed. A lower HFIAS score implies higher reported food security.

However, this relationship did not hold when this season's caterpillar sale and consumption were compared with food security during the following dry season (Multiple linear regression, $F_{2,36}$=0.47, p=NS). This suggests that greater caterpillar use in one season does not have effects on food security which carry over into the next year. It also suggests that the relationship shown in **Figure 7** is not due to more food secure households having more time or ability to collect caterpillars, but instead that caterpillar consumption and sale directly increase short-term food security for households.

Question	**Theme/category of response**	**Times mentioned**	**Explanation (N=Times mentioned) / *Notes***
Nutritional value	All in household eat a similar amount of caterpillars	3	
	Some in household eat more caterpillars than others	7	Younger (N=1), faster (N=2), stronger (N=1) individuals, & those who have a preference (N=1), eat more.
	Some households eat more caterpillars than others	5	(Some) Mossi don't eat caterpillars at all (N=3); households with many older individuals eat fewer (N=1); those who have a preference eat more (N=2).
Financial value	Some in household collect more caterpillars than others	9	Men (N=4) and children/younger people (N=6) collect more. Reasons for collecting more include: speed (N=1), early rising (N=1), and having a 'sense' (N=1). Collecting a lot of caterpillars is random (N=2) and difficult (N=1).
	Some households sell more caterpillars than others	N=6	Households with more people (N=3), more men (N=1) and more younger people/children (N=2) sell more caterpillars. Also, Mossi

			people (N=1), early risers (N=3), faster collectors (N=3), sell more.
Money from caterpillars is used for:	Food	10	
	Clothes/shoes	9	
	Cultivation	3	
	Other	5	Children (N=2), crockery (N=2), travel (N=1)
	Mention of poverty/food scarcity	4	
Main income source is:	Shea trees	4	
	Caterpillars	3	
	Other	6	Nere (N=2), Trees (N=1), shea nuts (N=1), commerce (N=1), health (N=1)
Financial importance of caterpillars?	Caterpillars are most important income source	5	
	Shea nuts are most important income source	5	
	Other	2	Most important income source is: nere (N=1), cultivation (N=1)
Food security	Varies by season	8	
	Rainy season is more food secure	7	
	Dry season is less food secure	7	
	Rainy season - other	8	Food abundant (N=4), leaves (N=3), maize (N=1)
	Dry season - other	11	Food scarce (N=3), hard/suffering/poverty (N=7), no leaves (N=1)
Do caterpillars decrease food insecurity?	Yes	9	
	Mention of poverty/food insecurity/suffering	9	
During discussion	Mention of poverty/food scarcity *without* prompting	11	

Table 3.i. Results of N=9 focus groups, summarised according to emergent themes.

3.3.4. Predictors of variation in caterpillar consumption and sale

During focus groups many respondents expressed a belief that some households, and people within households, collect more caterpillars than others, but reasons for this were diverse (**Table 3.i**). Youth and associated attributes such as strength and speed were common explanations for why some people collected more caterpillars. Ethnicity and gender were also cited as factors by a minority of respondents: they reported that individuals of Mossi ethnicity are early risers who collect many caterpillars to sell but do not eat them, and that men are faster collectors. Money from selling caterpillars is primarily used for food, but also to purchase items such as clothes, shoes, seeds and crockery.

Our analyses supported some of these observations (A4): Consumption of caterpillars was significantly associated with ethnicity and location (multiple linear regression, R^2=0.6, $F_{11,31}$=6.82, $p<0.001$). Mossi, Dioula and Dafi-headed households consumed more caterpillars. The ethnicity of the first wife of the male head of household was also a predictor of caterpillar consumption: households headed by women of Peul or Bwoba ethnicity consumed more caterpillars. Households located in Soumosso consumed fewer caterpillars than those located in Sitiena. There was no significant relationship between estimated household wealth and caterpillar consumption. These associations did not hold for the sale of caterpillars: the amount of caterpillars sold was not significantly associated with ethnicity, location or household wealth (multiple linear regression, R^2=-0.097, $F_{11,31}$=0.66, p=NS).

3.4. DISCUSSION

Edible insects are receiving increasing attention for their posited role in current and future food security (Van Huis et al. 2013a, Van Huis 2015), but data on the present contribution of edible insects to household level food security in food-insecure regions are sparse (Kelemu et al. 2015, but see Baiyegunhi et al. 2016). we therefore used a mixed methods approach to assess who currently benefits from the harvest of shea caterpillars in southwestern Burkina Faso, what those benefits constitute, and how this impacts the overall food security status of households at risk. we found that food security is significantly higher during the caterpillar season. Households that collected, consumed and sold more caterpillars were those that were more food-secure, suggesting that the association between caterpillars and higher food security may be a causal relationship. we found that the relationship did not persist out of caterpillar season, suggesting that caterpillar collection directly enhances immediate food security.

The link between edible insects and food security has been discussed widely. In areas where people have market access, edible insects contribute to food security via both nutrition and income (Van Huis et al. 2013a, Kelemu et al. 2015). This has been shown to be the case in South Africa, where Baiyegunhi et al. (2016) found that income from, and consumption of, the mopane caterpillar *Gonimbrasia belina* was positively associated with food security. However, this is the first study to our knowledge that has investigated the seasonality of insects' contribution to food security. we found that the collection and consumption of a seasonal edible insect does not confer greater food security on families throughout the year; policymakers should take this into account when developing strategies to combat food insecurity using edible insects.

We found that shea caterpillars were an important source of nutrition for many households. During caterpillar season, caterpillars were consumed more frequently than other sources of animal protein and the total frequency of animal protein consumption rose significantly as a result. Reported serving sizes suggest that caterpillars are eaten in large quantities, in dishes high in protein, fat, iron and zinc. This is particularly important given that protein malnutrition and anaemia are known to be common in rural West Africa (Schulte-Herbrüggen et al. 2017, Petry et al. 2016).

Caterpillars also provide a significant source of income for people in this region; most women reported that caterpillars or the combination of caterpillars and shea nuts were their most significant income source on an annual basis. In absolute terms and when proportional to household income, annual income from caterpillars was similar to that from shea nuts. When expressed as a proportion of overall household wealth the contribution of both caterpillars and shea is low; this may be because most wealth is held in assets rather than earned on an annual basis. Income from caterpillars is primarily spent on food, but also on other personal and household essentials.

Therefore, shea caterpillars may offer temporary alleviation of both malnutrition and poverty, both of which are prevalent in this region (Akombi et al. 2017). However, this study does not measure the bioavailability of nutrients for people consuming caterpillars, nor the immediate health implications of caterpillar consumption. Populations in this area would benefit greatly from research into confounding factors that may limit the nutritional potential of the caterpillars, such as different methods of preparation.

Previous research has highlighted the importance of shea nuts for women's livelihoods (Poole et al. 2016, Audia et al. 2015, Beczner et al. 2017); it is notable that in this area caterpillars are on a par with shea nuts in terms of income generation. This may mean that regions with caterpillars suffer less from poverty than those without caterpillars. However, caterpillar collection is tiring and time consuming, so there may also be trade-offs in the amount of energy used to collect caterpillars and energy needed to collect and process shea and other food crops. Furthermore, variation in climate and market price is known to impact household income and food security in this region (Wossen et al. 2017). This study took place over a short time period and does not take into account fluctuations in market prices of shea nuts or caterpillars, and how this may impact collection patterns and the relationship between caterpillars and food security; policymakers would benefit from future research that also looks at these external influences.

Finally, we found that consumption of caterpillars varies between households. The amount of caterpillars sold was not predicted by ethnicity, location, or household wealth (see S4), but the amount of caterpillars consumed varied by ethnicity and location. Importantly, the intersection between gender and ethnicity predicted caterpillar consumption to some extent. Households in which the male head of household was of Dioula ethnicity consumed more fresh caterpillars than people of Mossi ethnicity, but the same was not true for female heads of household. Dioula people have a long tradition of eating caterpillars, while the Mossi population in the area are largely migrants from areas without caterpillars. This suggests that ethnic background influences caterpillar consumption but that women may be more likely to adapt their caterpillar consumption and preparation to their husband's tastes, rather than vice versa. Some respondents raised concerns about how Mossi collecting practices (collecting very early in the morning and selling rather than eating the caterpillars) might negatively influence both the sustainability of the caterpillar population and the benefits the non-Mossi people are able to accrue from the caterpillars. This was not a common concern, but may be important: these results suggest that a minority of people experience underlying tensions based on ethnicity and migrant status. It is crucial that policymakers and future researchers working in this area take this into account.

3.5. CONCLUSION

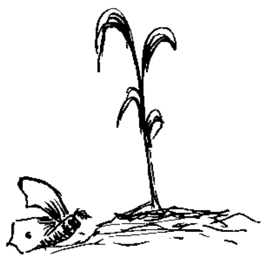
In this study, we report evidence that the collection, consumption and sale of edible caterpillars make a significant positive contribution to household-level food security on a seasonal basis in rural southwestern Burkina Faso. Edible insects have been advocated as potentially important to global food security; this study both exposes their limitations in terms of seasonality and emphasises their dual importance as a source of both income and nutrition. In this study we do not investigate the health implications of insect consumption, nor do we compare communities that harvest insects with those that do not. The study took place over two years (and two caterpillar seasons), which is too short a time period to consider the likely impacts of temporal variation in climate and market price. we recommend that future research considers these longer-term variables, and looks more closely at the relationship between insect consumption and health outcomes. we conclude that shea caterpillars in southwestern Burkina Faso are an example of an edible insect that is an important part of a widespread agricultural system, and that without the presence of caterpillars seasonal malnutrition and poverty would likely intensify.

The rains hail
the moths. Leaves will fall
But crops will grow.

雨は蛾の

予感で、葉が落ち

苗が増す



Chapter 4. Effects of defoliation by chitoumou on harvests of shea and growth of maize (*Zea mays*)

ABSTRACT

Edible insects are found in agricultural systems worldwide, and are an important source of food and income. However, many edible insects are also pests of important food crops, which raises the question of how far their presence might be costly to farmers in terms of reduced crop yields.

In this study we aimed to understand the impact of defoliation of shea trees by edible caterpillars on yields of shea and maize in a mixed agroforestry system in Burkina Faso, West Africa. We collected field data in two consecutive years. Our results suggest that tree defoliation by caterpillars has no effect on shea fruit yields, and that defoliation may have a positive effect on maize productivity.

We conclude that this appears to be an example of an agricultural system in which nutritionally and economically important plants and insects are both harvested by humans without risking yield reductions of harvested plants.

4.1 INTRODUCTION

Wild-harvested edible insects are an important source of food and income across much of the world (Van Huis et al. 2013a). This is particularly true in sub-Saharan Africa, where termites, locusts and caterpillars are traded and consumed, mostly in rural but also in urban areas (Kelemu et al. 2015, Illgner & Nel 2000). Edible insects are often harvested from agricultural systems. In many cases, this is because insects that feed on crop plants are deliberately collected as food (DeFoliart 1992, Van Itterbeeck & Van Huis 2012). For example, palm weevil larvae are harvested from many palm-based agroforestry systems worldwide (Binnquist & Shanley 2004), and weaver ants are harvested from fruit tree plantations in Southeast Asia (Payne & Van Itterbeeck 2017).

We know little about the interactions of edible insects with crop yields. The best data available are based on assumptions generalised across species in ways that even the authors admit are unlikely to be accurate (Wegier et al. 2017, Payne & Van Itterbeeck 2017). Some insects - such as grasshoppers and crickets – are collected at multiple points in the middle of their life cycle with the explicit aim of limiting crop damage. This presumably means that the harvested biomass of insects is not maximised, but crop yield is higher than it would have been if the insects had been left to mature. In such cases there is likely to be a trade-off between harvested biomass of insects and that of crops. How farmers respond to this trade-off may depend on demand – e.g. in parts of Mexico, edible grasshoppers are so prized that some farmers set aside fields of alfalfa specifically for the grasshopper crop (Cerritos and Cano-Santana 2008). Elsewhere farmers use insecticide to control outbreaks of these edible insects, apparently choosing higher crop yield over insect yield (Ecobichon 2001).

Other insects are harvested only at a specific point in their life cycle. Caterpillars are a good example of this: many are eaten only when in their final larval stage. This is the case for the mopane worm (*Imbrasia belina*), which is an economically important edible caterpillar throughout southern Africa (Gardiner 2006). The same is true for termite (*Macrotermes* spp) alates, harvested after their nuptial flight, which occurs in response to the first rains (Kinyuru et al. 2013). These insects are found in abundance, but only when in season. However, most are wild-harvested, and are not found in agricultural fields. Many larval insects feed on crops, but are small in size and not traditionally eaten.

This study looks at an exception to these patterns: an insect which is harvested as a larva which is also potential agricultural pest. The shea caterpillar *Cirina butyrospermi* (**Figure 8**) only feeds on the leaves of the shea tree (*Vitellaria paradoxa*). This is a wild tree that has been selectively retained in agricultural fields across western and sub-saharan Africa, a stretch of land known as the shea belt, with fields referred to as shea parklands (Maranz and Wiesman 2003). The nuts from the trees are collected to make shea butter, used in food, confectionery and cosmetics (Lovett 2010). Shea caterpillars are abundant in parts of these agroforestry systems, and are collected as food (Bonkoungou 2002). They are commonly harvested in their final instar before pupation, by which time they have usually caused extensive damage to the shea trees (**Figure 8**).

Figure 8. The shea caterpillar (Cirina butyrospermi), with scale (left, in cm); a shea tree (Vitellaria paradoxa) following defoliation by shea caterpillars (right).

Farmers in this region – and by extension, agricultural policymakers – are interested in the interaction between the edible caterpillars and their crops. Working in a rural landscape in the southwest of the shea belt, where shea trees are retained in fields of maize (*Zea mays*) and other crops, this study addresses this interaction in two different ways. Firstly, we ask whether defoliation by caterpillars has any discernible impact on the abundance of shea fruits in the following year. Secondly, we ask whether defoliation by caterpillars shows any association with the heights of maize crops under shea trees.

4.1.2. Shea agroforestry and shea caterpillars

Shea parklands are an agroforestry system estimated to dominate 3-4,500,000km^2 of the landscape across 21 African countries (Naughton et al. 2015); shea trees have been selectively retained for many years (Lovett and Haq 2000). The trees are a major source of income and cultural significance, and particularly benefit women through their use of the trees to collect edible and tradable goods (Boffa 2000). The presence of young and mature shea trees reduce maize yields by a mean of 65% and 76% respectively, across two seasons (Ogwok et al 2019).

Shea caterpillars are found in many parts of the shea belt (Anankware et al. 2017, Boffa 2015). Their range has not been mapped and while their life cycle has been documented (Remy et al. 2017), little is known of their ecology. They are harvested at the end of their larval life cycle, which usually falls in early to late August, after they have caused considerable damage to shea trees (**Figure 8**). Harvested caterpillars are an important source of nutrition and income for many subsistence farming households in the region (Anvo et al. 2016). In some parts of the shea belt where the caterpillar is not traditionally eaten as food, the caterpillar is considered a pest with insecticides sometimes used to combat it (Odebiyi et al. 2004). Yet even in such regions farmers are increasingly recognising the economic benefits of collecting caterpillars, and are learning to harvest them (K. Hien, pers.comm.). In most areas there remains a taboo on collecting caterpillars before they have reached their final instar, limiting any scope for flexibility over when to harvest caterpillars. However, some farmers are concerned about the impacts of caterpillar defoliation and caterpillar harvesting on their yields of shea and maize (Chapter 4 of this thesis).

In many parts of West Africa, women and men have different roles within the same landscape, and prioritise different crops (Rocheleau & Edmunds 1997). This is true of the study region, and therefore this study focuses on two crops: shea and maize. Shea is a commercially important crop for women across the shea belt (in the form of shea nuts, which are sold at market) (Elias 2015, Schreckenberg 2004). Maize is the staple food of the region; maize fields are usually owned and managed by men but women and children contribute substantial agricultural labour (Kevane & Gray 1999)

The impact of defoliation by shea caterpillars on shea and plant crop yields has not been quantified. Opinion is divided as to whether defoliation increases (Boffa 2015) or decreases (Dwomoh et al. 2004) subsequent harvests of shea nuts. Defoliation might increase light levels reaching maize plants growing underneath shea trees. In addition, shea caterpillars produce frass, which has been shown to have a positive effect on soil pH (increased alkalinity), calcium (C) and nitrogen (N) content, but not on phosphorus (P) or potassium (K) (Coulibaly et al. 2017); however, the impact of this soil enrichment on crops has not been quantified.

4.2 Materials and Methods

4.2.1. Study system

We collected data in Soumosso (Hauts-Bassins, 11°00'44", -004°02'45") and Sitiena (Comoe, 10°36'19", -004°49'03"), two administrative districts in southwestern Burkina Faso (**Figure 1**). Both are located in the Sudano-Sahelian climatic belt, and experience a long dry season punctuated by a short and unreliable rainy season in May-June (Maranz 2009). The majority of the population are smallholder farmers (Callo-Concha et al. 2012). The dominant crop – and dietary staple - is maize, although cotton (*Gossypium arboretum*) has become increasingly popular as a cash crop to supplement families' livelihoods (Gray and Kevane 2001). Millet (*Pennisetum glaucum*, referred to locally as 'petit mil', *Eleusine coracana*, referred to as 'mil africaine', and a red variant of *Eleusine coracana* referred to as 'mil rouge'), groundnut (*Arachis hypogea*) and sorrel (*Hibiscus sabdariffa*) are also widely grown. All agricultural fields measured (0.2-3ha, mean=1.1ha) had trees in them (4.2-69 trees per ha, mean=20 trees per ha) - predominantly shea (1.6-36 trees per ha, mean=15 trees per ha), although the African locust bean tree (*Parkia biglobosa*) is also common. Both of these trees are economically important (Gausset et al. 2005), and their primary products (shea nuts and locust beans) are mainly harvested, processed (into shea butter and soumbala respectively) and sold by women. The most prevalent ethnic groups are Dioula and Mossi in Soumosso, and Goin and Karaboro in Sitiena, although due to exogamy and economic migration many other ethnic groups are also present. Islam, Christianity and forms of animism are all practised at both sites.

4.2.2. Sampling strategy

We initiated this field study with 69 initial interviews in 2016, with male heads (N=54) and first wives (N=15) of households that owned >1ha of land and cultivated some maize, which is the staple food across the region. We did not record the exact variety of maize cultivated by each household; all maize crops were grown from unlabelled kernels purchased at local markets. Households likely to fit these criteria were identified by an employee of Le Centre Muraz (a malaria field research centre) in Soumosso (N=69), and by family members of BS (Bakary Sagnon) in Sitiena (N=25), following a snowball sampling strategy in which key informants – chosen for their understanding of research design and sampling – helped find further respondents (Young et al. 2018). Interviews followed a set structure to ensure quantifiable responses concerning land ownership, household size, and estimates of shea nut and shea caterpillar harvests. We recorded responses by hand. We found that men were able to answer questions about land ownership and crop cultivation, and women were able to answer questions about harvests of shea nuts and shea caterpillars.

In Soumosso we then used stratification by area of landholding and harvest level to select a representative subsample of 30 households whose field systems we then investigated further (Young et al. 2018). . This subset has similar land area, caterpillar harvest and household size to those households we discarded from our initial sample in terms of mean land area (t-test, t=1.1, p=NS), quantity of caterpillars collected (t-test, t=-0.9, p=NS) and household size (t-test, t=0.54, p=NS). In Sitiena, we interviewed 25 male heads of household and selected for our sample the N=23 households that owned >1Ha of land and grew maize. Our total sample comprised 53 fields owned by different households, 23 in Sitiena and 30 in Soumosso.
For each household, we measured the area of the field that the farmers told us would be used for maize in 2016. In two cases the farmer intended to use two separate ~1ha fields for maize; in both cases we selected one field, based on geographical convenience. We then measured the height and circumference of all trees in each selected field. To identify three shea trees in each field that represented size variation within that field, we ranked all shea trees in each field by size, divided these into three equal sized classes, and selected one tree at random from each size class. This gave a total sample of 157 trees (as two fields had only two shea trees in them).

We then surveyed a subsample of these trees on four separate occasions: (1) for caterpillar defoliation immediately following caterpillar season, in late August (in 2016, N=157 trees; in 2017, N=83 trees); (2) for shea abundance prior to caterpillar season, in July (in 2017, N=95 trees); (3) for crop height beneath trees during the growing season, in September-late October (in 2016, N=66 trees; in 2017, N=42 trees); (4) to examine how maize height related to cob productivity, immediately preceding harvest, in late October-early November (in 2017, N=36 trees). Each survey had to be completed within a certain time period, and we was unable to sample every tree for any given method; for this reason, none use the full sample of trees. When selecting sites to survey, we prioritised geographical spread to ensure sampling was not focused within a given area. We used the following methods for each survey.

4.2.1.1. Defoliation by caterpillars

As soon after caterpillar season as possible (within a 2wk window, necessary due to rapid regrowth) we noted levels of natural defoliation by shea caterpillars for each tree as follows: the observer stood under the tree in each cardinal compass direction, selected five leaf clusters at random and scored each on a scale of 0-100 for the extent to which defoliation had occurred. The observer also noted their overall impression of total tree defoliation, on a scale of 0-100. Three separate observers collected these data; to ensure concordance the first observer spent a day with each of the second and third observers, noting and then comparing the independently-made observations of each individual until all observations fell within 10% of one another. Scores for total tree defoliation showed substantial concordance (following McBride 2005) with the cluster-derived defoliation scores, as calculated by an overall mean of 20 observations (5 leaf clusters in each compass direction), in both years of data collection, 2016 (2016: Lin's Concordance Correlation Coefficient, N=157 trees, rho=0.82 (0.75-0.87), bias correlation factor = 0.99; 2017: N=83 trees, rho=0.82 (0.75-0.88), bias correlation factor = 0.97).

4.2.1.2. Shea abundance

The observer measured shea abundance (that is, the number of fruits, which corresponds to the number of nuts since the nut is found inside the fruit) in 2017 on a scale of 0-3 (0=None visible, 3=Abundant) for N=95 trees in Soumosso. We took five measures per tree: a branch was selected at random in each compass direction and scored from 0-3, and after observing the entire tree, we assigned one overall score from 0-3 to the tree. We checked inter-observer concordance as described above, and compared independently-made observations until all observations fell within the same category on the scale of 0 to 3. The measure of overall shea abundance showed poor concordance with the mean of the four observations in each compass direction (Lin's Concordance Correlation Coefficient, N=95, rho=0.62(0.51-0.71), bias correlation factor=0.88). There was no significant difference in shea abundance across the four compass directions (repeated measures ANOVA across 95 N/S/E/W scores, $F_{3,270}$=1.4, p=NS). We therefore focus for the rest of this chapter on the mean of four measures per tree.

4.2.1.3. Crop height

For each tree, we measured the height of 16 maize plants from base to tip in September 2016 and in September 2017. We measured 4 plants in each of the four compass directions. We selected these 4 plants based on their position at distances d/3, 2d/3, 4d/3, 5d/3 away from the trunk of the tree, where d=distance from the trunk to the canopy edge in the given compass direction. Maize plants were typically taller beyond the canopy. To gain a measure of the difference in height of plants growing outside and under the canopy for each tree, we first subtracted the mean height of the two plants under the canopy (at d/3 and 2d/3) from the mean height of those outside the canopy (at 4d/3 and 5d/3) (**Figure 9**), for each compass direction. We then calculated the mean of these difference values across our four directions to give a single measure per tree.

