AN INTEGRATIVE APPROACH TO MOSQUITO-BORNE DISEASE IN URBAN AREAS

by

MICHELLE V. EVANS

(Under the Direction of John Drake and Courtney Murdock)

Mosquito-borne diseases pose a threat to urban populations around the world. The process of urbanization involves changes to the biophysical, ecological, and socio-political landscape, all of which have important implications for mosquito populations and the diseases they vector. In this dissertation, I apply an integrative approach to explore how spatial patterns in urban landscapes may translate to spatial patterns in mosquito-borne disease by considering urbanization through an interdisciplinary lens. I considered the effects of microclimate, specifically temperature, on mosquito abundance, dengue transmission, and competitive interactions between two invasive mosquito species using an ecological approach. Then, I consider this question from an approach grounded in political ecology, aiming to understand the socio-political context in which urbanization happens for a more in-depth

understanding of mosquito-borne disease.

INDEX WORDS: [mosquito-borne disease, dengue, Aedes, urbanization, Anopheles]

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Dedication

To my family,

my parents, who encourage me in each new thing I undertake, Kevin, who supports me through the ups-and-downs of science, and Wahala, who always has time for a walk.

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It seems odd to present a dissertation as one's personal triumph, given how much of science, this dissertation included, is truly a team effort. I'd like to thank both of my advisors, John Drake and Courtney Murdock, and the rest of my committee - Rico Holdo, Jenn Rice, and Jerry Shannon - for asking the hard questions and challenging me throughout my time in graduate school. I'd especially like to thank my advisors for giving me the freedom to try new things in a big way, from setting up an experiment with 75 treatments to starting collaborations on the other side of the world. Your confidence in me inspired me when I couldn't always find the confidence in myself.

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Introduction

Nature, destroyed as such, has already had to be reconstructed at another level, the level of "second nature" i.e. the town and the urban. The town, anti-nature and non-nature and yet second nature, heralds the future of the world, the world of the generalized urban.

- The Survival of Capitalism: Reproduction of the Relations of Production Henri Lefebvre (1976)

The seductive implications of industrial production threaten to render us blind to monstrosity in all its forms by covering over both lively and destructive connections. They bury once-vibrant rivers under urban concrete and obscure increasing inequalities beneath discourses of freedom and personal responsibility. Somehow, in the midst of ruins we must maintain enough curiosity to notice the strange and wonderful as well as the terrible and terrifying.

- Art of Living on a Damaged Planet

Anna Tsing (2017)

By 2007, over 50% of the world's population lived in Lefebvre's future of the "generalized urban", and this proportion is expected to continue growing (United Nations 2018). Cities, which Lefebvre defines as the "anti-nature", have become the new norm. Defining the urban as a place separate from nature, and therefore produced by "unnatural" (e.g. human) processes, enables us to consider "the social, cultural, and political relations through which material and biophysical entities become transformed in the making of often unequal cities" (Lawhon, Ernstson, and Silver 2014), rather than focusing solely on the biophysical transformations themselves. As Lefebvre suggests, the urban is not a purely socio-political entity removed from nature, but a "second nature": a new form of entanglement between people and their environment, a socio-ecological system (Pickett et al. 2001). The word entanglement includes interactions in the conventional ecological sense, but also "the unfolding, often incidental attachments and affinities, antagonisms and animosities that bring people, nonhuman animals, and things into each other's world" (Nading 2014).

One such entanglement is that between humans, mosquitoes, pathogens, and the surrounding environment. This entanglement stretches back millenia, with evidence of the malarial parasite, *Plasmodium falciparum*, in the remains of Ancient Egyptians from over 4000 years ago (Nerlich et al. 2008). Indeed, mosquitoes in their current forms are the result of evolutionary and social processes arising from this entanglement that have resulted in phenomena such as the adaptation of the *Aedes aegypti* mosquito to human-modified environments (Brown et al. 2014) and anthropophilic blood feeding behaviors (Harrington, Edman, and Scott 2001. Human society has also been shaped by our interaction with mosquitoes. For example, the distribution of yellow fever in the Carribean determined the course of European colonization and subsequent independence movements (McNeill 2010), and malaria contributes to the self-reinforcing poverty-disease trap in certain tropical low-middle income countries (LMICs) (Bonds et al. 2010). Currently, there are over 350 million cases of mosquito-borne disease annually and they are unevenly distributed across the globe, with the majority in LMICs in the tropics (Franklinos et al. 2019). Within a city, the burden of mosquito-borne disease is also not evenly distributed, and there are many examples of intra-urban heterogeneity in the prevalence of mosquito-borne diseases (e.g. Lippi et al. 2018; Stewart-Ibarra et al. 2014; Misslin et al. 2016; Santos-Vega et al. 2016; Farinelli et al. 2018; Kabaria et al. 2016). Intra-urban heterogeneity in mosquito-borne disease burden is the result of the interaction of spatial patterns in humans, mosquitoes, and disease, which often in turn feedback and influence each other. Of the three, mosquitoes present an interesting focus for urban ecology as they easily bridge the social and ecological environments of a city and can be studied from an ecological lens, similar to other non-human organisms. In addition, public health interventions in cities rely on the control of mosquito populations through technologies such as larval source reduction, insecticide fogging, and sterile insect technique (Fonseca et al. 2013; Lees et al. 2015). Recent work has called attention to mosquito ecology, as opposed to simply abundances, and led to the consideration of the mosquito vector as "more than just a flying syringe" (Cator et al. 2018), implying that a deeper understanding of mosquito ecology across an urban landscape is necessary to understand mosquito-borne diseases across a landscape. However, investigations of mosquito dynamics in urban areas must also acknowledge the entanglement of mosquitoes with their living and non-living surroundings and include multiple perspectives.

Drivers of intra-urban heterogeneity in mosquito communities

This section provides a brief overview of the current state of the field regarding the drivers of intra-urban heterogeneity in mosquito communities, which have been extensively reviewed in recent publications (e.g. Gubler 2011; LaDeau et al. 2015; Eder et al. 2018; Weaver 2018). Drivers can be categorized into abiotic environmental factors (e.g. climate, habitat availability), biotic interactions (e.g. competition, host community composition), and socioeconomic changes accompanied with increasing urbanization (e.g. increased population densities, socio-economic inequalities, human mobility and movement). Abiotic environmental factors, such as temperature or habitat availability, can directly influence mosquito population abundances. Mosquito populations are also influenced by biotic factors, such as predation or competition, that may limit or facilitate population growth rates. The community composition of mosquitoes (i.e. which species are present and in what ratios) is also dependent on similar abiotic and biotic factors, as well as the diversity of host species that are present across the landscape.

As small-bodied ectotherms, mosquitoes are particularly sensitive to changes in temperature and their responses to temperature are often unimodal. Globally, this determines the ranges of mosquito species and the diseases they carry (Sinka et al. 2011; Rochlin et al. 2013; Kraemer et al. 2019; Mordecai et al. 2019, and presents a complex puzzle in the face of climate change due to the non-linear response to temperature (Tjaden et al. 2018; Ryan 2020). At a finer scale, temperature can influence the abundance of mosquitoes and their functional traits and behavior across a landscape (Murdock et al. 2017; Townroe and Callaghan 2014; Paaijmans and Thomas 2011). Generally, cities are warmer than their surrounding areas, due to the urban heat island effect, whereby relatively high amounts of impervious surface and heat-producing transport and