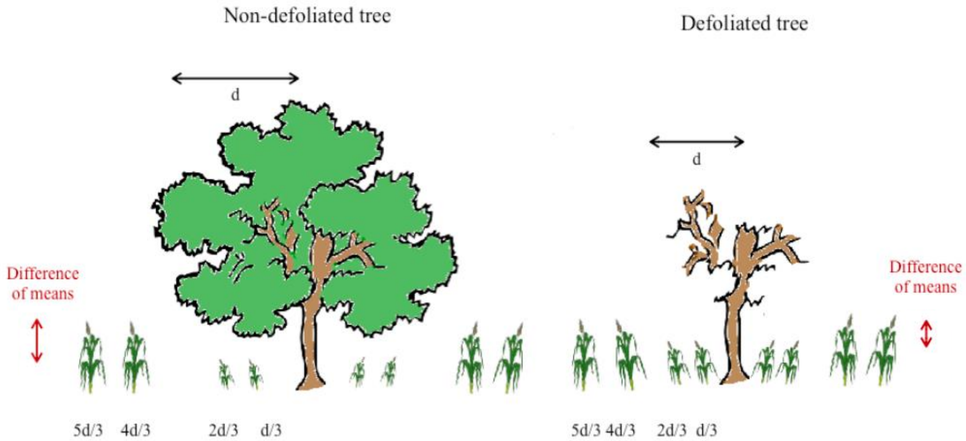


Figure 9. Diagram showing how measurements were taken for maize height, outside and under the shea tree canopy. Differences of means were calculated by subtracting the mean height under the canopy from the mean height outside of the canopy, in all four compass directions.

4.2.1.4. Crop productivity

The height of individual maize plants was used as a proxy for plant productivity. We checked the validity of this measure by measuring productivity directly, immediately prior to harvesting. We selected one tree at random from each of 9 fields (selected from the study sample based on geographic convenience and permission of owners), and heights of 4 maize plants near it were measured as described above but only for a single randomly chosen compass direction. We also measured the mass and abundance of their cobs.

4.2.3. Ethical approval

We obtained ethical approval for the study prior to both field seasons in 2016 and 2017, from the Department of Geography Ethics Review Group, University of Cambridge.

4.2.4. Statistical analyses

We used a repeated measures ANOVA to compare defoliation across compass directions in 2016 and 2017. We used a Spearman's rank correlation to look at the association between defoliation by caterpillars in 2016 and shea fruit abundance in 2017. We used a fitted linear model to look at the relationship between the difference in the height of maize plants under and beyond the tree canopy with the amount of defoliation by caterpillars in both years. We ran the same test looking at defoliation in 2016 and the difference in crop height in 2017. Finally, to assess the strength of using plant height as a proxy for yield, we ran a linear regression to look at the association between maize plant productivity and plant height.

4.3. RESULTS

We found no significant difference in defoliation across compass directions, in either year of data collection (for 2016 repeated measures ANOVA across 157 sets of N/S/E/W scores, $F_{3,452}$=0.2, NS; for 2017 repeated measures ANOVA across 83 sets of N/S/E/W scores, $F_{3,324}$=0.5, NS). This suggests caterpillars do not preferentially defoliate trees in any one direction; therefore all subsequent analyses use the overall mean of 20 observations per tree as the measure of defoliation.

Shea fruit abundance in 2017 did not show any association with defoliation by caterpillars in the preceding year (Spearman's rank correlation, r_s=0.011,N=84,p=NS) **(Figure 10)**.

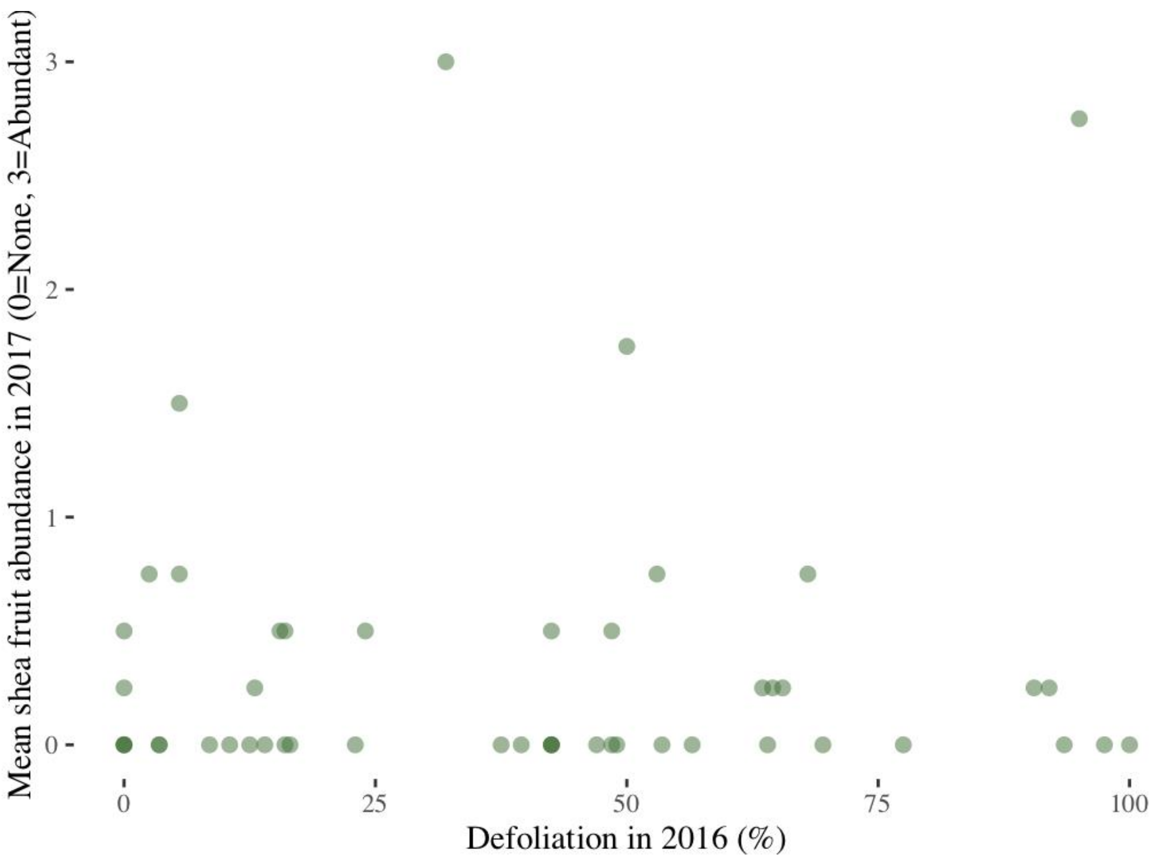


Figure 10. Defoliation (0-100%, continuous scale) in 2016 and mean shea abundance (0-3, ordinal scale) in 2017. Darker circles show overlapping data points. The relationship between the two is non-significant (Spearman's rank correlation, r_s=0.011,N=84,p=NS).

However, we did find evidence of a link between defoliation and maize growth **(Figure 11)**. In 2016, the difference between the height of maize plants beyond the tree canopy and under the tree canopy decreased with increasing defoliation (fitted linear model, N=66 trees, $F_{1,64}$=12.5, p<0.001; Fig5). There was no such association in 2017 (linear regression, N=42, $F_{1,40}$=1.9, p=0.17). This may be because deofliation was significantly higher in 2017 (Wilcoxon rank sum test, W=2660, p<0.001), when nearly all trees were defoliated to some degree (**Figure 11**).

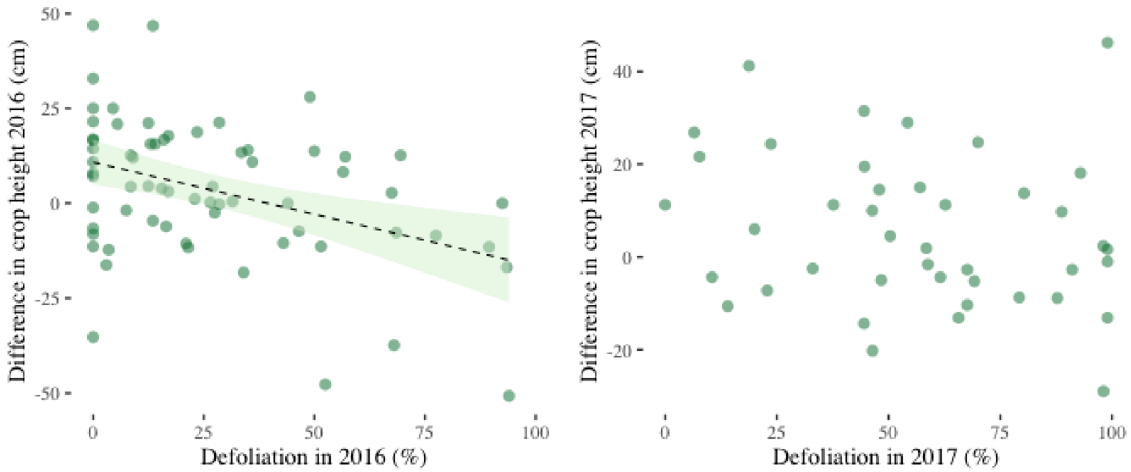


Figure 11. Correlation between defoliation (0-100%, continuous scale) and difference in crop height beyond and under the tree canopy. In 2016 (left; line shows fitted linear model, shaded area shows 95% confidence interval, N=66 trees, $F_{1,64}$=12.5, p<0.001), in 2017 (right; non-significant, N=42 trees, $F_{1,40}$=1.9, p=NS).

We found some evidence for a lagged effect of defoliation on crop height: there was a negative association between defoliation in 2016 and difference in crop height in 2017 (fitted linear model, N=34 trees, $F_{1,32}$=6.3, p<0.05) **(Figure 12)**. However, the statistical strength of this is less than the link between 2016 defoliation and difference in crop height in 2016 (**Figure 11**).

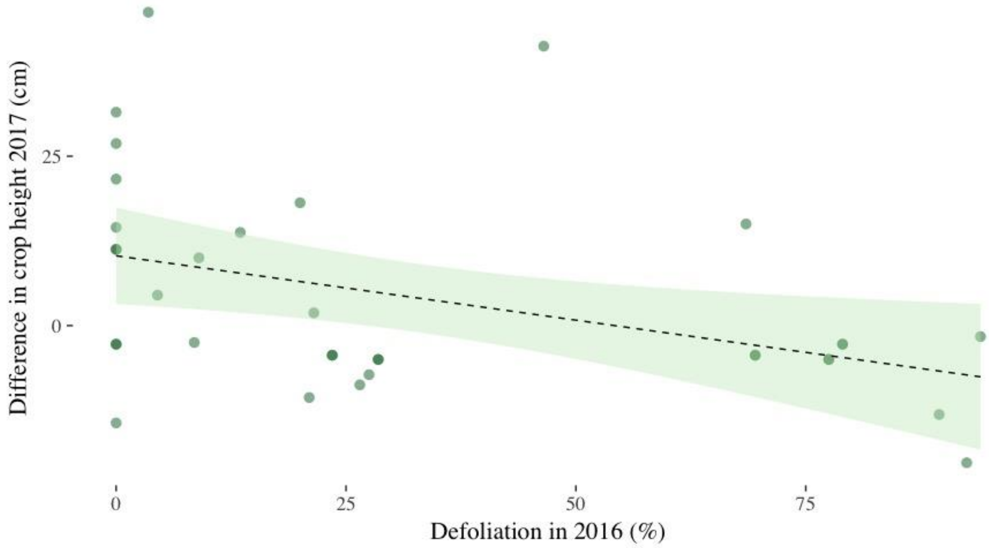


Figure 12. Defoliation in 2016 (0-100%, continuous scale) and difference in crop height beyond and under the tree canopy in 2017. Line shows fitted linear model, shaded area shows 95% confidence interval (N=34 trees, $F_{1,32}$=6.3, p<0.05).

Defoliation in 2016 did not predict defoliation in 2017 (fitted linear model, N=64 trees, $F_{1,62}$=0.74, p=NS).

The associations between defoliation and maize height may reflect links with maize productivity. Our measures of cob production showed that the productivity of each plant (total mass of maize cobs) was significantly positively correlated with plant height (linear regression, N=36 maize plants, adjusted R^2=0.62, $F_{3,32}$=19.9, p<0.001). Importantly, there was no significant interaction with whether or not the plants were under or outside of the canopy (t=-1.5, NS).

4.4. DISCUSSION

We found that individual trees are not consistently more or less prone to defoliation, suggesting that caterpillars do not seem to prefer certain trees in consecutive years. This suggests that the lagged association between maize growth and the previous year's defoliation is not mediated by its effect on the next year's canopy.

Despite highly variable (and sometimes marked) levels of defoliation of shea trees by shea caterpillars, we found no evidence of that caterpillar herbivory impacts shea fruit production – variation among trees in the abundance of shea fruit was not correlated with variation in their extent of defoliation the previous year. In contrast, in 2016 (but not 2017) we found a significant negative relationship between defoliation and the difference in the height of maize growing beyond vs under tree canopies: maize plants under trees grew relatively taller the more defoliated those trees. The correlation we observed between maize height and productivity suggests that height is a valid proxy measure for plant productivity and that the relationship between height and productivity is similar for maize plants growing under shea trees and beyond. Therefore the greater relative growth (in 2016) of maize plants under more heavily defoliated trees may in turn be associated with higher crop yields. The likely field scale impact of trees and their caterpillars on overall crop yield is relatively small: the mean area covered by shea trees in a given field is 316m^2, and the mean area of a field in this system is 1.13ha; therefore, shea tree canopy cover impacts a mean of approximately 2.82% of cultivated land.

The lack of any interaction between the extent of defoliation by shea caterpillars and the abundance of shea fruits the following year aligns with the perceptions of shea caterpillars by some members of the local community. Long-term residents of areas with a history of caterpillar use do not generally consider them to be pests. In two areas of Uganda, 50% and 58% of farmers reported increased fruit production following defoliation by caterpillars (Okullo et al. 2004), and an experimental study with seedlings suggested that defoliation did not adversely affect growth (Ugese et al. 2011). However, shea caterpillars have been referred to as destructive pests in scientific publications (e.g. Dwomoh et al. 2010), and in places where people are unfamiliar with the caterpillars (either because the people or the caterpillars have recently migrated to the area) there have been reports of pesticide use to combat caterpillar infestation (Odebiyi et al. 2004). Furthermore, there is a danger that if negative attitudes towards insects as food become more prevalent – a trend that has been observed in other parts of the world with globalisation (Van Huis et al. 2013a) – people may begin to react to caterpillars with pesticide use. The data reported here, which show that caterpillars do not have any discernible effect on the shea harvest, are important for the maintenance of the caterpillars and caterpillar-harvesting within this agricultural system. Similarly, the data here show that within a shea-dominant agroforestry system there is no negative association between defoliation by shea caterpillars and maize growth. The inconsistency between years in our result means we cannot conclude that there is a consistent positive association between these variables. It is possible that any relationship may fluctuate due to other factors that we did not account for, such as interannual climatic variation. Furthermore, the impacts of defoliation on yield may rely on multi-year patterns of defoliation and may not be discernible from data spanning only two annual cycles. However, to the extent that maize growth is greater under more heavily defoliated trees, one possible reason is that less radiation is intercepted by the shea canopy before reaching the maize leaves, A second potential mechanism is that caterpillar frass acts as fertilizer. A third potential mechanism is that that the frass may increase pathogen resistance. This has been observed in maize that has been exposed to the frass of another caterpillar (the Fall armyworm *Spodoptera frugiperda*) and may be due to the chitin content of the frass, which includes the chitinous skins of the first four larval stages (Ray 2015). There is a growing body of evidence for the efficacy of insect frass in promoting crop growth: for example, Thai farmers report that cricket frass is beneficial to their rice fields (Halloran et al. 2016); experiments using caterpillar frass to fertilise basil plants found a positive effect on leaf growth (Buenvinida and Tamban 2016); the application of cricket frass on farmers' fields in Canada has almost doubled yields of fresh hay (D. Goldin, pers. comm.). Likewise, frass from the shea caterpillar may prove to be another source of insect-derived fertilizer.

The results reported here reflect a correlational relationship, but this cannot be assumed to infer causality, as variables such as soil quality, tree age and tree health are not consistent across trees and may have affected our results. We need experimental data to establish causality, and this is an important avenue for future work. However, acquiring such data is complicated by the mobility of the caterpillars, which move between trees and are not easily deterred by commonly used insect deterrents such as tanglefoot and fluon.

4.5. CONCLUSION

We can conclude from this study that shea caterpillars do not appear to be pests in relation to either shea or maize, suggesting that where caterpillars harvesting takes place (or could), farmers should be actively dissuaded from using agrochemicals to combat these insects. There may be a positive effect of defoliation by caterpillars on the growth of maize underneath shea trees, but longer-term observations and further experiments are necessary to clarify the nature and strength of this relationship.

This is the first field study of the interaction between crop yields and the presence of an edible insect that is harvested at a single point in its life cycle. Unlike edible orthopteran pests, the shea caterpillars studied here do not have a discernible negative effect on crop yields. Instead, this insect does not appear to damage production of these economically important plants. We conclude that this appears to be an example of an agricultural system in which humans, as predators of both the plants and the insects in the system, are able to benefit in terms of harvesting both plant and animal matter without an apparent trade-off between the two.

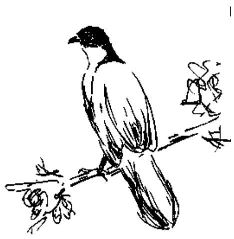
Edible insects are important for the livelihoods of smallholder farmers worldwide (Payne and Van Itterbeeck 2017, Kelemu et al. 2015, Van Huis et al. 2013a, Hanboonsong et al. 2013), and these results provide an optimistic framework for their sustainable exploitation under certain circumstances. However, the sustainability of the shea nut-caterpillar-maize system may be threatened by external factors. The market for edible insects is changing rapidly, with demand increasing among wealthier populations (Global Market Insights 2018, Payne 2014, Durst and Shono 2010). The climate is also changing, with increasing aridity in our study region and consequent decreases in crop productivity (Sonwa et al. 2017, Serdeczny et al. 2017). This may lead to management decisions that explicitly prioritise either the insects or the plants, shifting away from the current system. If this does happen, understanding and accounting for the nature of the interactions between these insects and plants will become increasingly important.

Birdsong says
The caterpillars
Are no hindrance.

鳥のさえずりに、

「毛虫って

許す」



Chapter 5. Bird abundance in a mixed agroforestry landscape containing chitoumou, the edible caterpillar *Cirina butyrospermi*

ABSTRACT

Agriculture is the greatest threat to biodiversity worldwide. Edible insects have been proposed as an environmentally friendly protein source, and many are found in existing agricultural systems. We investigated the relationship between bird abundance and deforestation, and between bird abundance and the presence of 'chitoumou' (*Cirina butyrospermi*), a commonly consumed edible caterpillar in an agroforestry system in southwestern Burkina Faso. We surveyed both cultivated (N=21) and uncultivated (N=15) sites. At each site we conducted four point count surveys of birds during caterpillar season. We recorded defoliation by *Cirina butyrospermi* as a proxy for the presence of the caterpillars. We also surveyed maize yield and tree density, both of which are expected to have a significant relationship with measures of biodiversity including bird abundance. 21 (out of 31 species detected on >30 counts) bird species were more abundant in uncultivated sites and none were more abundant in cultivated sites. Within cultivated sites, six species showed a positive correlation between abundance and defoliation by caterpillars, and one showed a negative correlation. We found no significant association of overall bird abundance with maize yield, tree density or the extent of defoliation by caterpillars across cultivated sites. We conclude that in this low-intensity agroforestry system, the presence of the edible caterpillar *Cirina butyrospermi* does not have a significant association with either higher or lower bird abundance.

5.1. INTRODUCTION

Human activities are causing a significant decline in global biodiversity (Newbold et al., 2016). Of these activities, habitat loss and degradation through the expansion and intensification of agriculture threaten the greatest proportion of mammals and birds (Tilman et al., 2017). Wildlife-friendly farming, in which crops are cultivated in a way that supports wild species, is one strategy that may combat this (Pywell et al., 2012). However, such systems tend to be lower-yielding (Green et al., 2005) and only support a limited range of species (Phalan et al., 2011). Higher yields are crucial given that food production via agriculture is necessary to support our expanding human population: we may need to produce up to 70-100% more food by 2050 (Godfray et al., 2010). Data suggest that we can achieve this yield increase using intensified farming techniques, but that it will be crucial to combine such a strategy with measures that preserve biodiversity via land sparing - ensuring that land not needed to meet food demand is set aside (or restored) for wild nature (Phalan et al., 2014). To work towards achieving this– higher yields at the lowest possible cost to biodiversity - we must understand the relationship between yield and biodiversity in different agricultural systems worldwide. Bird abundance is a commonly used proxy for overall biodiversity (Nagy et al., 2017), which is why we chose to use this measure in the present study.

Yield data, especially when measured in relation to measures of biodiversity including bird abundance, tend to focus on yields of one or more global commodity crops (Fischer et al., 2017). However, over 50% of the world's major food crops are grown by smallholder farmers in Latin America, sub-Saharan Africa and Southeast Asia, many of whom use mixed cropping systems (Samberg et al., 2016). In such systems, the same patch of land may support several non-commodity cultivars, and/or edible wild plants (Félix et al., 2018), complicating yield measurement. This is because some non-commodity food plants may be valued for their taste and micronutrient content rather than for those components which may be more readily aggregated across products, such as caloric or protein content.
Mixed systems that support non-commodity foods also commonly share space with livestock. As one example, duck-rice farming systems in southeast Asia (Zheng et al., 2017) can be beneficial for farmers in terms of improving both crop yield and overall profit (Hossain et al., 2005). The same may be true for agricultural crops from which nutritionally and economically valuable edible insects are also harvested. The FAO (Food and Agriculture

Organisation of the United Nations) published reports in 2010 (Durst et al., 2010) and 2013 (Van Huis et al., 2013a) that drew attention to this type of mixed system. Edible insects in agricultural fields provide ecosystem services and disservices that include indirect influences on both crop yields and measures of biodiversity that include bird abundance (Payne and Van Itterbeeck 2017). Some prominent examples of this include orthopteran insects that consume the main crop, such as *Locusta migratoria* in parts of Africa (Mohamed 2015), *Oxya* spp. in China and parts of Southeast Asia (Chen et al., 2009) and *Sphenarium purpurascens* in Mexico (Cerritos and Cano-Santana 2008). Their herbivory is thought to reduce crop plant production, and therefore the abundance of these species is likely to correlate negatively with plant crop yields. Others edible insects include hymenoptera that consume crop pests, such as *Oecophylla smaragdina* (Van Mele 2008), *Vespa mandarinia* (Feng et al., 2010) and *Vespula* spp. (Payne and Evans 2017) in Asia. If their presence of these species reduces the presence of crop pests through predation, their abundance may be positively associated with plant crop yields. Both types of insect provide farmers with an additional yield of animal protein that can be consumed and sold.

There are few data on the potential relationship between the presence of edible insects in agricultural systems with yield, profit for farmers, and greenhouse gas emissions: the harvest of *Sphenarium purpurascens* grasshoppers in Mexico reduces the density of eggs the following season, reduces costs of insecticides and adds to farmers' incomes (Cerritos and Cano-Santana 2008). Feed conversion ratios for the same species are low (i.e. more efficient) compared to conventional livestock, and therefore they may have an indirect association with levels of biodiversity in the form of reduced environmental pollution (Wegier et al., 2018), which may in turn cause an increasee in bird abundance. Ultimately, data are too scarce to draw any conclusions about the relationship between edible insect harvesting and the environmental impacts of agricultural practices, and there are currently no data that directly address the relationship between edible insects and bird abundance. It is likely that the relationship between edible insects and bird abundance in agricultural systems will vary greatly according to both the species of insect and the type of system, but that broadly speaking, the impacts of any edible insect on bird abundance will be most marked in birds that consume the insects in question.

For this study, we looked at an edible insect that is harvested from shea parklands in West and Central Africa: *Cirina butyrospermi*, locally known in Burkina Faso as "chitoumou", or the “shea caterpillar” (chenille de karite). *C.butyrospermi* caterpillars eat the leaves of the shea tree, causing extensive defoliation. The term *shea parklands* refers to fields within the shea belt, which ranges across West and Central sub-Saharan Africa (Maranz and Wiesman 2003) and is characterized by shea trees growing in agricultural fields of densities up to 36 trees per ha (Payne et al., in press). This system has been created by the intentional retention of shea trees during forest clearance (Elias 2013). Shea trees produce fruits and nuts that are a significant source of income and nutrition for people in this region (Pouliot 2012). Shea caterpillars eat the leaves of shea trees. Defoliation by the shea caterpillar has no discernible relationship to shea yield, and no negative association with the yield of maize, which is the dominant staple crop in the region (Payne et al., in press). They do, however, provide a source of protein-rich food (Anvo et al., 2016) that is important for food security (Payne et al., in review). There is no significant difference between household profits from caterpillars and household profits from shea nuts in the current study system (Payne et al.,, in press). Overall, prior research shows that the edible insect *Cirina butyrospermi* adds value to shea parklands.

The shea belt is also home to a wide range of bird species (Söderström et al., 2003). In Burkina Faso, forest clearance for agriculture has intensified since the 1970s and continues today (Paré et al., 2008). Some land in this landscape is left temporarily fallow, but amongst sites of fallow land, more recently cultivated areas have been found to support higher species richness (Söderström et al., 2003). On land that is currently cultivated, previous surveys have shown that the selective retention of shea trees and edible weeds within cultivated land promotes bird richness and abundance, but that palearctic migrants favour fields with fewer trees (Usieta 2014). In the same study, yields did not differ significantly in relation to these variables. Many birds do thrive in this landscape, but their relationship to *Cirina butyrospermi* has not yet been considered.

In this study we ask what predicts bird abundance in an agroforestry landscape from which edible caterpillars are harvested. We compare bird abundance in cultivated and uncultivated sites; we test which variables affect abundance of individual bird species across cultivated sites, and finally we consider predictors of aggregate abundance across cultivated sites. We consider as our key variables that may predict bird abundance: tree density, shea tree density, agrochemical use, maize crop yield, and defoliation by caterpillars as a proxy for caterpillar abundance.

5.2. METHODS

5.2.1. Study system

We collected data for this study in the shea belt villages of Soumosso (Hauts-Bassins, 11°00'44", -004°02'45"), Koba (11°00'52.1", -003°59'42.2) and Sitiena (Comoe, 10°36'19", -004°49'03"), characterised by shea-dominant agroforestry with few patches of uncultivated land. The majority of the population are reliant on smallholder agriculture. Maize (*Zea mays*) is the dominant crop. Other common crops include: Millet (*Pennisetum glaucum* and *Eleusine coracana*), groundnut (*Arachis hypogea*) and sorrel (*Hibiscus sabdariffa*). Many households supplement their diet with wild foods and foods purchased at local markets (Cox et al., 2018). Most households also keep some livestock, including chicken, guinea fowl, donkeys, goats, pigs and cattle. Few people own vehicles and bicycles are the most common mode of transport. Cotton (*Gossypium arboretum*) is also grown as a cash crop by some farmers. Nomadic herders also range through the landscape and keep cattle and goats.

5.2.2. Sampling

We chose cultivated sites using stratified sampling of households in Sitiena (N=21), Soumosso (N=13) and Koba (N=18) that had at least 1ha of land that was intended to be used for maize in 2016. Our sample was stratified by household size as described in detail in Payne et al., (in press). Cultivated sites (fields designated for maize) ranged from 0.16ha to 2.14ha with a mean area of 0.88ha and a mean perimeter of 427m.

We selected uncultivated sites for comparison; these are 1ha areas of land that are not currently used for crops, were considered to be forested (as opposed to temporary fallows) by key informants and are located within the same region as all field sites. To select uncultivated sites, we first identified forest patches via information from key informants. We then selected 20 1ha sites within these to match cultivated sites by distance from nearest road, because roads are known to have a major influence on bird abundance (Benitez-Lopez et al., 2010). The patches were highly fragmented (mean area 14.7ha, range 3.2ha-26.6ha, mean perimeter 2800m), and may have been used as agricultural land in the past; none were primary forest. All cultivated survey sites, forest patches and uncultivated survey sites are shown in **Error! Reference source not found.**.

We used the Global Land Analysis and Discovery (GLAD) database to estimate forest canopy cover for all sites (Hansen et al., 2010) in QGIS (QGIS 2015). Mean canopy cover in 2010 ranged from 0.4% to 12.5% within uncultivated sites (median 8.68%), and 0% to 12% within cultivated sites (median 2.5%). Overall, uncultivated sites had significantly higher mean canopy cover than cultivated sites (Wilcoxon rank sum test, $W_{51,20}=109.5$, $p<0.001$). To compare the canopy cover of uncultivated sites with protected forests within our study region, we used the Protected Planet database (protectedplanet.net) to identify protected areas within a 40km radius of the survey sites. Eleven classified forests fell within or overlapped with this area: Dinderesso, Koulima, Dan, Kua, Nabere, Niangoloko, Boulon, Bounou, Toumousseni, Beregadougou and Sources de la Volta Noire. The mean canopy cover in these protected areas ranged from 0% to 41% (median=8.4%), and was not significantly different from canopy cover in our uncultivated sites (Wilcoxon rank sum test, $W_{11,20}=106$, $p=0.887$). However, the reported areas of these sites (median=5000ha) were significantly greater than the areas of the forest patches (median=14.7ha) recorded in this study (Wilcoxon rank sum test, $W_{7,9}=54$, $p<0.05$).

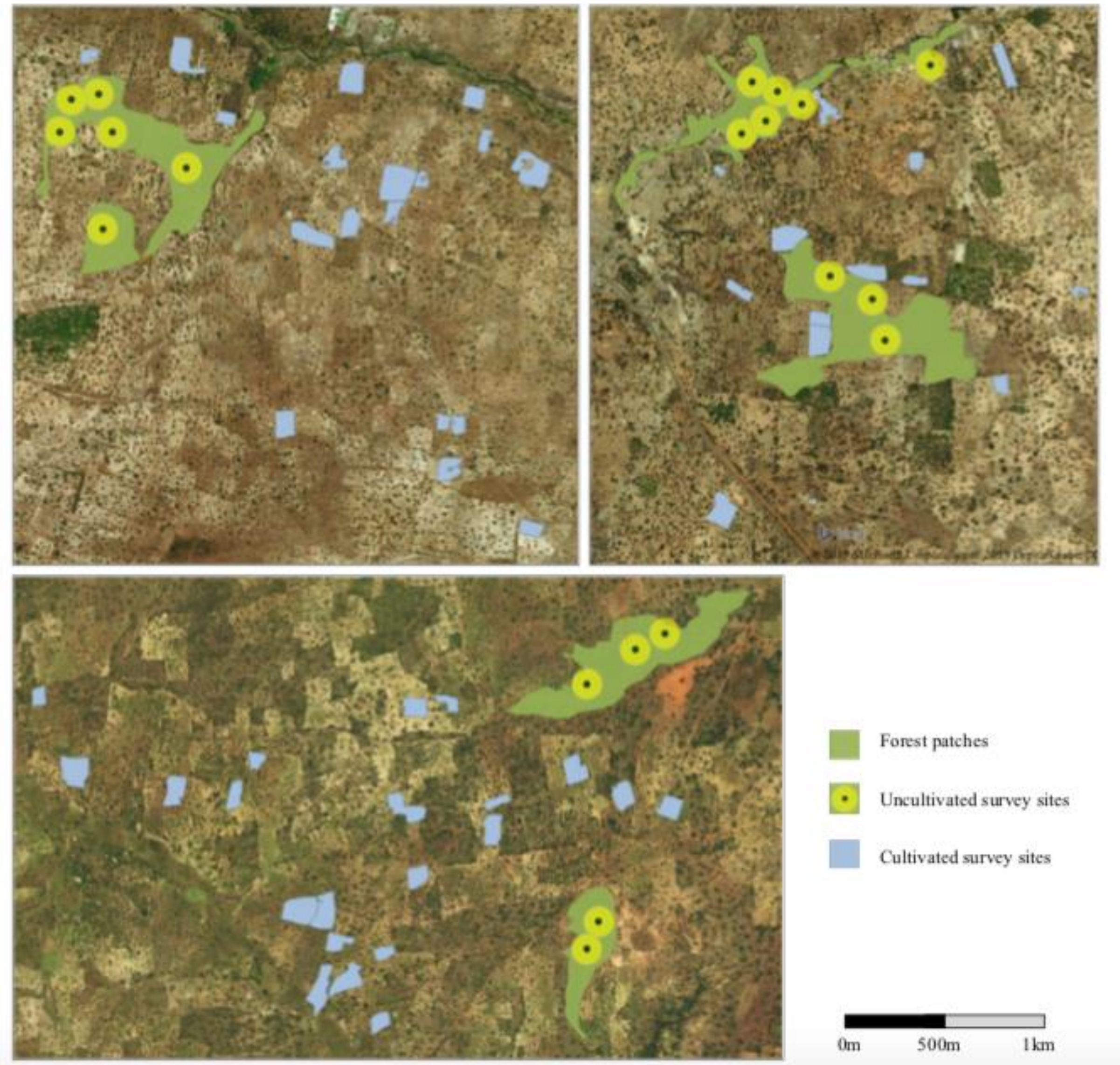


Figure 13. Maps showing the distribution and size of forest patches, uncultivated survey sites (dark points show where each forest survey was made; yellow circles represent an 85m radius, the maximum range of each survey) and cultivated survey sites (point counts took place in the centre of each cultivated site) in Soumosso (A), Koba (B) and Sitiena (C)

5.2.3. Bird counts

We (MM, CP, BS) carried out point count surveys at all cultivated (N=62) and uncultivated (N=20) sites during 2016 and 2017. We surveyed each site in each year, once in the morning (from 30min before sunrise to 3h after sunrise, following Phalan 2010) and once in the evening (from 3h before sunset to 30min after sunset), in July-August 2016 and repeated these surveys in June-August 2017. This was during the rainy season, and therefore also the caterpillar season. This is also when palearctic migrants begin to arrive.

After a 5 minute settling-in period, we conducted 10 minute surveys of all birds within a 100m radius of our point. We detected birds and estimated their group size using both auditory and visual cues. MM was present for all surveys and verified all recorded birds; all surveys were conducted with three observers with the exception of <10 surveys conducted with three individuals. We estimated the distance from our point to a given recorded species using a laser rangefinder and/or handheld GPS. We did not count flyovers. When analysing the data we discarded all observations >85m, so the final counts represent all recorded species within an 85m radius, following Williams (2016).

5.2.3. Bird density estimates

Following Phalan (2010) and Williams (2016), we used the R package *Distance* (Buckland et al., 2012) to calculate species-specific detection functions for all species with >30 observations. We fitted six models for each species, using or omitting habitat type (cultivated or uncultivated) as a discrete covariate or tree density (trees per ha) as a continuous covariate, and using hazard-rate or half-normal key functions. We discarded models that failed to converge. We examined fitted models visually for feasibility using the R package *mrds* (Laake et al. 2018) to check goodness of fit quantile-quantile plots and by checking the shape of the detection function. For each species we selected the model with the lowest Akaike Information Criterion (AIC) value. Using this process, we did not select any models that used tree density as a covariate; the majority of selected models used habitat as a covariate or did not use a covariate. We did not calculate individual detection functions for species with <30 observations. Instead we grouped these species by diet and body size and calculated detection functions for each group of species.

We generated estimates for the abundance of each species at each site using the selected detection functions. We used estimates based on this process to compare abundance in cultivated vs uncultivated sites, but used raw count data to model effects of our predictor variables on species-specific and overall bird abundance within cultivated sites, as described below.

5.2.4. Independent variables

In cultivated sites, we measured tree density and shea tree density; we counted all trees over 5m tall and divided this by the total field area in ha to give us a count of trees and shea trees per ha. Tree density ranged from 4.2 – 69 trees per ha with a median of 18. Shea tree density ranged from 1.6 – 36 trees per ha with a median of 13.

We interviewed farmers on three occasions: one preliminary interview in 2016, one follow-up interview in February 2017 after the 2016 harvest, and one follow-up interview in January 2018 after the 2017 harvest. We asked about prospective and retrospective agrochemical use on all three occasions. Farmers gave us an estimate of the times they had sprayed and/or intended to spray their field with herbicide or insecticide that year. We used retrospective estimates from 2016 and 2017, grouped herbicide and pesticide together because not all farmers clearly differentiated between them, and calculated the mean times sprayed per growing season for each field. We chose to use times sprayed rather than the number of bottles used because farmers stated that they used standard recommended quantities of spray per ha. We did not ask for timings of pesticide application; many farmers reported that they delayed spraying until after caterpillar season in order to avoid contaminating the caterpillar harvest.

During interviews in February 2017 and January 2018 we asked farmers to estimate the yield of maize harvested from their field. Several local measures were used to estimate yields; we consulted with at least two local informants per measure to convert these into kg of maize cobs. Our estimates for yield are means taken from interview responses in both years.
We estimated defoliation by caterpillars for three selected trees per cultivated site. We measured the height of all trees at each cultivated site, and stratified each site by height into ‘low’, ‘medium’ and ‘high’ trees. We selected one tree at random from each stratum. We surveyed the defoliation caused by caterpillars immediately following caterpillar season using methods described in Payne et al. (in press), giving an overall estimate of the percentage of defoliation for each tree. For current analyses we grouped defoliation estimates from 2016 and 2017 and used the mean of both.

Due to constraints on our time and resources we did not obtain measures of defoliation for every cultivated site, as leaves regrow rapidly. Due to difficulties in reliably reaching all farmers we were not able to obtain estimates of yield and agrochemical use for some cultivated sites. These limitations reduced the number of bird survey sites for which the full suite of independent variables was available.

5.2.5. Species-specific abundance in cultivated and uncultivated sites

We compared detection-corrected density estimates (hereafter abundance) of birds in cultivated and uncultivated sites for each species in turn. Data were right-skewed, that is, for each bird, there were many sites with zero observations. We ran Kruskal-Wallis tests for each species to compare abundance in these two different habitats. We calculated epsilon-squared as a measure of effect size, following Mangiafico (2016).

5.2.6. Variables associated with species-specific abundance across field sites

We then tested for associations between our potential predictor variables and species-specific bird abundance across cultivated sites. Following Harrison et al., (2018), we first tested for collinearity (high correlation coefficients) and multicollinearity (measured by Variance Inflation Factors, or VIFs) between our independent variables. Using the recommended Pearson correlation coefficient cut-off value of $r \geq 0.7$ for collinearity between variables (Dormann et al., 2013), we found collinearity between density of trees, density of shea trees, yield and agrochemical use (**Error! Reference source not found.**).

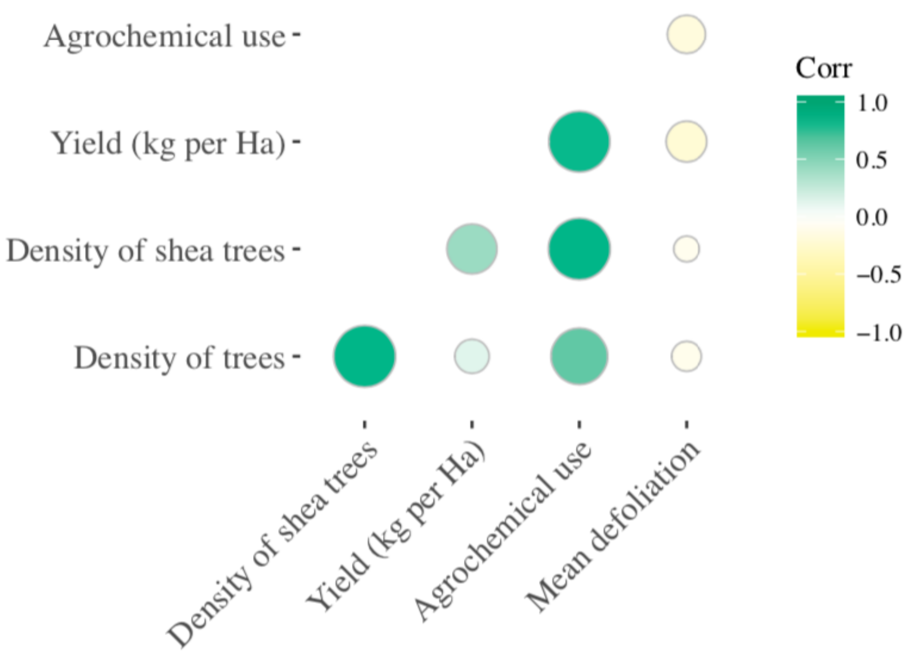


Figure 14 Correlation plot showing collinearity between variables originally proposed for our model.

Density of trees	Density of shea trees	Yield (kg per ha)	Agrochemical use	Mean defoliation
5	7.5	8.3	18	1.1

Table 5.i. Table showing VIFs (Variance Inflation Factors) for each variable.

We found some multicollinearity between these variables, since VIFs equal or exceed a value of 5 (**Table 5.i**; interpretation following James et al., 2013). Agrochemical use exhibited the highest multicollinearity with a VIF of 18. Following Quinn and Keough (2002)'s recommendation of a cut-off of 10, we excluded this variable from future analyses. When determining which of the remaining variables to keep, we followed Harrison et al.,' (2018) in excluding less biologically relevant variables in the case of collinearity. We therefore excluded density of shea trees, reasoning that overall tree density is likely to have a more generalised association with bird abundance.

Our choice of fixed effects was driven by the directional hypotheses that (1) tree density will show a positive association with bird abundance and (2) maize yield will show a negative association with bird abundance, and the non-directional hypothesis that (3) defoliation by caterpillars will show an association with bird abundance.

Following this process, we were left with three fixed effects for our models: density of trees, maize yield and defoliation of trees by caterpillars.

Our species-specific model was:

Count ~ Tree density + Maize yield + Defoliation + offset(log(Max count))

We fitted a generalised linear models with Poisson error distribution and the log link function using the *lme4* package in R (Douglas Bates et al. 2015). We scaled all independent variables. The output predicts counts of each bird species per effective area surveyed, that is, within an 85m radius of each survey point. To back-transform scaled variables we used the *DMwR* package (Torgo 2010), for visualisation of the results we used the *effects, ggcorrplot, ggplot2* and *ggthemes* packages (Fox and Hong 2009, Kassambara 2018, Wickham 2016, Arnold 2018).

We considered that the following species traits could shape the responses of birds to our fixed variables:

Interactions with tree density: we predicted that abundance of birds with higher dependence on forest will be more strongly positively correlated with tree density (Harvey and Villalobos 2007), and that abundance of migrant birds will be more abundant in fields with fewer trees (Usieta 2014).

Interactions with maize yield: we predict that abundance of birds with decreasing populations will show a stronger negative association with maize yield, since increasing agricultural intensification threatens abundance of some bird species (Phalan 2014).

Interactions with defoliation: we are interested in the possible relationship between defoliation by caterpillars and the population trends of bird species, since caterpillars have been harvested as food in this area for at least 30 years and during a time of increasing environmental degradation (DeFoliart 2002). We do not propose a directional hypothesis relating to this potential interaction.

We therefore used Birdlife's online database (Birdlife 2017) to identify the level of forest dependency, migratory status and current population trend for each species in our dataset. All observed species fell into one of three categories for forest dependency: non-forest, low forest dependency, and medium forest dependency; one of three categories for migratory status: full migrant, nomadic, and not a migrant; and one of four categories for current population trend: increasing, decreasing, stable and unknown. We used these categories to visualise the results of the species-specific models.

5.2.7. Variables associated with overall bird abundance across field sites

Finally, we modelled the relationship between the same fixed effect variables with data from all species, using a generalised linear mixed model with Poisson error distribution and log link . We fitted a baseline model and three additional hypothesis-driven models, as a stepwise exploratory exercise (following Harrison et al., 2018). For all models we specified an offset of specie-specific maximum count value, to avoid the artificial inflation of effect sizes by more abundant bird species.

Our baseline model used only tree density and maize yield as fixed effects. Given the lack of prior research on the association between caterpillars and bird abundance, we had no directional hypothesis concerning the fixed effect of defoliation, so we did not include this in our baseline model.

To account for the non-independence of data relating to the same site or species, we included random intercepts of site and species.

Our baseline model was:

$$\text{Count} \sim \text{Tree density} + \text{Maize yield} + \text{offset}(\log(\text{Max count})) + (1|\text{Site}) + (1|\text{Species})$$

This model has 5 parameters; 647 observations are included; the ratio of data points to parameters exceeds the recommended minimum (n/k=10) (Harrison et al., 2018). We scaled the variables. The output predicts counts of birds per effective area surveyed.
We ran two additional models that build on our baseline model:

Model 1 Count ~ Tree density + Maize yield + Defoliation + offset(log(Max count)) + (1|Site) + (1|Species)

Model 2 Count ~ Tree density * Forest dependency * Migratory status + Maize yield + Defoliation + offset(log(Max count)) + (1|Site) + (1|Species)

For Model 1 we incorporated defoliation as an additional parameter. Adding defoliation reduces the number of observations that inform the model (N=216), but only increases the parameters to 6, meeting the criteria for the recommended minimum. For Model 2 we incorporated interaction factors of forest dependency and migratory status, interacting with tree density. This model had 16 parameters for 216 observations and thus met the criteria for the recommended minimum. We did not run a third model incorporating current population trend as a further interaction factor because to do so would have increased model parameters beyond the recommended minimum; more data would be required to test such a model. For model comparison we employed all-subsets selection using the *MuMIn* package (Barton 2018).

5.2.8. Summary of statistical analyses

Our results describing bird abundance in cultivated and uncultivated sites represent the output of the species-specific models (described in detail in 5.2.3.), which were fitted using the R package *Distance.* Our results describing the effects of our predictor variables (tree density, maize yield and defoliation, described in 5.2.4.) on species-specific and overall bird abundance represent the output of generalized linear models using raw count data. The species-specific models (described in detail in 5.2.5.) use the log of the maximum count (e.g. highest count for that species at any site) as an offset. The model of overall bird abundance (described in detail in 5.2.6.) also used the log of the maximum count as an offset, and used the random effect of site and species.

5.3. Results

5.3.1. Species-specific abundance in cultivated and uncultivated sites

The majority of bird species (N=21 of a total of N=31 species with >30 observations) were more abundant in uncultivated sites than cultivated ones; this effect was statistically significant ($p < 0.05$) for 21 species. Whilst 11 species were more abundant in cultivated patches, this association was significant ($p < 0.05$) for only one species. Most species classed as forest dependent (low or medium) were more abundant in uncultivated sites (**Error! Reference source not found.**). Considering only species for which the effect size was moderate to strong (i.e. epsilon-squared > 0.08), 21 were more abundant in uncultivated sites and only one in cultivated sites.

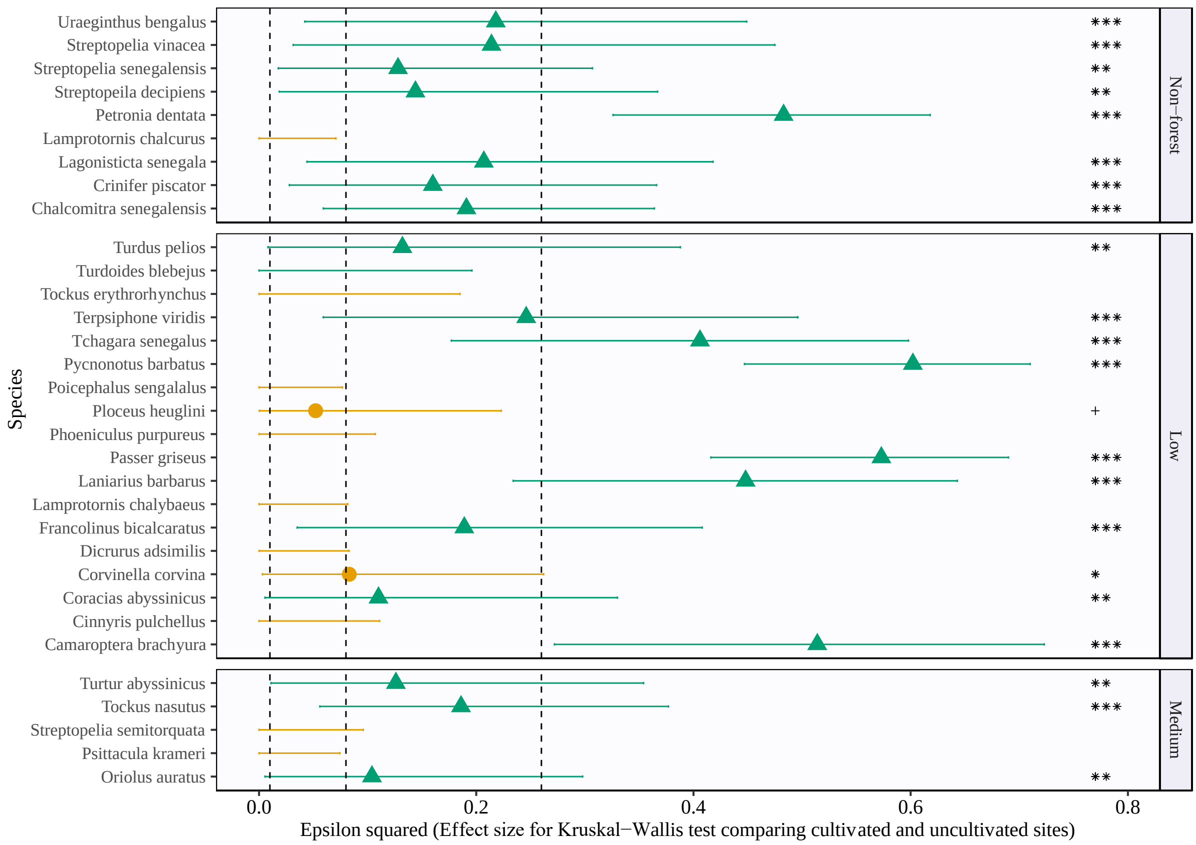


Figure 15 Forest plot showing epsilon-squared values for Kruskal-Wallis test comparing median abundance in cultivated and uncultivated sites. Error bars show bootstrapped 95% confidence intervals. Orange circles indicate a higher abundance in cultivated sites; green triangles indicate a higher abundance in uncultivated sites. Transparency of each point corresponds to p-value (higher p-values are more transparent), which is also indicated as

follows: + p<0.1, * p<0.05, ** p<0.01, *** p<0.001. Dashed lines indicate cut-offs for effect size: >0.01 is considered a small effect size, >0.08 is considered a medium effect size, >0.26 is considered a large effect size (Mangiafico 2016).

5.3.2. Variables associated with species-specific abundance across cultivated sites

Comparing across cultivated sites, the effect of tree density on bird abundance was weak. Only four species showed a significant association with tree density, none of which were migrant species (**Error! Reference source not found.**); of these, two species had a negative a ssociation (beta values = -1.1 and -0.63 respectively) while two had a positive association (beta values = 1.18 and 0.51 respectively)). All other associations were not statistically significant (p>0.05). Similarly, only two species showed a significant association with reported maize yield, one of which was positive and the other negative (**Error! Reference s ource not found.**). Finally, seven species show a significant association with defoliation, and of these six are positively correlated (**Error! Reference source not found.**).

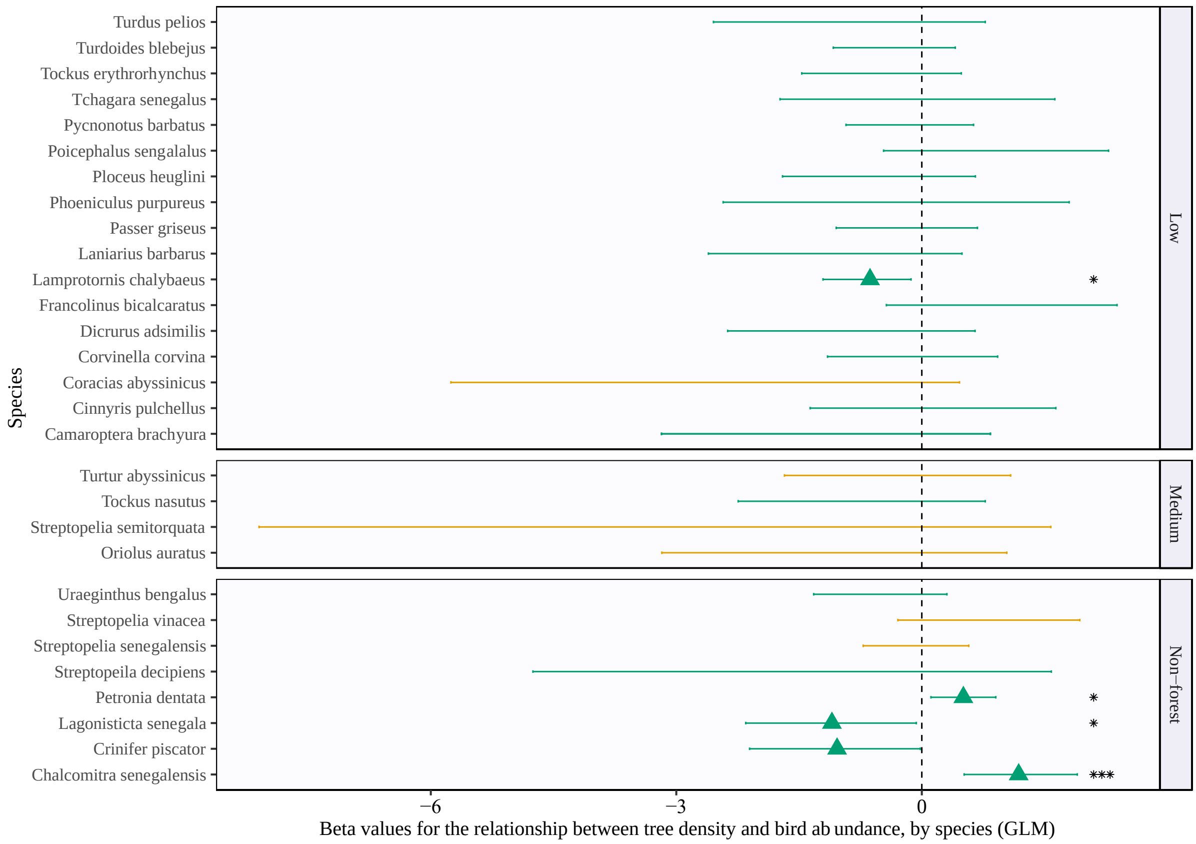


Figure 16 Forest plot showing beta values for the relationship between bird abundance and tree density, by species. Orange circles indicate non-migrant species; green triangles indicate migrant species. Species are grouped by forest dependency (Low, Medium or Non-forest, shown on right-hand axis). Transparency of each point corresponds to p-value (higher p-values are more transparent), which is also indicated as follows: + p<0.1, * p<0.05, ** p<0.01, *** p<0.001. Error bars represent 95% confidence intervals.

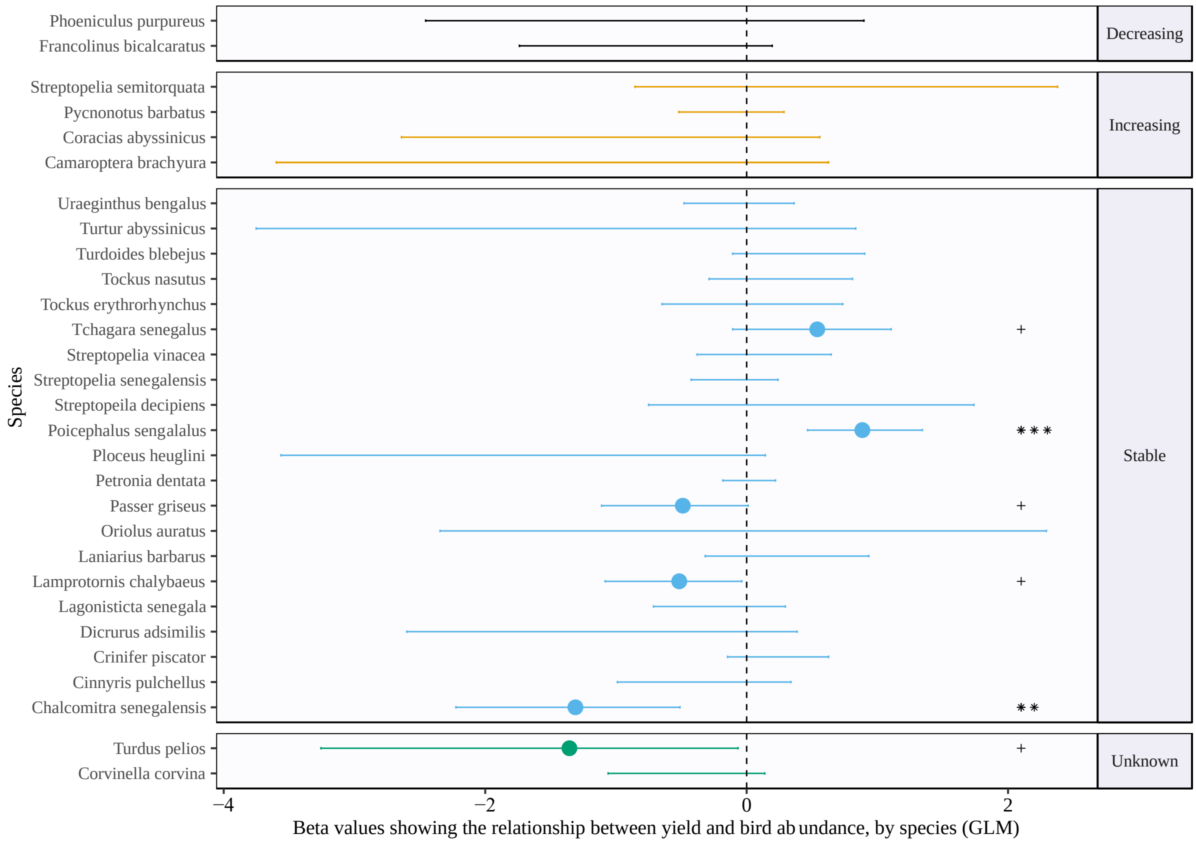


Figure 17 Forest plot showing beta values for the relationship between yield and bird abundance, by species. Species are grouped by population trend (Decreasing, Increasing, Stable or Unknown, shown on right-hand axis). Transparency of each point corresponds to p-value (higher p-values are more transparent), which is also indicated as follows: + p<0.1, * p<0.05, ** p<0.01, *** p<0.001. Error bars represent 95% confidence intervals.

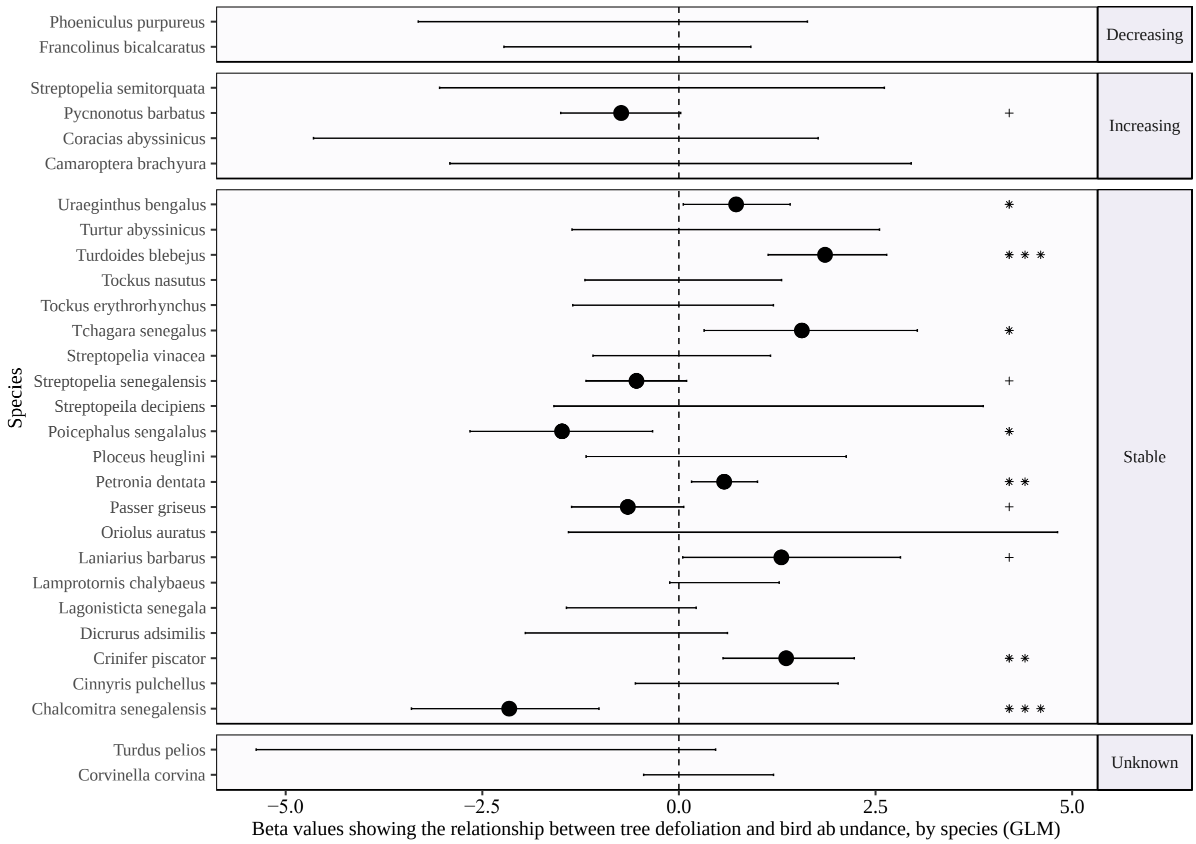


Figure 18 Forest plot showing beta values for the relationship between defoliation and bird abundance, by species. Species are grouped by population trend (Decreasing, Increasing, Stable or Unknown, shown on right-hand axis). Transparency of each point corresponds to p-value (higher p-values are more transparent), which is also indicated as follows: + p<0.1, * p<0.05, ** p<0.01, *** p<0.001.

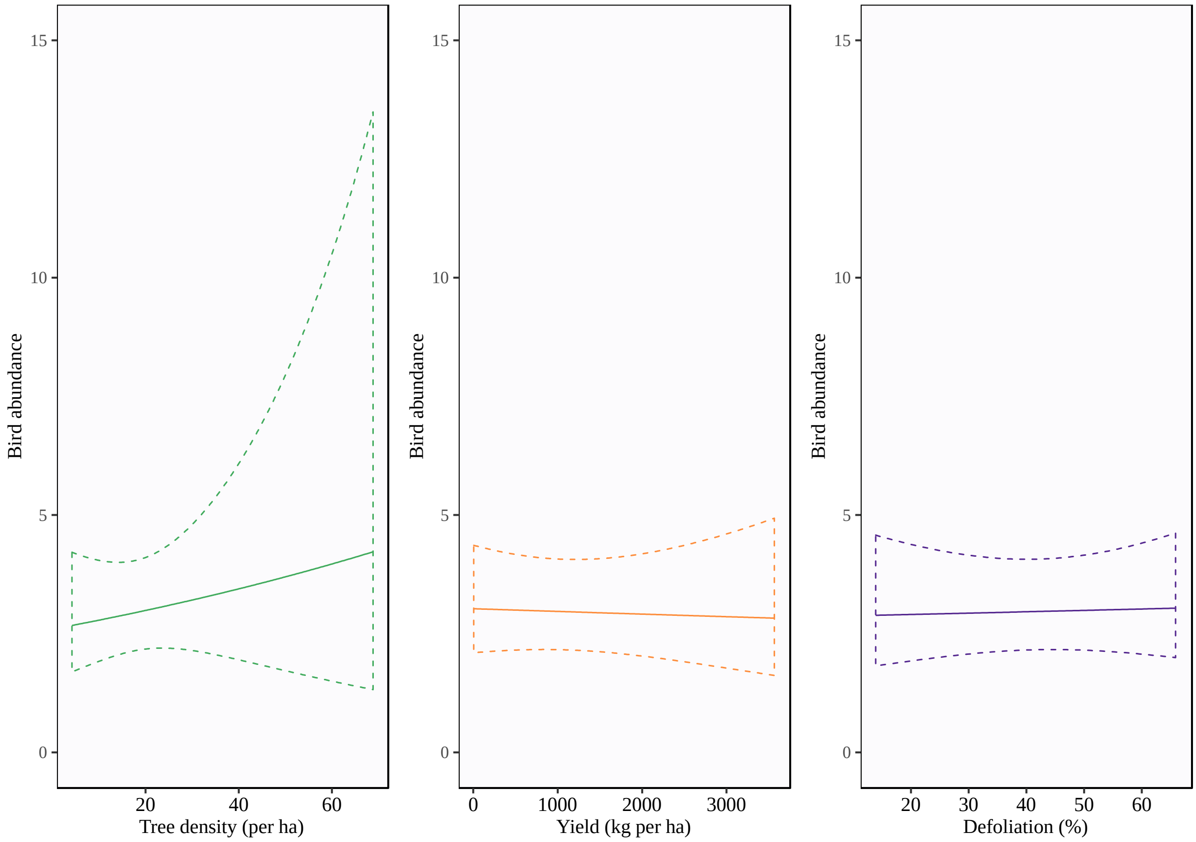
5.3.3. Variables associated with overall bird abundance across cultivated sites

The model that best fit with the data was Model (1), which is our baseline model with defoliation as an additional predictor variable. This model had the lowest AICc (corrected Akaike Information Criterion), representing a substantial improvement on both the baseline model and the null (intercept-only) model (**Table 5.ii**).

Model	Parameters	AICc
(1) Baseline model + defoliation	6	1223
(2) Baseline model + defoliation + migratory status and forest dependency (interacting with tree density)	16	1227
Baseline model	5	3970
Null model (no fixed effects)	3	9353

Table 5.ii. Table showing candidate models with No of parameters and AICc, ordered by AICc.

The effects of tree density, defoliation and maize yield on bird were weak (beta=0.16, 0.04 and -0.026; p = 0.54, 0.87 and 0.84 respectively) (**Error! Reference source not found.**). T he strongest predictor was tree density, which had a positive effect on bird abundance, though the confidence intervals of this parameter overlapped 0, suggesting that a negative effect is also compatible with our data.



	Tree density (per ha)	Yield (kg per ha)	Defoliation (%)
Beta value	0.16	-0.026	0.041
Standard error	0.23	0.13	0.25

Figure 19 Summary of the fit of each fixed effect according to the selected model; table showing beta values and standard error for each variable. We scaled all fixed effects prior to running the models; figures shown in the graphs are back-transformed; shaded areas show confidence intervals.

5.4. Discussion

Despite cultivated sites representing low-intensity systems which retain some features of the native vegetation, the majority of bird species in this landscape prefer uncultivated habitat, and only one prefers cultivated habitat, though several show no statistically clear preference.

This replicates previous studies that have found higher bird abundance in uncultivated land across a wide variety of agricultural systems (e.g. Phalan 2010, Williams 2016). Our species-level data did not include any birds with high forest dependency (according to Birdlife 2017), suggesting that forest species are not present in this landscape. This is likely to be due to the highly fragmented nature of the remaining forest patches. Among the species that we did observe, level of forest dependency was not associated with preference for uncultivated over cultivated habitat. This may be in part due to factors other than canopy cover that drive preferences for uncultivated land, such as a relative lack of human disturbance and higher diversity of food sources. Among cultivated areas, the lack of significant association between tree density and bird abundance is contrary to our expectations, as is the lack of interaction with migrant status or forest dependency. This may reflect the fact that all sites in this system have relatively low (<12%) canopy cover, but none are completely deforested and there is a relatively high median number of trees per ha (18). It may also reflect the limited statistical power of our data due to the low number of observations that we were able to use to inform the model.

There was no clear association between bird abundance and maize yield in this system. This may be due in part to inaccurate reporting of yields, as data were collected via interviews rather than direct measurement. It may also reflect scale: the fields in this study cover small areas and may be adjacent to fields where more wildlife-friendly farming practices are used, and this may cause a spill-over effect. It may also be related to the delay in the timing of agrochemical application until after caterpillar season in order to avoid chemical contamination of the caterpillars; bird counts were done prior to most agrochemical application.

In contrast to our other predictor variables, defoliation by caterpillars did appear to have a significant association with the abundance of some bird species, though the direction of this effect varied between species. This is a novel and unexpected result that warrants further investigation. There may be an additional variable that influences both the presence of caterpillars and the presence of birds in this system. For example, both birds and caterpillars may prefer fields managed by farmers who till their soil less intensively, who enter their fields less frequently, and/or who allow more weeds to grow amongst their crops.

Our overall model that considers the abundance of all species present suggests that, in a mixed low intensity agroforestry system with patches of uncultivated land, tree density, yield and defoliation by caterpillars do not drive overall bird abundance. Weak associations with these variables may exist, but these are not picked up by the current study.

The current study has significant limitations. Firstly, the sample size is limited. We do not have adequate data to test all of our variables across all field sites, therefore we have relied on a very small number of counts for our analyses, and this may have obscured some relationships between these variables and bird abundance. Secondly, we rely heavily on reported and retrospective estimates of yield and agrochemical use, rather than direct measurements. This introduces a wide margin of error, as farmers may over- and underestimate both metrics.

This is the first study to look at the relationship between the presence of edible insects and biodiversity in an agricultural system. Using defoliation by caterpillars as a proxy for the presence of caterpillars, and using bird abundance as a proxy for biodiversity, we do not find any significant associations between these two variables in a low intensity agroforestry system. Many bird species are less abundant in cultivated areas compared to uncultivated areas, suggesting that maintaining patches of uncultivated land will be important for biodiversity conservation in this landscape. Overall this study shows that within a range of relatively low-intensity farming practices, differences in farming practices and caterpillar abundance do not appear to influence biodiversity. This may be due to the high retention of trees in fields and the delayed use of agrochemicals. The stability of this system of low-intensity smallholder agroforestry cultivation with edible caterpillars would almost certainly change with scaling-up of agricultural land clearance, as biodiversity is significantly higher in uncultivated sites. This stability may also change with if more intensive farming or caterpillar-harvesting practices are adopted, as these may threaten biodiversity in ways that are not apparent at the current scale.

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Chapter 6. Discussion

In this thesis I have presented and analysed data that describes the contributions of chitoumou, the shea caterpillar, to food security, agriculture and biodiversity in West Africa. My findings add to a growing scientific literature on edible insects and have significant implications for policy-makers and farmers in this part of the world. This study also highlights the wider importance of understanding the role of edible insects in agricultural systems, and attests to the value of using a participatory approach throughout the research process.

6.2 Policy-makers: Caterpillars are important for seasonal food security

For policy-makers, the most important finding in this thesis is the contribution that caterpillars make to seasonal food security. Food security is higher during caterpillar season (**Figure 6**), and is predicted by the quantity of caterpillars collected, eaten and sold (**Figure 7**). This association therefore holds even for households that collect and sell, but do not eat, caterpillars; the overwhelming majority of households in this region engage with the caterpillar market regardless of cultural food preferences. I also found that income from caterpillars is comparable to income from shea (**Figure 5**). Shea has been hailed as "women's gold" in this region, that is, as a wild-collected food resource that can provide economic empowerment and independence to rural women and marginalized groups (Pouliot 2012). In this region, caterpillars too play this role.

The implications of these findings for policymakers are threefold. Firstly, the caterpillar market is pivotal in ensuring food security for many people living in rural areas. Any fluctuations in the price of caterpillars and in the viability of the caterpillar trade, particularly during caterpillar season, could exacerbate food insecurity in this region. Conversely, regulations that stabilize this trade and incentives that promote it, could increase food security. Secondly, the security that the caterpillars confer is seasonal (**Figure 6**). Initiatives that target food insecurity should recognize the seasonal nature of the contribution of caterpillars. In regions where caterpillars are harvested, such initiatives should ensure that baseline measures of food security are taken outside of caterpillar season, and any seasonally limited interventions should target times of year that fall outside caterpillar season. Thirdly, the importance of shea trees lies not only in the economic and nutritional value of shea nuts, but equally that of the shea caterpillars they harbour. Combined, these represent the greatest income source for female heads of household (**Figure 23**). Changes in farming practices that may incentivize the destruction of shea trees will cause a substantial economic loss for households in this region and could consequently exacerbate food insecurity.

6.3 FARMERS: TREES ARE OF HIGH ECONOMIC AND NUTRITIONAL IMPORTANCE

For farmers, the relationship between caterpillars and crop growth is the most immediately relevant finding of this thesis. Firstly, I found no evidence that defoliation by caterpillars has a negative impact on yields of either shea (**Figure 10**) or maize (**Figure 11**; **Figure 12**). This confirms the prevalent belief in the villages where I collected my data and challenges the term 'pest' used by previous researchers – and farmers in other regions – to describe the caterpillars. It is crucial that farmers across the shea belt understand that despite extensive defoliation the caterpillars are by no means a pest in the traditional sense. Indeed, they may mitigate the negative impact of shea trees on crop growth beneath the trees, though this relationship was only evident from data in one, not both, years of this study (**Figure 11**).

The second main finding relevant to farmers echoes one of the key messages for policy-makers: shea trees are pivotal to food security (Chapter 3). This is crucial knowledge for smallholder households in the shea belt where men are traditionally responsible for managing the privately-owned crops, and women are responsible for managing the communally-owned trees (Gausset et al. 2005). Where shea trees appear to inhibit crop growth, the priorities of men and women may therefore come into conflict. In particular, commodity crops such as cotton are almost exclusively grown by men. Commodity crop yields promise short term economic benefits to farming households, and the shade conferred by shea trees may seem undesirable in this context, leading to the felling of shea trees in agricultural fields. Yet the annual economic and nutritional significance of these trees due to both shea nuts and caterpillars (**Figure 5**; **Figure 6**; **Figure 23**) suggests that such strategies, when used by farmers, are likely to sacrifice longer term financial and nutritional benefits for short term gains. Unfortunately, severe food insecurity may encourage shot-term decision-making (Ericksen 2008).

Thirdly, my lack of success in systematically rearing caterpillars on alternative substrates (Appendix C) reinforces the importance of the sustainable management of shea trees in this system. Caterpillars grown on artificial feeds did not survive in either a university lab (**Figure 33**) or field lab (**Figure 32**) setting. This suggests that it will be challenging to find an alternative feed for shea caterpillars, let alone one that is economically viable and readily accessible to smallholder farmers. At present, living shea trees remain essential for the successful exploitation of shea caterpillars. Farmers wishing to reap the benefits of the shea caterpillar harvest must ensure that their shea trees are not felled for short-term gain.

6.4 SUSTAINABILITY: CULTURAL RULES MAY BE CRUCIAL

The results presented in this thesis also have implications for understanding and supporting the sustainability of shea caterpillars in low-intensity agricultural systems. The presence of shea caterpillars in my study system currently increases food security on a seasonal basis (**Figure 6**), has no negative impact on yields of maize (**Figure 11**) or shea (**Figure 10**), and no discernible association with biodiversity (**Error! Reference source not found.**). This s uggests that caterpillars do not threaten the current status of these important aspects of the system. However, the system is by no means perfect: there is a clear need for higher yields (Diarisso et al. 2016), higher year-round food security (Frongilo and Nanama 2006; also **Figure 6**);); restoring lost biodiversity would also be desirable (Dayamba et al. 2016; Sachs et al. 2009). Efforts to facilitate such changes may alter the place of caterpillars in the system.

Furthermore, market demand for caterpillars is likely to change in coming years. There is an increasing consumer interest in edible insects (Ahuja and Deb 2018), and an increasing emphasis on ethically sourced insects (Müller et al. 2016). One of the global companies catering to this demand at present uses shea caterpillars for its main products – FasoPro. If competitors emerge and consumer demand continues to increase, the price of caterpillars could become unstable. An increase in price would have an initially positive impact on rural livelihoods but could incentivize unsustainable behaviour such as the breaking of cultural taboos regarding harvesting practices. Harvesting is currently only permitted in the early hours of the morning, and buyers refuse to purchase caterpillars that are not in their final instar. In southern Africa, mopane worms (*Gonimbrasia belina*) were once subject to similar taboos but increasing demand has precipitated a rise in destructive harvesting methods that contradict such taboos. Mopane worms are currently subject to unpredictable fluctuations in population, and this is considered to be a direct result of such practices (Makhado et al. 2012). In the event of increased market demand for shea caterpillars, farmers, buyers and policymakers alike must act to mitigate this risk, particularly via measures that prevent overharvesting.

6.5 Future research priorities: Extend the seasonal importance of caterpillars

The findings presented here also have important ramifications for future research to improve regional food security, agricultural yields and biodiversity. Firstly, it is clear from Chapter 3 that although caterpillar collection confers seasonally-limited food security, there is no year-round benefit for collectors. The same may or may not be true for the impacts of caterpillar consumption on physical health; further research could test this using anthropometric measurements and blood tests in both seasons to measure prevalence of markers of malnutrition, such as stunting, wasting and blood hemoglobin levels. It may also be appropriate to run randomized controlled trials looking at the longitudinal effects of caterpillar consumption on these parameters. Seeking to rear caterpillars in enclosed systems, as discussed in Appendix C, is a complex and highly resource intensive processs that has not yet been optimized under laboratory conditions, let alone in a commercial and/or smallholder context. Therefore, it may be more pertinent for future researchers who aim to reduce food insecurity to investigate ways of safely extending the shelf life of caterpillars in a humid climate without refrigeration. Currently, households do not dry and store large quantities of caterpillars, choosing instead to eat fresh caterpillars and sell most of their surplus (**Figure 22**). Safe preservation and storage techniques, combined with palatable and nutritious methods for preparing preserved caterpillars, could incentivize households to save more of their surplus, either for sale or consumption at a later date. This is particularly important given that during caterpillar season the shea caterpillars are eaten in quantities that exceed daily protein requirements (**Figure 25**), yet out of caterpillar season household diets have comparably little animal protein (**Figure 4**). Safe preservation and storage techniques, such as sun drying in solar dryers and the use of natural desiccants to absorb moisture during storage, may facilitate a longer period of adequate protein provision. Such studies are rare in edible insect research (but see Klunder et al. 2012), yet may be widely applicable due to the inherent seasonality of many wild and semi-cultivated edible insects. The price of caterpillars is lowest during caterpillar season; for households who benefit from the income gained form selling caterpillars, safe preservation and storage would facilitate sale at other times of year when prices are higher, potentially increasing the financial benefits of the caterpillar harvest.

Thirdly, while I have in this thesis addressed key questions relating to the interaction of caterpillars with agricultural yields and found that no negative relationship exists (Chapter 4), the exact mechanisms are unclear and warrant experimental study. The significant association between defoliation by caterpillars and maize growth under trees recorded in 2016 (**Figure 11**) does suggest the possibility of a mechanism that links these phenomena. Obvious candidates are the addition of caterpillar feces to the soil, which may act as a fertilizer, and increased photosynthesis facilitated by tree defoliation. Further research could usefully test these mechanisms independently through field experiments using caterpillar feces and fertilizer, and varying degrees of sun exposure.

Fourthly, I did not find any discernible relationship between agricultural yields, tree density, caterpillar defoliation and bird abundance (**Error! Reference source not found.**). This may b e due to insufficient sampling effort, since previous studies have found negative associations of bird abundance with yield (Phalan 2010, Williams 2016), and given the greater abundance of birds in uncultivated areas (**Error! Reference source not found.**) one would expect to see a positive association with tree density in cultivated areas. Therefore, further research could replicate these surveys using a larger sample size. A further study could also look at other indicators of biodiversity, such as plant or insect diversity, which may respond differently to caterpillar defoliation. It may also be feasible to conduct a longitudinal assessment of these measures and how they interact with yield, tree density and defoliation. Given that this system is already degraded and relies on low-intensity agriculture, changes are likely to be subtle, but identifying trends in such systems is crucial to monitoring biodiversity and identifying the factors that may precipitate declines. It would also be useful to collect data from higher-intensity systems in a comparable climatic zone, as this might shed light on potential future changes in farming linked to increased mechanization or other means of intensification.

Finally, this thesis shows the value of using a participatory approach to research from the development stages onwards. Though I began my pilot study with several questions that had been shaped by my own reading, discussions with stakeholders including smallholder farmers shaped the eventual focus of this study. I worked together with smallholder farmers throughout, and their insights and suggestions have proved invaluable. Their guidance helped me to select an appropriately representative sample, to test their own assumptions about caterpillars with quantitative systematic methods, and to ensure that my results will be useful and relevant to the people whose livelihoods depend on this system. Future researchers could expand upon this approach by using technology to enable farmers to collect data independently, and to have access to and control over this data following the study (e.g., van Etten 2011). Such methods will further expand the impact of scientific research to the livelihoods of smallholder farmers worldwide.

6.6 Shea caterpillars in comparative perspective

In conclusion, the results presented in this thesis have contributed to our knowledge of the costs and benefits of the shea-caterpillar cultivation system in Burkina Faso. The main findings are summarized in **Figure 20**, which depicts these relationships: farmers benefit from shea trees, crops and caterpillars due to their contribution to food security; crop growth is hindered by shea trees but this may be ameliorated by caterpillars; birds bear the costs of agriculture due to the clearance of forested land.

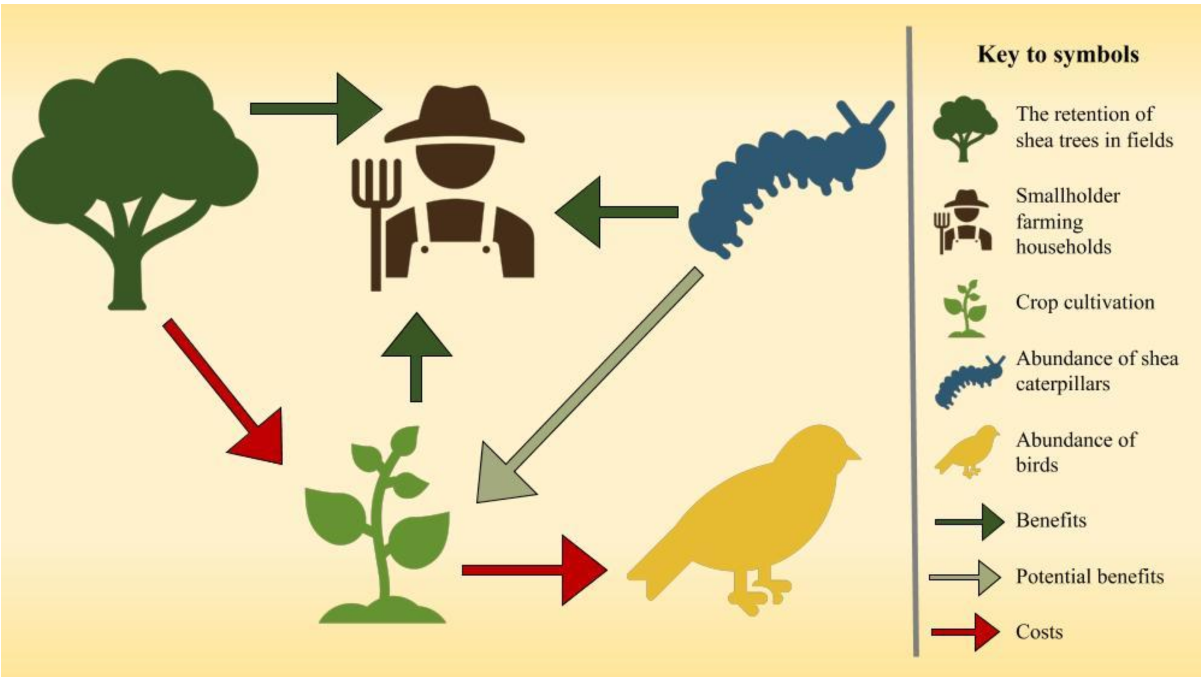

Figure 20 Diagram showing the relationships between key parts of the study system: shea trees confer benefits on farmers but hinder crop growth; crops are beneficial to farmers but

costly to birds, which are more abundant in forested areas; caterpillars are also beneficial to farmers and may be beneficial to crop growth.

Overall, although this study system is unique to a single region of the world, my thesis shows the importance of investigating and quantifying the importance of edible insects to food security, agriculture and biodiversity. A diverse range of insect species are harvested as food from traditional agricultural systems worldwide, and each species will have its own unique costs and benefits to its human harvesters. The caterpillars studied here are harvested in their final instar immediately prior to a long period of pupation: this is a life stage at which they are nutrient-dense and likely to experience a low survival rate. This is likely to increase their palatability and also pre-empts the dangers of over-harvesting, enabling humans to collect large quantities without harming the harvest in the following year. The target food species of this caterpillar is not an annual crop but a perennial tree, the shea tree. Given the lack of association between defoliation by caterpillars and tree productivity, it seems likely that the tree has co evolved strong defence mechanisms in response to defoliation by caterpillars. These factors combined are likely to be responsible for the main finding of this thesis: that shea caterpillars confer benefits to farmers in the form of economic and nutritional provisioning, and do not confer any discernible ecosystem disservices such as crop damage or detrimental effects on biodiversity.

6.7 CONCLUSIONS

This thesis highlights the importance of understanding the dynamics of edible insects in agricultural systems when considering the sustainability of the global food system. The problems of environmental degradation and food insecurity are deeply interlinked and both disproportionately affect smallholder farmers. Multiple stakeholders are working towards increasing demand for edible insects as a way of providing a sustainable alternative to conventional livestock, yet alongside this the livelihoods of millions of smallholder farmers already depend to some extent on edible insects harvested from existing agricultural land, among them the households whose data is represented in this thesis. The shea caterpillar is one example of an edible insect that contributes multiple services to human harvesters, without any discernible disservices. While these qualities cannot be generalized to all such insects, the shea caterpillar is unlikely to be unique in this respect. Therefore, researchers and policymakers concerned with mitigating food insecurity and environmental degradation via edible insects should consider too those insects that are harvested from existing cropland, and how they may play a role in the future of the global food system.

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Appendix A. Chapter 3, supplementary material

A1. Amount of caterpillars collected, consumed and sold

When asked about the total quantity of caterpillars collected during interviews >1 month after caterpillar season, women (N=45) reported collecting a median of 4.26kg (IQR=10) of caterpillars during the season, with values ranging from 0kg to 39kg per person. Respondents reported spending a median of 30 hours (IQR=35) per season collecting caterpillars, at a median rate of 0.0278kg per hour (IQR=0.0352). This is a significantly lower rate (Wilcoxon rank sum test, W=356, $p<0.001$, for both measures) than the kg per hour collection rate recorded via participant observation (median=0.044, IQR=0.021) and same-day opportunistic interviews (median=0.038, IQR=0.038).

Responses to structured interview questions about the consumption and sale of caterpillars showed that, on an annual basis, respondents consumed a median of 0.263kg (IQR=0.425kg) of fresh caterpillars and 0kg (IQR=2.1kg) of dried caterpillars and sold a median of 3.33kg (IQR=4.41kg) of caterpillars. Reasons for selling fresh caterpillars rather than drying them included the need for money in the short term, the risk of spoilage during long term storage, and the higher palatability of fresh caterpillars.

A2. NUTRIENT CONTENT AND CONTRIBUTION OF CATERPILLARS AND CATERPILLAR DISHES

Our nutritional analysis shows that 100g of fresh shea caterpillars exceeds half of the recommended daily intake of protein, iron and zinc (150%, 63.7% and 173% respectively) for a woman of reproductive age (**Table A.i**).

	Energy (Kcal)**	**Protein (g)****	**Fat (g)****	**Fibre (g)****	**Calcium (mg)*****	**Iron (mg)*****	**Zinc (mg)*****
Content per 100g fresh weight	413	60	13.9	4.8	67.5	15.6	8.5
GDA/RNI*	2000	40	70	20	1000	24.5	4.9

Table A.i. Energy (Kcal), macronutrient (protein, fat, fibre) and micronutrient (Ca, Fe, Zn) content of shea caterpillars per 100g fresh weight and dietary reference values.*GDA/RNI =Guideline Daily Amount / Recommended Nutrient Intake, for a woman of reproductive age, according to UK/WHO guidelines **From Anvo et al. (2016); ***From this study.

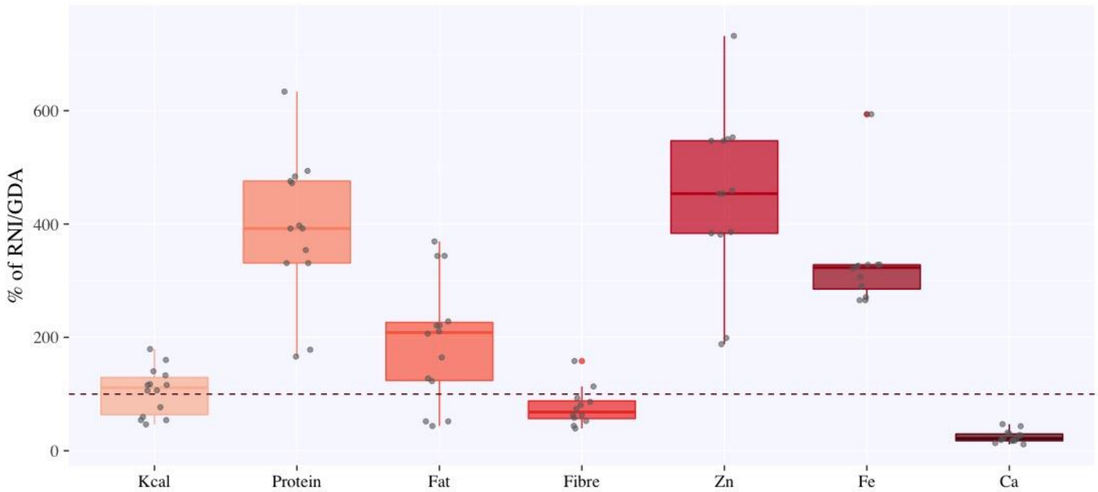

Figure 21. Nutritional composition of N=14 caterpillar dishes described during 24-h recall surveys. Each dish represents the proportion reported as an individual serving size for that dish. Dashed line indicates 100% of GDA/RNI.

Caterpillar dishes, as reported during 24h dietary recall surveys, also contained high amounts of these nutrients (**Figure 21**). The mean mass of caterpillars consumed was 247.5g (range =

100-400g). On five of these occasions, the caterpillars were dried prior to cooking, but the serving size for these (mean=245g, N=5) was not significantly different (Wilcoxon rank sum test, W=37, NS) from the portion size for fresh caterpillars (mean=249g, N=13). Caterpillar dishes (single portion) contained a median of 395% (IQR=145), 232% (IQR=42.8) and 456% (IQR=165) respectively of the recommended daily intake for Protein, Iron and Zinc. Dishes also contained high amounts of fat (median=209%, IQR=102), due to the oil used during the cooking process.

Caterpillars were consumed significantly more frequently during caterpillar season, when they were also consumed more frequently than either meat or fish is consumed during the dry season (**Table A.ii**).

Comparison		**P value**
Between seasons		
Caterpillars (C) +	Caterpillars (D) -	**<0.001**
Caterpillars (D) -	Fish (C) +	**<0.001**
Caterpillars (C) +	Fish (D) -	**<0.001**
Fish	Fish	1
Fish (D)	Meat (C)	0.07
Fish (C) +	Meat (D) -	**0.04**
Meat	Meat	1
Meat (D) -	Caterpillars (C) +	**<0.001**
Meat (C) +	Caterpillars (D) -	**0.04**
During caterpillar season		
Meat -	Caterpillars +	**<0.001**
Meat	Fish	0.05
Fish -	Caterpillars +	**<0.001**
During the dry season		
Meat	Caterpillars	0.06
Meat	Fish	0.06
Fish +	Caterpillars -	**<0.001**

Table A.ii. Results of post-hoc Tukey test comparing the frequency of animal protein consumption during the caterpillar season and during the dry season, based on responses to post-HFIAS questions. Significant p-values are highlighted in bold. (C) denotes the caterpillar season, (D) denotes the dry season. +/- indicates the higher/lower median consumption.

A3. Financial contribution of caterpillars

Women reported that more caterpillars were sold (median=3.33kg, IQR=4.41kg) than consumed fresh (median = 0.263kg, IQR=0.425kg) or dried (median=0kg, IQR=2.1kg) (**Figure 22**).

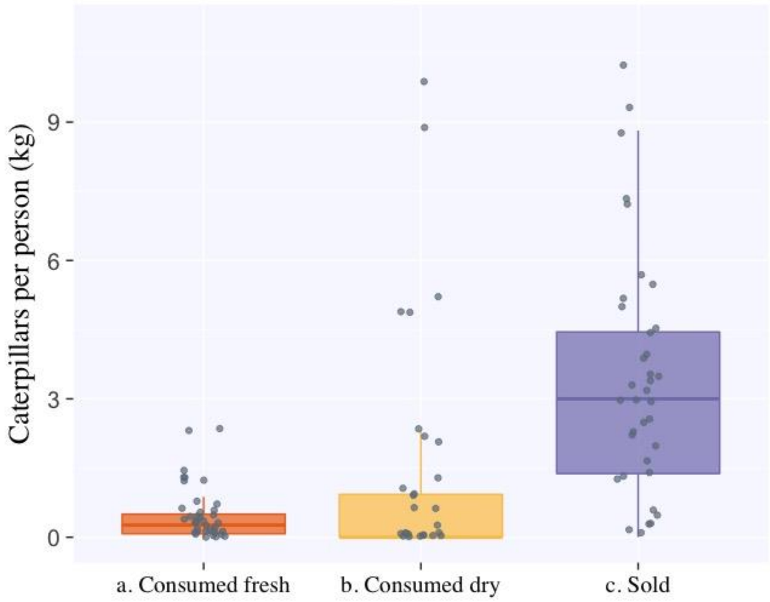

Figure 22. Caterpillars consumed fresh, consumed dry, and sold, per person in N=49 households, in 2016, according to responses to structured interview questions. Plots shows the median and interquartile range; error bars show the largest and smallest values within 1.5 times the interquartile range above and below the 25th and 75th percentiles respectively; outliers have been removed to show the data more clearly but were not removed for analyses or descriptive statistics.

We asked the question 'what is your main income source?' to 8 focus groups (N=19 people). Of these, 6 people responded 'caterpillars', 3 responded 'shea', 7 responded 'shea trees – for both shea and caterpillars' and 3 gave other answers (fields, health and Nere), as shown in **Figure 23**: Five respondents considered caterpillars to be their most important income source, but when discussing income many respondents considered the shea trees in a more general sense to be a key source of income due to a combination of both shea nuts and caterpillars.

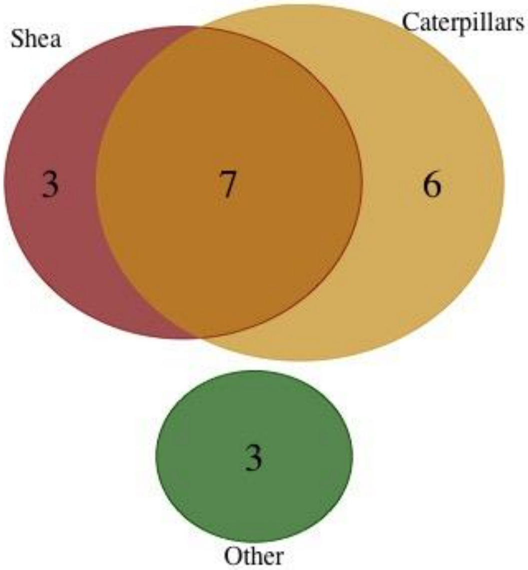

Figure 23. Venn diagram showing focus group participants' responses to the question "What is your main income source?"

A4. Caterpillars, food security and ethnicity

We used multiple linear regression to determine whether village, ethnicity and household wealth predict the consumption and sale of caterpillars. Consumption of caterpillars is predicted by the ethnicity of the male head of household, the ethnicity of the head of household's first wife, and by village, but not by household wealth (multiple linear regression, R^2=0.6, $F_{11,31}$=6.82, p<0.001, **Table A.iii**). Households headed by a man of Mossi, Dioula or Dafi ethnicity consumed more caterpillars. Households in which the first wife of the male head of household was Peul (also known as Fulani in English) or Bwoba consumed more caterpillars. Households located in Soumosso consumed fewer caterpillars. The amount of caterpillars sold is not predicted by any of these variables (multiple linear regression, R^2=-0.097, $F_{11,31}$=0.66, p=NS).

Predictor variable		Coefficient	P value
Village			
	Sitiena	0.79	NS
	Soumosso	-3.2	**<0.001**
Ethnicity of male head of household			
	Dafi	5.2	**<0.01**
	Dioula	4.9	**<0.001**

	Mossi	3.7	**<0.01**
Ethnicity of first wife			
	Bwoba	3.1	**<0.05**
	Dioula	0.17	NS
	Mossi	0.3	NS
	Peul	3	**<0.05**
Household wealth estimate		-1.5e-07	NS

Table A.iii. Table showing the coefficients and p-values of a multiple regression analysis (R^2=0.6, $F_{11,31}$=6.82, p<0.001), where consumption of caterpillars is the independent variable, and village, ethnicity of male head of household, ethnicity of first wife, and household wealth, are the predictor variables.

Nourishment

From caterpillars -

Nonpareil

毛虫を

食うなら

豊かすぎだ

Appendix B. The nutritional role of insects as food: A case study of chitoumou, an edible caterpillar in rural Burkina Faso

ABSTRACT

Insects are frequently promoted as a nutritious food. Yet they are a diverse class, and few data are available on their dietary role. In this paper, we present novel data on the nutritional role of 'chitoumou', the edible caterpillar *Cirina butyrospermi*, in the diet of rural smallholder farmers in southwestern Burkina Faso. We collected detailed dietary data via 24-h recall interviews (N=64), which we conducted with women who were predominantly responsible for making decisions on food preparation for their households (N=16) during and out of caterpillar season. We found that ethnicity did not predict caterpillar consumption. Diets that contained caterpillars were richer in protein ($p<0.05$) and calcium ($p<0.05$), key nutrients for combating malnutrition in this region. We conclude that edible insects play an important nutritional role among smallholder communities in southwestern Burkina Faso, but that more data are required to confirm the bioavailability of nutrients found in caterpillars, the effect of the cooking process on caterpillar nutritional quality and consequent health outcomes for people that consume them. To inform policy and the way in which insects are promoted as food, it is imperative that further research is done to quantify the nutritional role of edible insects in current human diets.

B1. INTRODUCTION

With the arrival of caterpillar season in mid-July, the villages of southwestern Burkina Faso are transformed. For the next three weeks of the rainy season, villagers rise in the middle of the night and eagerly harvest the caterpillars. They are the caterpillars of the Cirina butyrospermi *moth, and their abundance during this period means you cannot walk the village paths without coming across groups of caterpillars marching across the dry earth between trees. Their food source, the shea trees (*Vitellaria paradoxa*, formerly* Butyrospermum parkii*), teem with the insects, and people can amass loads of up to twenty kilograms within only three hours of collecting. Men, women and children partake in the* *harvest with delight. Their bounty, cooked with chilli, onions and soumbala (fermented locust beans), will make many delicious meals. If they have visitors, they tell them that the caterpillars are not only tasty but also promote good health and urge them to try them.*

This scene – rural villagers enjoying a seasonal abundance of edible insects and advocating their nutritional value – is found in many parts of the world (Evans *et al.,* 2017). Meanwhile, insects are being promoted as a healthy and sustainable food on a global scale: they are now sold in high-end retail outlets (Pope 2017), in popular chain restaurants (Trimble 2017), in supermarkets in Europe (Jones 2018, Olsen 2017), and even as a snack at a North American baseball game (Vinh 2017). Amongst this avid marketing of insects as food, their nutritional value is much lauded (Scott-Dixon 2018).

However, insects are a diverse class, and as such there is great diversity in the nutritional composition of insects that humans use as food. The current list of insects known to be used as food worldwide has over 2000 entries comprising nine orders (Jongema 2017). Many of these insects are eaten at different life stages, which has a major impact on nutritional composition: larvae, for example, tend to be far higher in fat than their adult counterparts. Raubenheimer and Rothman (2013) amalgamated data on the nutritional composition of 86 insects eaten by humans. They found that the protein:fat ratio ranged from 27:1 to 0.32:1. To say insects are high in either fat or protein is a generalization that disregards this diversity. Given the amount of variation seen in micronutrient content even across one insect species, generalisations about the micronutrient content of insects are also not supported by data. It follows that the nutritional role of insects also varies according to species, location, and dietary context.

To ascertain the nutritional role of a food, and to predict its effects on health, we need to look beyond its nutritional composition to its dietary context (WHO 2003, Hu 2002). Previous analyses of specific insects have included recommendations that certain insects are suitable for combating malnutrition, for example crickets and locusts because of their high protein content (Tao 2016), and caterpillar cereal because of its high iron content (Bauserman *et al.* 2015). In terms of nutrients that are key for combating diseases associated with overnutrition, several insects are similar to commonly consumed meat and may therefore be a cheaper and more environmentally friendly source of animal protein (Payne *et al.,* 2016). These findings and conclusions are both species- and context-specific.

Such studies are based on assumptions about diets in a given context, which are informed by knowledge about the diet and health status of a given population (Scarborough *et al.,* 2007). This often comes from large-scale dietary surveys (e.g., Whitton *et al.,* 2011) and longitudinal health monitoring (e.g. Tjønneland *et al.,* 2007). Insect consumption has rarely been recorded on large-scale dietary surveys; therefore, to understand the nutritional role of insects, we need to record how they are eaten, in what quantities, and in combination with what other foods. Detailed dietary data of diets that include insects can be used to paint a more detailed picture of their actual nutritional value.

In this study we look at the nutritional role of a widely consumed edible insect in the traditional diets of agriculturalists in West Africa. The insect in question is the edible caterpillar *Cirina butyrospermi*, locally known as 'chitoumou'. These caterpillars are a seasonally important food for rural smallholder farmers in southwestern Burkina Faso, although even when they are abundant, not everyone chooses to eat them. In this study we ask what nutrients these caterpillars contribute to the diets of people who choose to consume them.

Edible insects are thought to contribute to people's livelihoods not only as a direct source of nutrition but also via their market value (Kelemu *et al.,* 2015): even people who do not eat the caterpillars sell them in large numbers, creating a source of revenue (unpublished data). This, too, may contribute to improved nutrition. Therefore, we also ask whether diets are more nutritionally adequate during caterpillar season, regardless of actual consumption of caterpillars.

B2. Materials and Methods

B2.1. Study site

Figure 24. Preparation of freshly collected caterpillars involving washing and precooking (right); a prepared dish of caterpillars ready to be eaten (left).

We conducted this study in the villages of Koba, Soumosso and Larama, in the Hauts-Bassins region of Burkina Faso (**Figure 1**). The main method of subsistence combines smallholder cultivation and animal husbandry with the collection of wild foods. The agricultural system is shea-dominant agroforestry. Maize is the staple crop; rice and millet are also grown. Caterpillar season comes after the first rains, during the main growing period when people are engaged in heavy agricultural labour on a daily basis. Machine use is rare and most cultivation is done by hand or cattle-drawn plough. Caterpillars are collected in the early hours of the morning, cooked fresh to eat at home (**Figure 24**), sun-dried for later consumption, and/or sold at local markets and to buyers who visit from nearby cities. The most prevalent ethnicity is Dioula although there is also a large Mossi migrant population, and people of other ethnicities including Bobo, Peulh, Dafi and Bwaba. Islam, Christianity and forms of animism are all practised.

B2.2. Sample

We selected N=16 individuals from a wider sample of N=59 females who were predominantly responsible for making decisions on food preparation for their households and had previously been interviewed about food insecurity status (unpublished data). Our decision to interview these women was based on their influential roles in food preparation decisions and thus their acumen for providing the most valid responses to dietary interview questions. This subsample was stratified based on food security status and ethnicity. The two ethnicities, Dioula and Mossi, were selected because Dioula were reported to follow a tradition of eating the caterpillars of *Cirina butyrospermi,* while Mossi individuals, as more historically recent migrants to the region, reportedly often do not. Individuals of Dioula and Mossi ethnicity were thus chosen for the sample because we wanted to compare the daily intakes of occupants of the same region and of similar measured levels of food insecurity status when they included and did not include caterpillars. N=8 women were Mossi ethnicity and N=8 women were Dioula ethnicity. The subsample was stratified so as to be representative of the range of food insecurity status present in the original sample. Food insecurity status was based on categories generated by Household Food Insecurity Access Scale (HFIAS) surveys (following Coates *et al.,* 2007). There are four possible categories: category 1 represents food secure households; category 4 represents severely food insecure households. To be representative of the food insecurity status diversity present in the original sample, the subsample should have contained one individual from HFIAS 1 for both ethnicities, one individual from HFIAS 2 for both ethnicities, two individuals from HFIAS 3 for both ethnicities and four individuals from HFIAS 4 for both ethnicities (N=16). This stratification was achieved for HFIAS categories 2-4 but an individual from HFIAS 1 and of Mossi ethnicity was not available from the original sample and was therefore substituted with an individual of Mossi ethnicity and from HFIAS 2. An individual of Dioula ethnicity and of HFIAS 1 was available. Participants in the subsample were selected from the original sample using a random number generator application to avoid selection bias.

B2.3. Ethics and consent

All interview, survey and focus group protocols were developed in accordance with the Research Ethics Review Group, Department of Geography, University of Cambridge, which follows the Policy on the Ethics of Research developed by the University Ethics Committee (available online: https://www.research-integrity.admin.cam.ac.uk/files/policy_on_the_ethics_of_research_involving_human_participants_and_personal_data_oct_2016.pdf). Since low levels of literacy were common among the participants in this study, consent was acquired orally and recorded before interviews began.

The research was explained to participants in French or in their own language by trained field assistants. Participants were informed that they were free to opt out at any point, and that their contribution to the research would not result in direct financial gains. Information provided to participants and the oral consent declaration can be found in Appendix A, Cox et al. (2018).

B2.4. Interviews

Participants (N=16) were interviewed and asked to report every item of food or drink they had consumed during the previous twenty-four hours, and to estimate the quantity of each. The accurate reporting of time according to the 24-hour clock was uncommon among the participants in the sample, with individuals tending to round up to the nearest hour instead. Participants were asked to provide their waking and consumption times, and these were then used by the interviewers during the surveys. We therefore consider the impact of subjectivity in reporting the time of day to be negligible using this method.

Data collection for caterpillar season was the period between 22nd July 2017 and 12th August 2017, since 12th August 2017 was the last day when women reported finding any caterpillars. The period from 13th August 2017 to 16th September 2017 was out of caterpillar season. We aimed to interview all sixteen participants four times each; twice during and twice out of caterpillar season. Of the sixteen participants, ten were available for all interviews as intended and six were not available for interview on all occasions. Further details are given in Appendix B, Cox et al. (2018).

We used an interview protocol based on the multiple-pass method for 24-h recall surveys (Biro *et al.,* 2002). We asked respondents to recall all foods and drinks consumed during the previous 24 hours, and to estimate portion sizes. Average interview length was twenty-five minutes, and we conducted all interviews in the morning to aid recall (Huybregts *et al.,* 2009). To maximise accuracy of recall we used the multiple pass method (Wrieden *et al.,* 2003): for the first pass respondents recalled all foods and beverages consumed during the previous 24 hours; for the second pass respondents identified when and where foods were consumed; for the third pass we recalled the report to the respondent to prompt for any forgotten items. Finally, we reviewed and confirmed with the respondent all items recorded. We used household measures to aid estimates of portion size. Interviews were conducted in

Dioula, Mori (the language of Mossi ethnicity) or French, as per the participant's preference, with the assistance of trained field assistants who were fluent in all three languages. Interview questions were written in English by SC and translated into French and Dioula by CP, Flora Some (field assistant) and Poda Nambepierre (local collaborator). Field assistants were provided with interview questions in French and translated from these into Dioula or Mori when necessary. Several Dioula interviews were conducted by SC in Dioula using the translation and under the supervision of the field assistant present.

The protocol was as follows:

Go to participant's house.
Ask if participant consents to be interviewed.
If consent not given, apologize and move on to next household. If participant consents, record the reading of consent information to the participant and their provision of oral consent, either in their first language or a language in which they are fluent and comfortable. Ensure participant's full understanding.
Provide a brief overview of what will be asked and why: 'I'm going to ask you to tell me everything you ate yesterday because I want to have an honest record of people's diets in this area. Your name will be removed from the answers you provide, so the interpreter and I will be the only people to know your answers.'
Ask if participant has any questions and provide answers.
Ensure interview setting is as comfortable as possible for all parties.
Begin interview. Questions in French and in Dioula (with English translations) are given in Appendix C and Appendix D, Cox et al. (2018).

B2.5. Data analyses: food matching

For all interview data, we retrospectively converted portion sizes to grams using 'FAO/INFOODS Density Database Version 2.0' (Charrondiere *et al.*, 2012a). We matched food items with energy and nutritional compositional values from the West African Food Composition Table (Charrondiere *et al.*, 2012b). When an exact match was not possible, food items were matched with values available from other published sources (Anvo *et al.*, 2016, Greffeuille *et al.*, 2010, Nordeide *et al.*, 1996); if these were unavailable, we used the mean of the values for several similar items (in accordance with the 'INFOODS Guidelines for Food Matching' - Stadlmayr *et al.*, 2011). Where information was not available regarding water content in recipes, we substituted a likely amount based on reported recipes.

B2.6. Data analyses: comparison with reference measures

The WHO (World Health Organisation), in collaboration with WFP (World Food Programme), UNICEF (United Nations Children's Fund) and UNHCR (United Nations High Commissioner for Refugees), provides a document with guidelines for nutritional recommendations to combat malnutrition (World Health Organisation 2004). This is based on a 2100Kcal daily intake for an hypothetical adult and is specifically designed for populations at high risk of malnutrition. It covers many micronutrients considered crucial for preventing micronutrient deficiency, in such a scenario. We deemed this to be an appropriate measure given the prevalence of malnutrition and particularly micronutrient deficiency in rural West Africa (Akombi *et al.*, 2017, Petry *et al.*, 2016).

We calculated the mean daily intakes of macro- and micronutrients per person; these daily intakes were compared with the corresponding WHO (2004) recommendations.

B2.7. Data analyses: statistics

We used R Studio version 1.1.442 for all statistical analyses.

We used the data of N=13 participants with at least one interview during and one interview outside caterpillar season (N=13). If participants had two interviews during one or both of the seasons, the season was represented by the average of the values collected for that season. We used paired Wilcoxon signed rank tests to estimate the difference between total intake of calories, macro- and micronutrients, during and outside caterpillar season.

We then used the data of N=9 participants with at least one interview reporting caterpillar consumption and one interview where caterpillars had not been consumed. If a participant did not have at least one interview reporting caterpillar consumption and one interview not reporting caterpillar consumption, they were not included in this group. When a participant had multiple interviews reporting caterpillar consumption or multiple interviews not reporting caterpillar consumption, the mean of the values from these interviews was used to represent that participant's intake when they consumed or did not consume caterpillars. We used paired Wilcoxon signed rank tests to estimate the difference between total intake of calories, macro- and micronutrients, when they included or did not include caterpillars in their diet.

The high margin of error in converting firstly actual dietary intake to reported estimates, and secondly converting locally consumed ingredients to known ingredients with reported nutrient composition data, elevates the risk of Type II Errors. Therefore, while we consider $p<0.05$ to be our threshold for significant results, we also report results where $p<0.1$ with the caveat that these are tentative findings.

B3. RESULTS

Intakes deficient in macronutrients were not the norm: most participants reported intakes that contained energy, protein and fat in excess of recommended daily intakes (**Figure 25**). However, for several micronutrients considered key in situations where malnutrition is prevalent, many intakes were below recommended levels. The median values for dietary content of thiamine (76%, 0.68mg), riboflavin (58%, 0.82μg), folate (86%, 140μg), and vitamins A (10%, 52μg), C (54%, 15μg) and D (0.76%, 0.029μg), all fell below 100% of the required daily intake. Iron intake was also frequently insufficient, with 45% of intakes (N=13) falling below 100%.

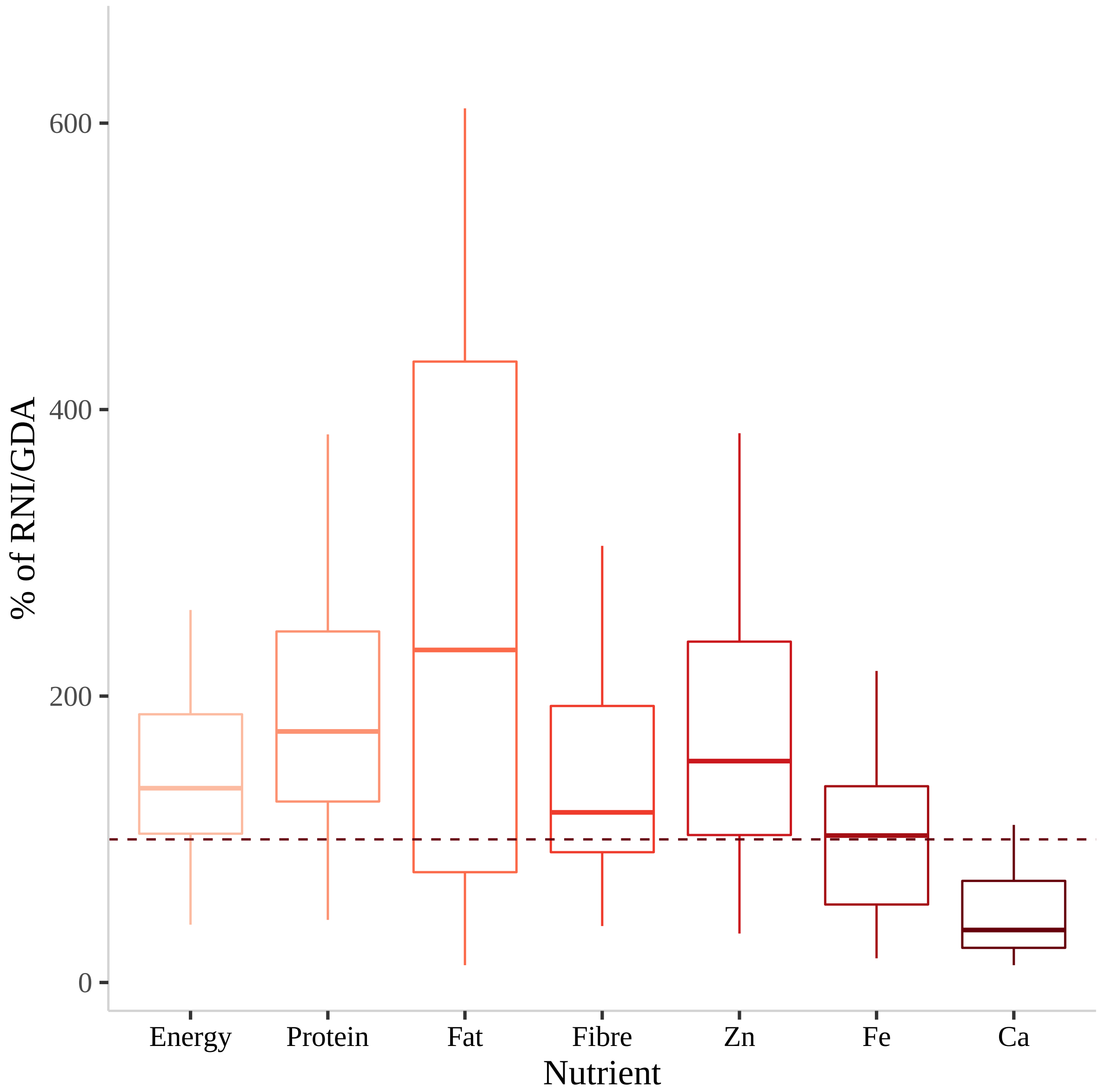

Figure 25. Boxplot showing daily nutrient content in reported intakes (N=29). 25 intakes represent an average nutrient content of two surveys taken during the same season; for 4 intakes when individuals were only available once, these represent nutrient content of a single survey. The dashed line shows the threshold for an intake containing 100% of the recommended daily amount according to WHO/WFP/UNHCR/UNICEF guidelines (World Health Organization 2004).

Fifty six percent (N=9) of individuals interviewed (N=16) reported eating caterpillars in at least one of their dietary surveys. Of these, five individuals were of Mossi ethnicity and four were Dioula. Of the participants who did not report eating caterpillars, three were Mossi and four were Dioula (**Table B.i**). There was a weak effect of seasonality in reports of caterpillar consumption, with higher caterpillar consumption during caterpillar season (Chi-squared test, χ^2=3.2, d.f.=1, p=0.075), but there was no difference based on ethnicity (Chi-squared test, χ^2=0, d.f.=1, p=1).

			During caterpillar season		**Outside caterpillar season**	
Participant ID	**Ethnicity**	**HFIAS category**	**Interview 1 Caterpillars?**	**Interview 2 Caterpillars?**	**Interview 3 Caterpillars?**	**Interview 4 Caterpillars?**
1	Dioula	1	N	Y	Y	NA
2		2	Y	N	N	N
3		3	N	Y	N	N
4		3	N	N	N	N
5		4	N	N	N	N
6		4	Y	Y	N	N
7		4	N	NA	NA	NA
8		4	Y	N	N	N
9	Mossi	2	Y	N	NA	NA
10		2	N	N	N	N
11		3	Y	Y	Y	NA
12		3	Y	N	N	N
13		4	N	N	N	NA
14		4	N	N	N	Y
15		4	N	N	N	N
16		4	N	Y	N	N

Table B.i. Ethnicity and HFIAS category recorded for participants and the interviews for which participants were available. Caterpillars collected during caterpillar season can be sun-dried and stored for later consumption. Interviews reporting caterpillar consumption outside caterpillar season therefore refer to these dried caterpillars.

Intakes containing caterpillars, regardless of season, were higher in protein (paired Wilcoxon signed-rank test, V=5, $p<0.05$) and fat (paired Wilcoxon signed-rank test, V=7, $p<0.1$) than intakes not containing caterpillars (**Table B.ii**). The median protein content for intakes not containing caterpillars was 58g (interquartile range (IQR)=49), just below the 60g minimum recommended by the WHO, while intakes containing caterpillars were very rich in protein with a median of 160g (IQR=92) (**Figure 26**). Fat content of intakes both containing (median=108g, IQR=180) and not containing (median=86g, IQR=63) caterpillars fell above the recommended 42g minimum for fat intake.

	P-values for difference between intakes with caterpillars (N=9) and without caterpillars (N=9)	**P-values for difference between intakes during caterpillar season (N=13) and outside caterpillar season (N=13)**
Energy	0.36	0.15
Protein	0.039*	0.41
Fat	0.074^{+}	0.89
Vitamin A	0.91	0.12
Thiamine	0.2	0.048*
Riboflavin	0.5	0.68
Vitamin C	0.43	0.41
Vitamin D	0.93	0.19
Iron	0.098^{+}	0.41
Calcium	0.012*	0.5
Niacin	0.098^{+}	0.3
Potassium	0.55	0.094^{+}
Zinc	0.91	0.17

Table B.ii. Results of paired Wilcoxon signed-rank tests comparing nutrient intake with and without caterpillars, and during and outside of caterpillar season. *= significant at $p<0.05$:

+=significant at p<0.1. This table includes all macro- and micronutrients considered important for combating malnutrition (World Health Organisation 2004).

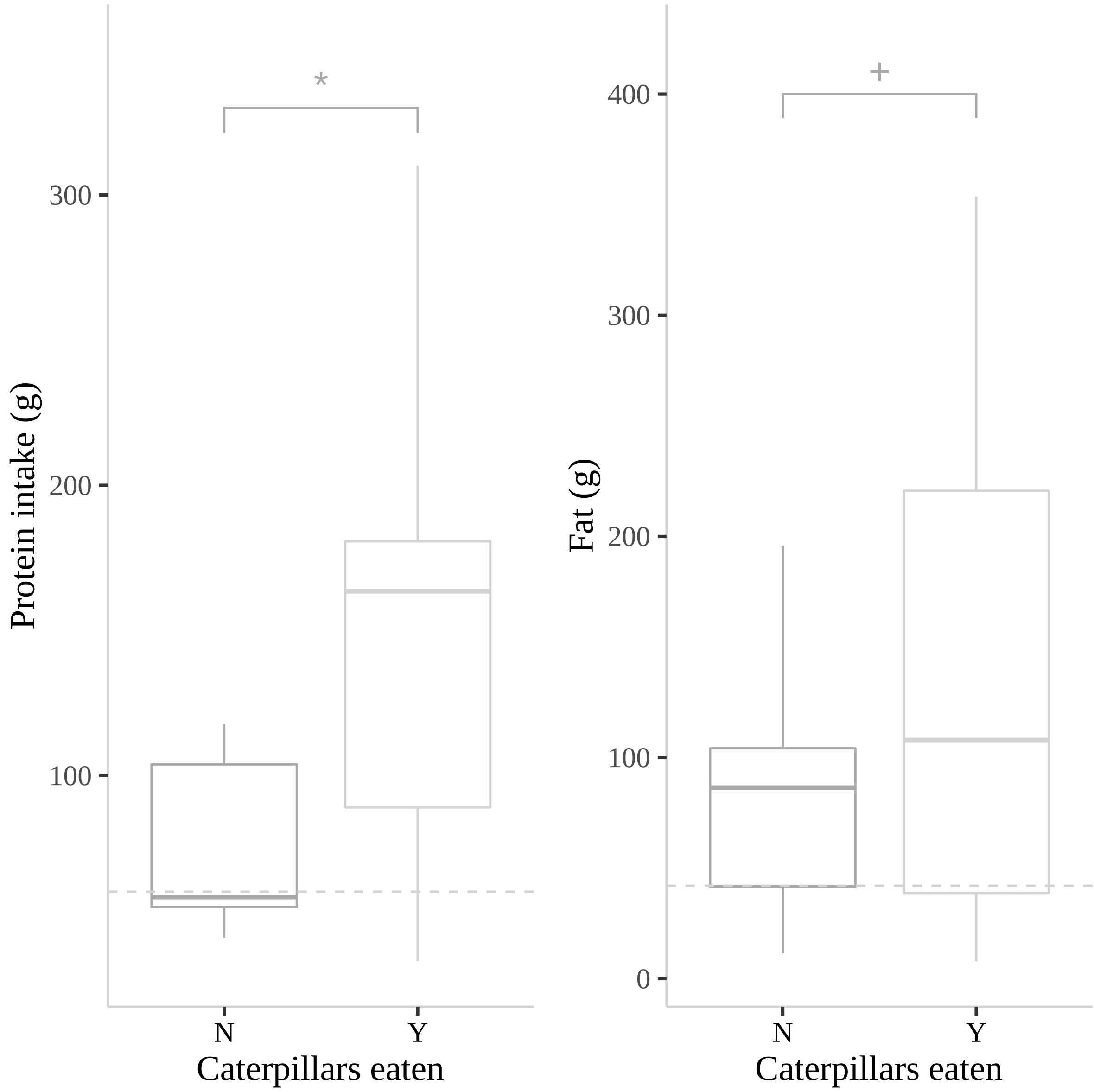

Figure 26. Boxplots showing daily protein (g) and fat (g) consumption for intakes when caterpillars were and were not eaten. The dashed lines show the threshold for an intake containing the recommended daily requirements according to WHO (2004) guidelines: 60g of protein and 42g of fat. *= significant at p<0.05: +=significant at p<0.1.

Iron, calcium and niacin content of intakes were also higher when caterpillars were eaten (Wilcoxon signed-rank tests, Iron: V=8, p<0.1; Calcium: V=2, p<0.05; Niacin: V=37, p<0.1; **Figure 27**). For both iron and niacin, the inclusion of caterpillars means that median intake

(38mg of iron; 16mg of niacin) exceeds the minimum recommended intake by WHO (22mg of iron; 12mg of niacin), while in intakes without caterpillars it falls below this level (19mg of iron; 7.6mg of niacin). Calcium content is higher in intakes with caterpillars but the median intake (910mg in diets containing caterpillars; 300mg in intakes not containing caterpillars) does not reach the 1000mg Recommended Dietary Allowance (RDA) of the Institute of Medicine (IOM) (Ross *et al.* 2011).

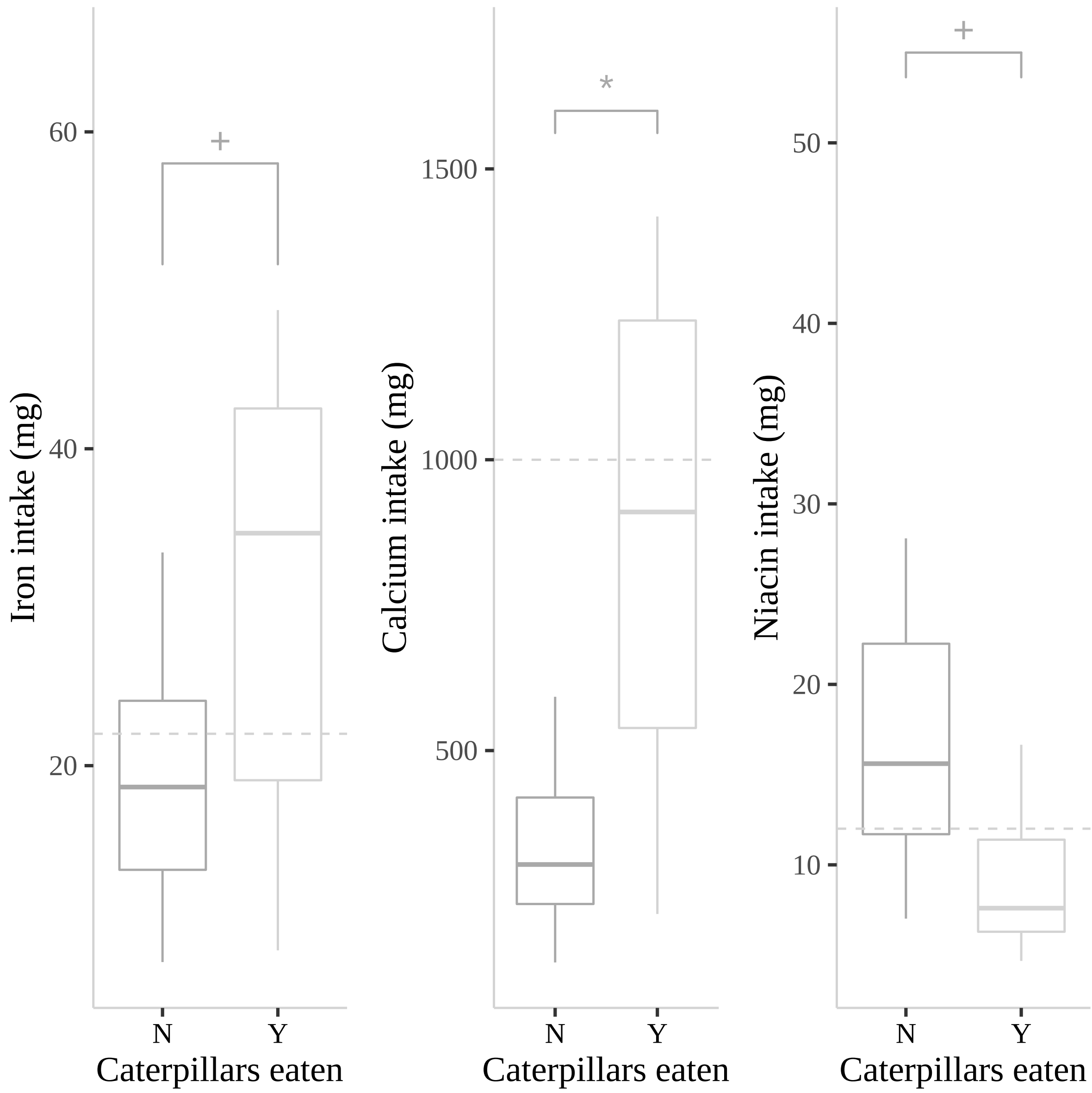

Figure 27. Boxplots showing daily iron (mg), calcium (mg) and niacin intake (mg) for intakes when caterpillars were and were not eaten. The dashed lines show the threshold for a diet containing the recommended daily requirements according to WHO guidelines (22mg of iron; 12mg of niacin), or 100% of the Recommended Dietary Allowance (RDA) according to

the Institute of Medicine (IOM) (Ross *et al.* 2011) (1000mg of calcium). *= significant at p<0.05: [+]=significant at p<0.1.

The only nutrients for which there was a seasonal difference in nutrient content of diets were potassium and thiamine (**Figure 28**). Both were higher out of caterpillar season (Wilcoxon signed-rank tests, potassium: V=70, p<0.1; thiamine: V=74, p<0.05). In the case of thiamine, the median value for diets both during (0.57mg, IQR=0.36) and out of (0.71mg, IQR=1.8) caterpillar season was below the WHO recommended intake of 0.9g. The median values for potassium content were 1900mg (IQR=1800) during caterpillar season and 2600mg (IQR=2200) out of caterpillar season.

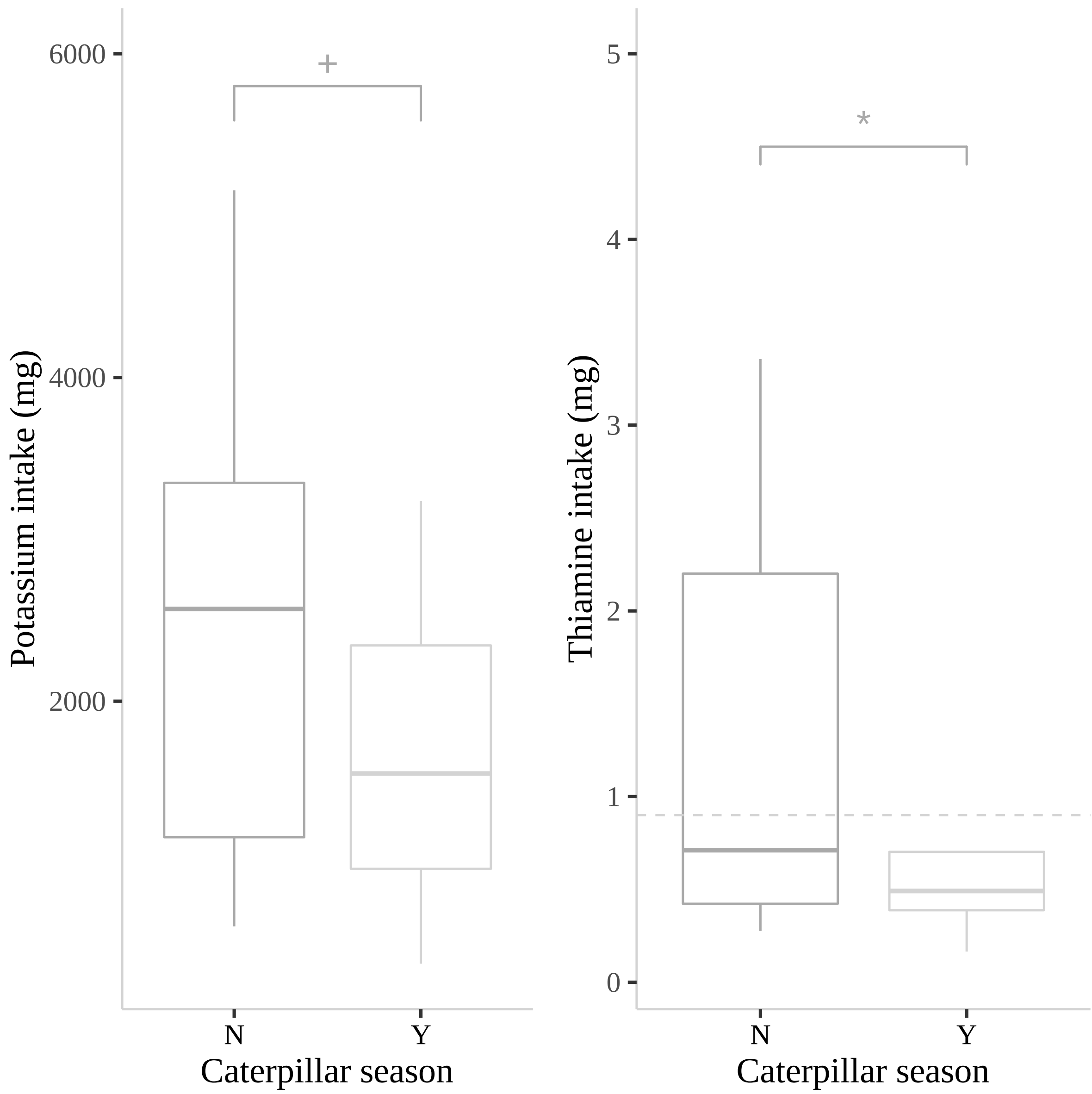

Figure 28. Boxplots showing daily potassium (mg) and thiamine (mg) intake for intakes during and out of caterpillar season. The dashed line shows the threshold for a diet containing the recommended daily requirement of thiamine according to WHO guidelines: 0.9g. *= significant at $p<0.05$: $^{+}$=significant at $p<0.1$.

B4. DISCUSSION

Edible insects have been advocated as a nutritious food that may help combat malnutrition in high-risk regions of the world (Meyer-Rochow 1975, Van Huis 2013a). However, while data are available on the nutritional composition of insects (e.g. Brand Miller *et al.,* 1993, Rumpold and Schlüter 2013, Bukkens 1997), little is known about their nutritional role in actual diets. In this study we used 24-h dietary recall surveys in a region where the edible shea caterpillar is seasonally abundant and widely eaten to ascertain the nutritional contribution of caterpillars to diets. We found that individuals of both ethnicities represented in the study consumed caterpillars. Daily intakes including caterpillars were significantly higher in protein and calcium. The only nutrient that differed significantly during and out of caterpillar season was thiamine, which was higher out of caterpillar season. In this region, the consumption of caterpillars does significantly increase intake of key nutrients, but there is no evidence that the occurrence of caterpillar season – via extra income gained by the sale of caterpillars – also confers nutritional benefits.

Previous literature has suggested that edible insects may be a seasonally important source of protein and micronutrients (Bukkens 1997). We found that when individuals consumed caterpillars, their overall daily intake contained significantly more protein and calcium, and to a lesser extent fat, iron and niacin. Protein is important for brain development (Laus *et al.,* 2011), and although we did not find prevalence of a deficiency in dietary protein among study participants, protein-energy malnutrition is common in west Africa (Akombi *et al.,* 2017). Promoting caterpillar consumption may therefore be a useful strategy for combating protein-energy malnutrition in southwestern Burkina Faso.

Caterpillars may also be important for combating micronutrient deficiency. Daily intakes that included caterpillars were significantly higher in calcium, which helps to prevent certain diseases (Kennedy *et al.,* 2003) and is particularly important for pregnant women in aiding child growth (Scholl *et al.,* 1997). Deficiency of calcium, particularly in association with other micronutrient deficiencies, inhibits metabolic pathways and can lead to clinical symptoms (Branca and Ferrari 2002). We found that a deficiency in key micronutrients was a common feature of the intakes reported in this study and that there was a weak association between intakes containing caterpillars and intakes that were richer in iron and niacin. Deficiencies in iron and niacin may exacerbate symptoms of calcium and other micronutrient deficiencies (Branca and Ferrari 2002). Micronutrient deficiency affects one third of the world's population (Biesalski and Black 2016) and is particularly prevalent in west Africa (Petry *et al.,* 2016). Our results suggest that caterpillars may play a role in curbing the severity of micronutrient deficiency in southwestern Burkina Faso.

Seasonality also affected the nutrient content of intakes: those recorded out of caterpillar season contained higher quantities of thiamine, and to a lesser extent, potassium. Low thiamine intake was common in this study. Thiamine deficiency disease (beriberi) can lead to child mortality (Barennes *et al.,* 2015); potassium deficiency can contribute to stunting (Branca and Ferrari 2002). Seasonal differences in levels of these micronutrients in the diet may be caused by the seasonal availability of foods that contain or are deficient in these nutrients. Identifying such foods is beyond the scope of this study, but communities in this region may benefit from policies that promote year-round consumption of foods that are high in thiamine and potassium.

In addition to being used as food, caterpillars are also sold and are an important income source in this region. Women report that their overall food security is higher during caterpillar season (unpublished data), yet diets recorded during caterpillar season were not significantly higher in any key nutrients than diets out of caterpillar season. This suggests that the extra income generated by the sale of caterpillars may not be used to provide a more nutrient-rich diet. However, this study did not look at the amount of money individuals made from caterpillars, which may indeed predict diets higher in key nutrients. Policy in this area would benefit from further research examining the relationship between the sale of caterpillars and individuals' nutritional status.

Prior to conducting this study, we had been advised that, for cultural reasons, Dioula people eat caterpillars while Mossi people do not. However, we found that ethnicity did not predict caterpillar consumption. This suggests that cultural aversion to eating caterpillars is less prevalent than previously believed, and that some migrant families in this area without a history of caterpillar consumption do currently consume caterpillars. The burgeoning edible insect industry aims to create a more environmentally friendly food system through providing an alternative to livestock yet is currently held back by entrenched attitudes of disgust towards insects as food (DeFoliart 1999). Further research into the reasons for adoption of insect consumption by people who are newly exposed to an insect-eating culture could be very significant for the future of this industry.

There are several important limitations to this study. Firstly, we only investigated women's diets. Women prepare most of the food for the household, so similar patterns may be expected for men's diets. However, men may supplement household meals with food hunted, gathered or purchased elsewhere. In other societies, men are also known to consume more vertebrate meat than women (Fagerli and Wandel 1999, Prattala *et al.*, 2006). These factors may mean that the nutritional contribution of caterpillars to men's diets may differ from the results reported here.

Secondly, this study did not look at actual health outcomes of diets containing caterpillars. Although we report quantities of nutrients in diets, we do not know the extent to which these nutrients are bioavailable. This is a major problem with dietary recommendations that are based on nutrient composition alone (Hambidge 2010) and may be particularly relevant for edible insects since their properties as food are not well researched.

Furthermore, we do not know whether higher intake of the key nutrients discussed here actually affects the prevalence of macronutrient or micronutrient malnutrition for women in the study population. Caterpillars, as is the case with many edible insects, are only available for a short period, and their consumption may not be adequate to achieve health outcomes.

Both industry stakeholders and policymakers would benefit from further research addressing these unknown factors, all of which may mediate the nutritional role of edible insects.

B5. CONCLUSIONS

Overall, we can conclude that in southwestern Burkina Faso, caterpillars make a significant nutritional contribution to women's daily diets by increasing their intake of protein and calcium. This is the case both for women from a culture that traditionally consumes caterpillars, and for migrant women whose traditional culture rejects caterpillars as food, suggesting that taboos against insects as food can be broken. This study has shown that edible insects play an important nutritional role on a seasonal basis; further research is necessary to determine whether their inclusion in diets also makes a positive contribution to health outcomes, particularly the prevalence of protein-energy malnutrition and micronutrient deficiency.

Appendix C. Rearing the edible caterpillar *Cirina butyrospermi* on substrates developed for related Lepidoptera

ABSTRACT

Edible insects are important for food security, but there is a risk that promotion of wild-harvested edible insects could lead to overexploitation. The shea caterpillar *Cirina butyrospermi,* known as chitoumou, is a popular edible insect in West Africa. Previous experimental trials have found that it is possible to rear chitoumou on fresh shea leaves. However, fresh shea leaves are also limited in spatial and temporal supply. For this study we aimed to identify an alternative feed that could be used by rural farmers as a rearing substrate for chitoumou. We developed six test diets and ran two rearing trials in parallel, one in a field lab set up in a rural village and one in a university lab. In the university lab, we used fresh shea leaves as a control diet; in the field lab we did not use a control diet. The test diets we developed were based on artificial feeds used successfully to rear other saturnid and noctuid larvae. All caterpillars in both settings died within a few days of being reared on all seven diets, including those fed on the control diet in the university lab. The reasons for this are unclear.

C1. Introduction

The global food system is under increasing pressure from population growth and climatic change (Tilman et al. 2011). It is imperative that we find new ways to increase yields of food, and particularly yields of edible protein (Godfray et al. 2010). In 2013 the FAO highlighted a potentially rich source of protein with a relatively low environmental footprint: edible insects (Van Huis et al. 2013a). Since then, companies, researchers and entrepreneurs have developed methods of farming several species of insect for human consumption (Halloran 2018).

However, some of the most highly valued food insects are still harvested from wild land (Van Huis 2016). If insects continue to be promoted as a source of food there is a real risk that wild populations may be exploited in ways that could threaten future harvests (Yen 2015a). This is the case for a number of species worldwide; one of the most commercially significant is the mopane worm, the edible caterpillar *Gonimbrasia belina*. Mopane worms are traditionally collected from mopane woodlands when they come down to the ground to pupate. In response to increased demand for these insects, some collectors have begun to shake or even chop trees down in order to harvest the caterpillars before they are fully grown. Collectors report extreme fluctuations in inter-annual caterpillar populations, and this may be linked to these destructive harvesting practices (Sithole 2016). There is a real risk that the same patterns may emerge as demand increases for chitoumou. Chitoumou are subject to increasing attention as a source of food (BBC 2017), and demand for chitoumou may further increase with population movement in this region, as people move into its range from elsewhere (Sanfo et al. 2017). Developing methods for enclosed rearing of this species would be highly beneficial in preventing overexploitation of wild populations and ensuring future food security.

In natural conditions, *Cirina butyrospermi* produces a single generation every year. In southwestern Burkina Faso, the caterpillars burrow into the ground to pupate in July/August. They remain underground until the following May/June, when they emerge as moths. The moths are short-lived and do not feed. They mate and lay eggs on the bark and branches of shea trees. Shea trees are found throughout agricultural fields in the region and have wide commercial and cultural importance due to their nuts, which are harvested for consumption and sale. The eggs hatch into first instar larvae, which then feed on the leaves. The caterpillars pass through five instars before they are fully mature; this takes an average of 33.3 days when the caterpillars are kept in laboratory conditions feeding on shea leaves (Rémy et al. 2018). It is possible to break the diapause using the insect growth hormone 20-hydroxyecdysone, causing the adult moths to emerge early (Bama et al. 2018). Therefore, in laboratory conditions, it would be possible to have more than a single harvest per year if suitable food were available. The caterpillars require fresh shea leaves in order to grow, and young leaves are not available year-round nor in all regions. Developing a feeding substrate is therefore the key next step in being able to increase production of shea caterpillars through enclosed rearing.

C2. METHODS

C2.1. Feed

We developed feeds based on diets used for other Lepidoptera (saturnid and noctuid moth larvae) reared in captivity, and also used a control diet of fresh shea leaves. These are summarized in **Table C.i**. We (Darja Dobermann, Charlotte Payne and Athanase Badolo, hereafter DD, CP and AB) developed methods for preparing the feeds in the university and field labs, detailed in **Table C.i**.

Name of feed	***Target species***	***Composition***
1. Mopane starter mix	Gonimbrasia belina[1]	Corn flour (75g), whole wheat flour (75g), wheat bran (75g), dried yeast powder (25g), glycerine (125g), honey (125g). Mix dry ingredients; mix wet ingredients; mix together; let stand for 24h.
2. Mass rear mopane mix	Gonimbrasia belina[1]	Corn flour (37.5g), wheat germ (37.5g), wheat bran (37.5g), brewer's yeast (12.5g), chicken mash (125g). Blended for 2 mins. Add milk (41.6g), castor oil (41.6g) & water (166.6ml). Mix; let stand 24h.
3. Spodoptera diet mix	Spodoptera spp[2]	Wheat germ (36g), casein (16.5g), sugar (14.6g), yeast (7.1g), Wesson's salt (4.7g),

		methyl paraben (0.47g), Vanderzant vitamin mixture (2.5g), acsorbic acid (1.6g), agar (9.4g), linseed oil (0.94g), hot water (432.8ml). Mix dry ingredients; mix agar and water and cook over heat for 7min (stir at least twice during this time); allow to cool to 65ºC; mix together.
4. H. armigera diet mix	Helicoverpa armigera[2]	Chickpea flour (50g), yeast (15g), Wesson's salt mix (3.5g), methyl paraben (1g), ascorbic acid (1.5g), carbendazim (0.34g), Vanderzant vitamin mix (4g), agar (6.5g), hot water (360ml). Mix dry ingredients; mix agar and water and cook over heat for 7min (stir at least twice during this time); allow to cool to 65ºC; mix together.
5. Silkmoth handbook mix	Saturnidae[3]	Casein (18.9g), wheat germ (16.2g), inositol (0.6g), Wesson's salts (5.4g), sugar (18.9g), cellulose powder (2.7g), powdered dried kale leaves (8.2g), methyl paraben (1g), Vanderzant vitamin mix (2.5g), ascorbic acid (2.3g), agar (13.5g), hot water (300g), linseed oil (1.5g), water (165g). Boil agar in hot water for 10min. Mix dry ingredients with cold water in blender; allow agar and water mixture to cool to 70ºC; mix together.
6. Mulberry chow (Bombyx mori)	Bombyx mori[4]	Mulberry mix (125g), water (337.5g).
*7. Fresh shea leaves **(control)***	Cirina butyrospermi[6]	NA

Table C.i. Experimental diets used in this study, target species and recipe composition. Recipes make ~500g of feed. Table footnotes are as follows: 1. Ghaly et al. (2009); 2. Standard lab mix; 3. Gardiner (1982); 4. silkwormstore.co.uk/silkworm-food-2/; 5. Spirulina

0.9g, Oat fibre 0.8g, Spinach 0.7g, Broccoli 0.7g. Kale 0.7g, Wheat Grass 0.6g, Barley Grass 0.6g, Watercress 0.5g, Tomato 0.5g, Carrot 0.5g, Golden Flaxseed 0.5g, Chlorella (Broken Cell Wall) 0.35g, Oregano 0.35g, Yucca root 0.3g, Beetroot (0.8% Nitrates) 0.25g, Rosemary 0.25g, Thyme 0.2g, Avocado Juice Powder 0.2g, Alfalfa Sprouts 0.2g, Soy Sprout 0.2g, Parsley 0.2g, Basil 0.2g, Sumac Bran (96% tannin) 0.15g, Kelp 0.01g, purchased from: https://www.amazon.co.uk/BULK-POWDERS-Complete-Greens-Unflavoured/dp/B00IXIWC7A/ref=sr_1_5?keywords=bulk+powders+super+green&qid=1554732358&s=gateway&sr=8-5; 6. Rémy et al. (2018).

C2.2. Egg collection

We collected wild caterpillar eggs (**Figure 29**) from shea trees near to Po and Soumosso (**Figure 30)**, by cutting branches with secateurs. Prior to transportation and/or use we kept all eggs in a tissue-lined plastic containers without lids to maintain airflow.

Figure 29. Wild-collected *Cirina butyrospermi* eggs, with scale.

Figure 30. Map showing locations of Po (Nahouri, 11° 10' 2.9", -1° 9' 36") and Soumosso (Hauts-Bassins, 11°00'44", -004°02'45"), where we collected wild *Cirina butyrospermi* eggs for this study.

C2.3. Diet preparation

DD prepared the dry ingredients for all diets; these were shipped to Burkina Faso in sealed labelled plastic bags with detailed instructions on how the diets should be prepared for subsequent use. For the preparation of all diets we added water to the dry ingredients and mixed this thoroughly. In the field lab, we used well water for this. In the university lab, we used distilled water. Diet 2 (Mass rear mopane mix) also required that we add milk; we used milk powder (Nido Lait Entier Poudre Instantané, owned by Nestlé) dissolved in the proportion of powder to water recommended on the packaging.

C2.4. Experimental settings

We ran two experimental trials in parallel. The first is in our field lab, which we set up in Guiriko Organic Farm in the village of Soumosso (**Figure 31**). We ran this trial without the aid of electricity (e.g. for refrigeration or temperature control) in order to mimic conditions that could be achieved by smallholder farmers in this region. Poda Nambepierre (PN) acted as our field technician; he is knowledgeable about the local fauna and flora, is a respected member of the village and likely to share his experiences with many others local to the area. His involvement meant that we were made aware early on of traditional ecological knowledge that could help facilitate the experimental methods, and that the lived experience of running the trials was effectively disseminated amongst other villagers. We used a room with earthen walls, which is a common feature in most houses in the village, with the aim of maintaining a consistent temperature and humidity within the parameters identified by Rémy et al. (2018) as suitable for *Cirina butyrospermi* rearing: 23-30°C and 58-84% humidity.

The second experimental setting was a laboratory in the Department of Entomology at the University of Ouagadougou, hereafter referred to as the university lab. We employed Aboubakar Sanon (AS), a graduate student in the Department of Entomology, as our lab technician.

C2.5. Field lab

For our field lab experimental trial we only used eggs collected in Soumosso. PN was our responsible for the trials, trained by CP following a protocol developed by CP, DD and AB. Training took one day, followed by ad hoc monitoring of the trials. PN monitored the egg clusters for signs of hatching. When eggs showed signs of hatching he moved the larvae to the selected feed substrate one by one using a small paintbrush, following advice in Gardiner (1982). PN freshly prepared all substrates as needed, using dry ingredients and local well water. No refrigeration was available, so substrates were used within 24h of preparation. The substrate was placed on a wooden platform inside an 18” pop-up mesh cage designed for insects (**Figure 31**). PN added fresh substrate every 48hrs or more often if necessary, and weighed it before and after use. The cages were kept in a room with earthen walls (**Figure 31**) and PN monitored the temperature and humidity on a daily basis.

Figure 31. Photos showing the cage and wooden platform structure (left), the room in which cages were kept in the field lab (top right), and fresh substrate preparation in the field lab (bottom right)

C2.6. University lab

Our university lab was in Ouagadougou, and for these experiments we used eggs collected from both Po and Soumosso. We transported the eggs by hand in plastic buckets without lids, to maintain airflow. AS was responsible for the trials, trained by AB following a protocol developed by CP, DD and AB. Training took one day, followed by ad hoc monitoring of the trials. AS monitored the egg clusters for signs of hatching. When eggs showed signs of hatching he moved the larvae to the selected feed substrate, again one by one using a small paintbrush. AS freshly prepared all substrates as needed, using dry ingredients and distilled water. Substrates were refrigerated to maintain freshness, and were used within 72rs of preparation. The substrate was placed on a wooden platform inside an 18” pop-up mesh cage designed for insects, as in the field lab setting (**Figure 31**). AS added fresh substrate every 12hrs, and weighed it before and after use.

C2.7 Statistical analysis

We ran survival analyses using the R package *survival* (Therneau and Grambsch 2000). We generated Kaplan-Meier curves for caterpillars on each diet and in each location. The Kaplan-Meier estimator (Kaplan and Meier 1958) is a method widely used in medical studies (Stalpers and Kaplan 2018) and also adopted by ecologists (Cox 2018) to calculate the probability of survival at different life stages for all test diets. In order to then understand the relationship of the covariates diet and location (field lab or university lab), we built Cox proportional hazards models designed to enable the comparison of multiple covariates (Anderson and Gill 1982), to compare the two using the R package *survival*.

C3. RESULTS

In the field lab, the temperature ranged from 27.1 – 39.7°C, and humidity ranged from 62 – 82%. Larval mortality rate was high for all six diets recorded, no larvae lived beyond 22 days, the mortality rate was not recorded for the control diet, and additional larvae were added on an ad hoc basis throughout the experiment (**Figure 32**). In the university lab, the temperature and humidity ranged from 29.5 - 32°C, and 58 – 67%. Larval mortality rate was high for all seven diets recorded, with no larvae living beyond 13 days (**Figure 33**).

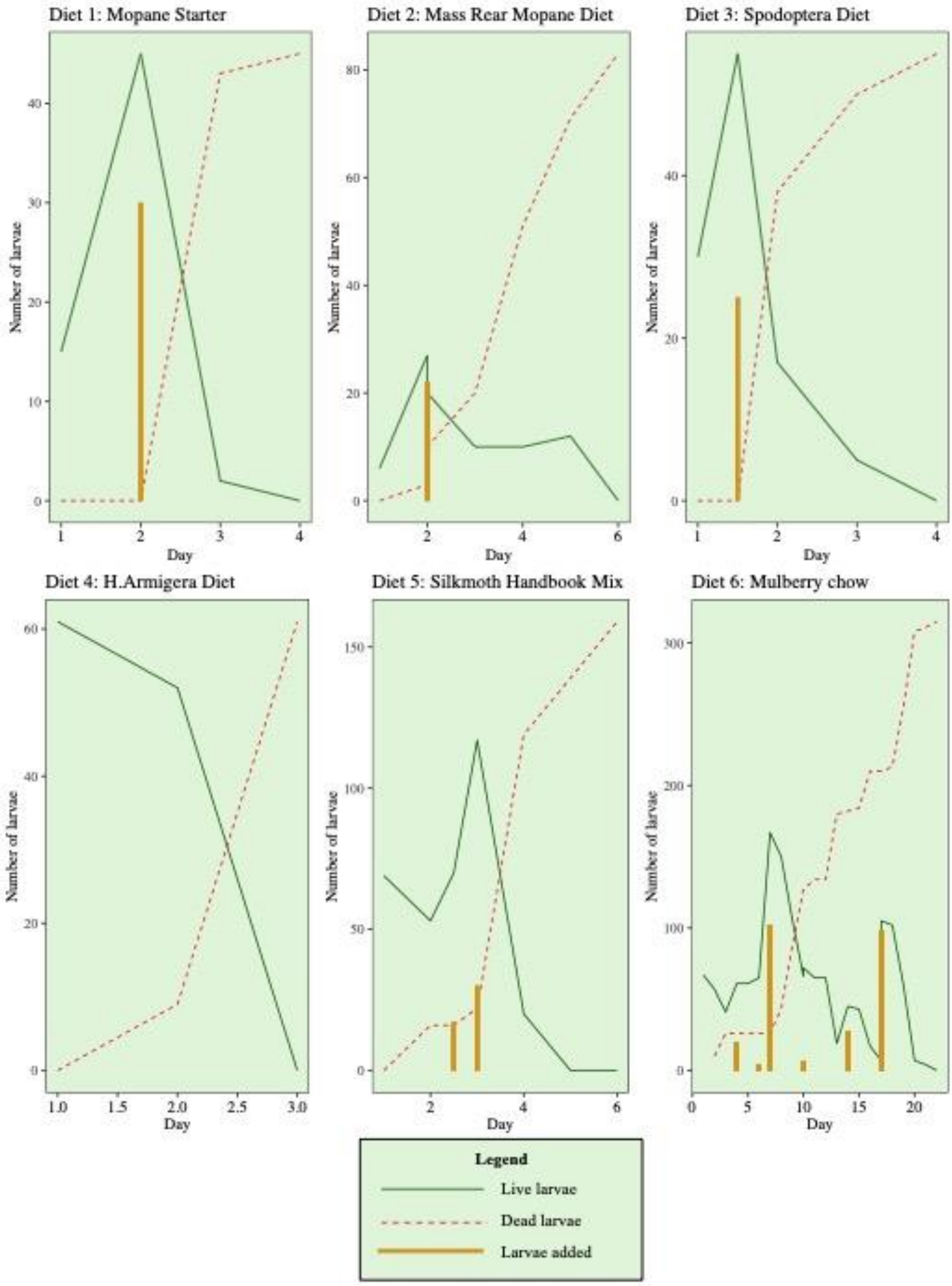

Figure 32. Graphs showing the fate of larvae in field lab trials testing different diets.

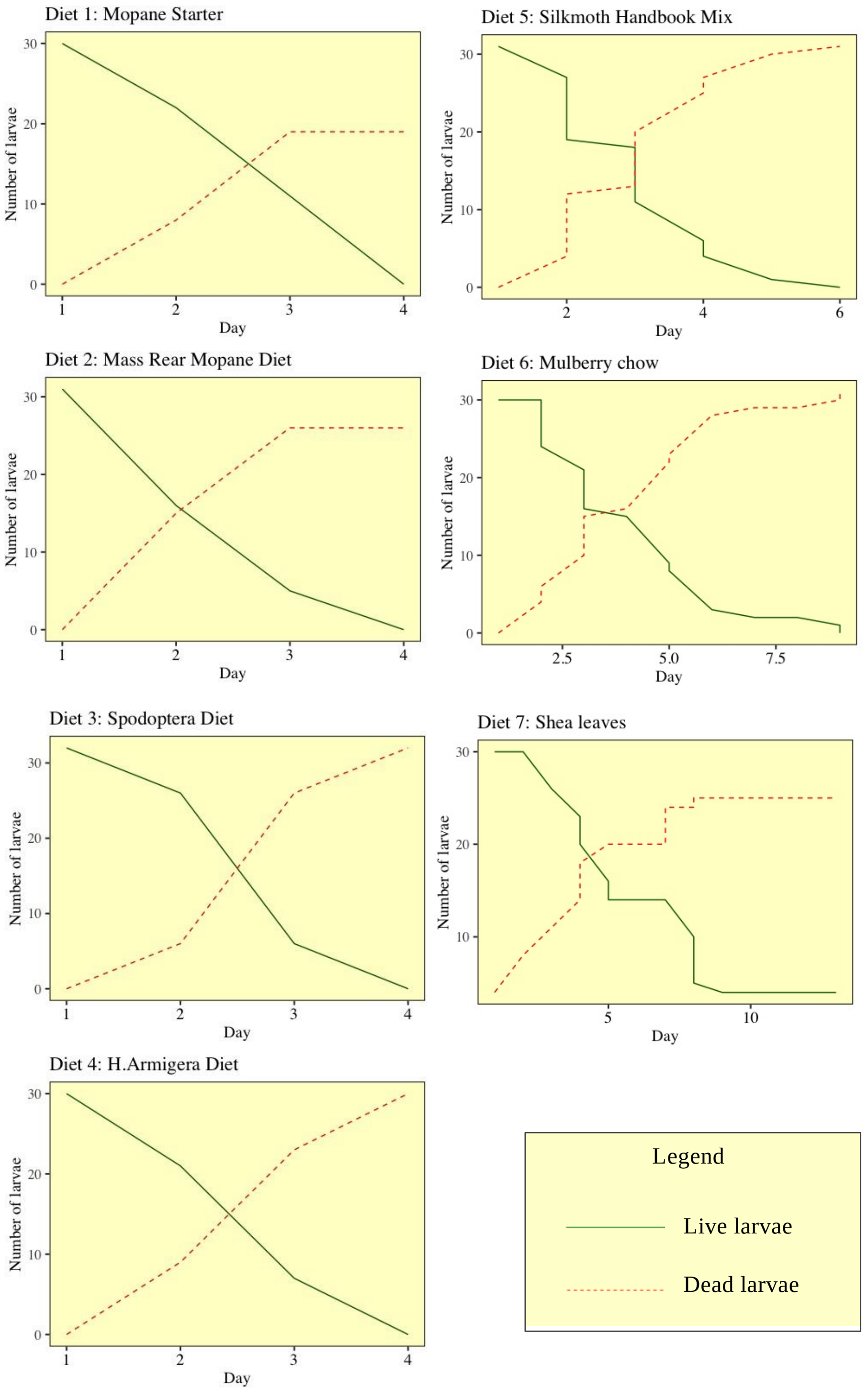

Figure 33. Graphs showing the fate of larvae in university lab trials testing different diets.

The probability of survival for caterpillars living on all diets dropped rapidly during the experimental period, albeit with a slightly shallower curve – indicating a slower drop in survival probability over time – for caterpillars fed on Mulberry Chow and on the control diet of shea leaves (**Figure 34**).

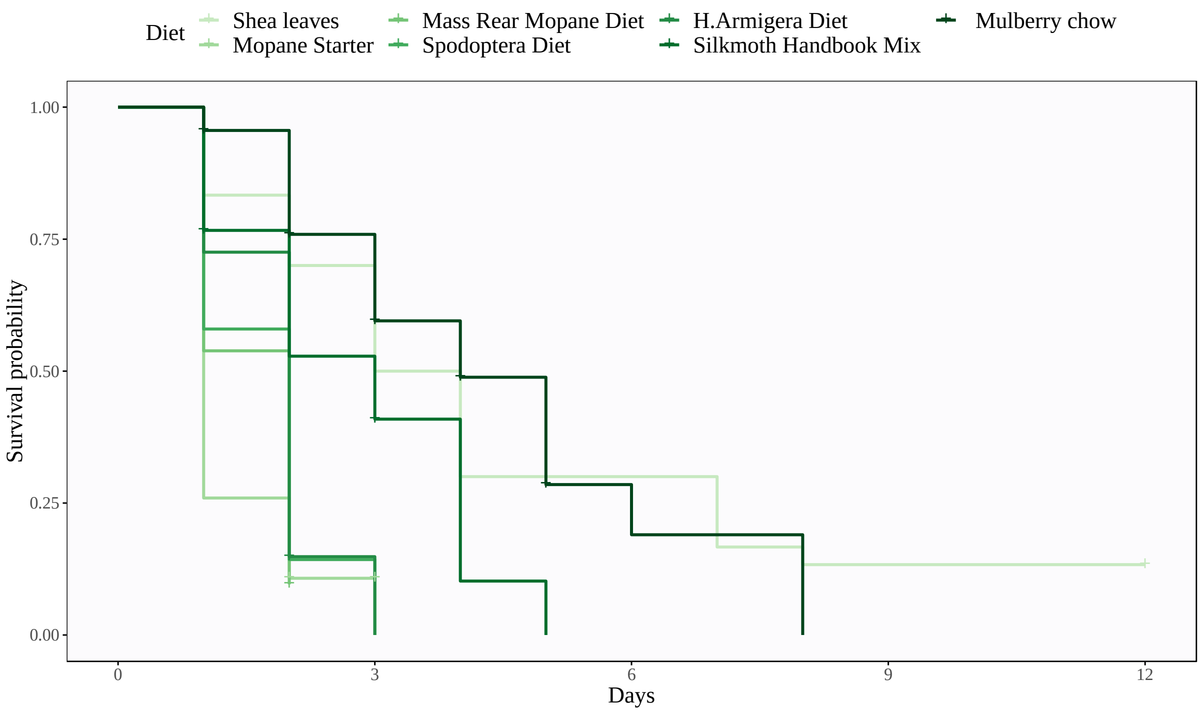

Figure 34. Graph showing Kaplan-Meiers curves estimating the survival probability for caterpillars fed on different diets, in both lab and field settings.

All diets except mulberry chow significantly raised the risk of death compared to the control diet of shea leaves (**Figure 35**). The university lab also significantly raised the risk of death compared to the field lab for caterpillars, regardless of diet (**Figure 35**). However, it is important to note that no reliable data were recorded for the control diet in the field lab setting.

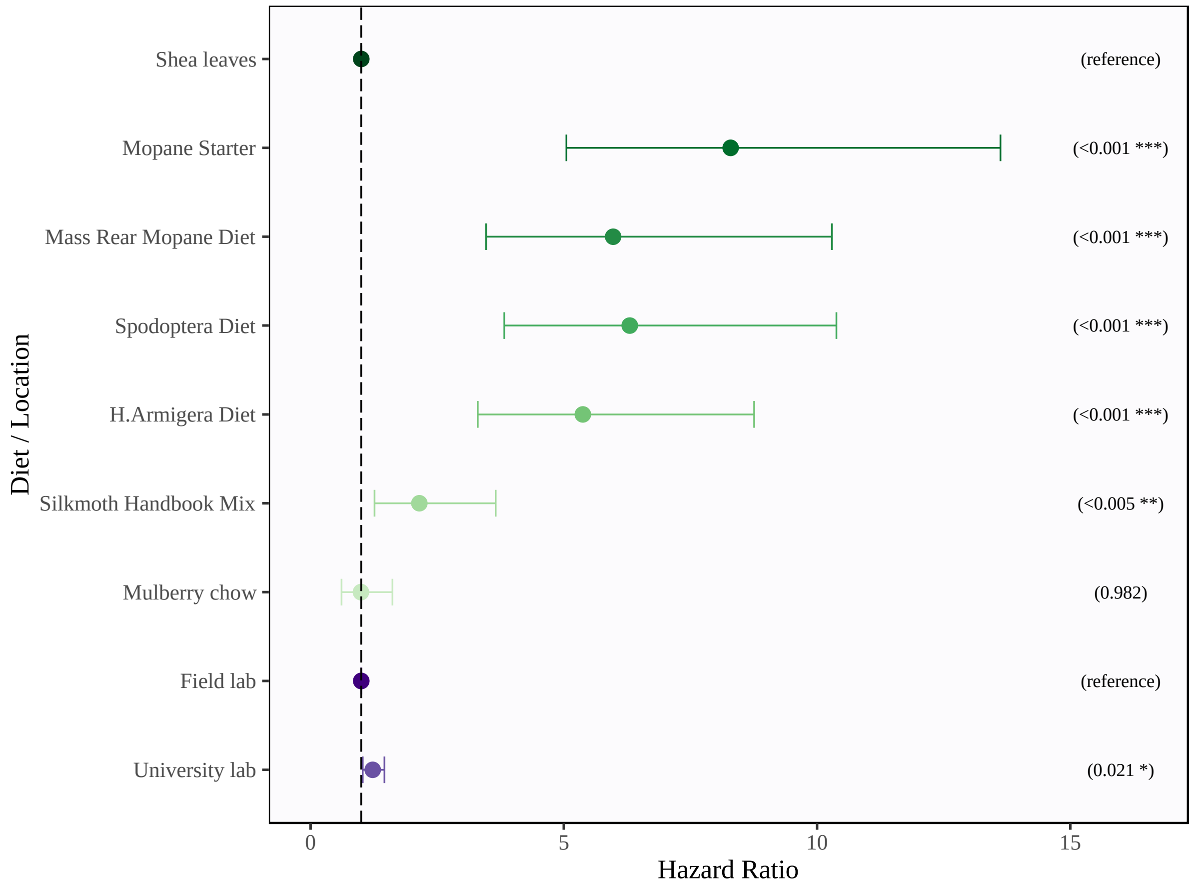

Figure 35. Forest plot showing the hazard ratios (relative risk of death) for caterpillars reared on different diets (greens) and in different settings (purples). Lines indicate 95% confidence intervals. P values are listed on the right hand side and indicate a significant difference from the reference value. The reference value is shea leaves for diet and field lab for setting.

C4. Discussion

The results suggest that none of the tested artificial feeds is suitable as a rearing substrate for the edible caterpillar *C. butyrospermi.* However, the control diet in the university lab was also unsuccessful, and was not recorded in the field lab setting; we failed to replicate previous trials that successfully reared young larvae to maturity on fresh shea leaves (Rémy et al. 2018). High temperatures could have contributed to the failure of the trials: Rémy et al. give 23-30°C as parameters for *C. butyrospermi* survival; both the field and university labs recorded temperatures exceeding this (39.7°C and 32°C respectively). Previous experiments have found that exposure to heat stress can cause mortality in Lepidopteran larval development (York and Oberhauser 2002). However, these temperatures are not uncommon in the landscapes in which shea caterpillars are found naturally. Also, survival rates were higher in the field lab despite higher recorded temperatures. Therefore there is likely to be another variable present in these enclosed systems that had a severe negative effect on survival compared to the caterpillars' wild habitat.

One variable that may have contributed to the failure of the trials could have been the handling of the caterpillars. Both trials were run by individuals with no prior experience rearing Lepidoptera, and young larvae are particularly fragile (Gardiner 1982). A single day of training and ad hoc monitoring may not have been adequate.

Mulberry chow was the only artificial diet that did not differ significantly from the control diet in terms of survival rate. This is a promising result, as mulberry chow does not use shea leaves as its base, but instead uses mulberry leaves. This suggests that it may be possible to rear the specialist feeder *C.butyrospermi* on a diet based on mulberry leaves, which is a profitable and sustainable strategy for rearing *B. mori* (Hamamura 2001). However, it will first be important to understand the parameters that cause a high death rate amongst even caterpillars fed on shea leaves in an enclosed system.

Overall, it is unclear why the trials met with such little success compared to previous trials with the same caterpillar. Future experiments should ensure that individuals running the trials receive more than a day's training, and that all trials are regularly monitored by a person with prior experience rearing Lepidoptera.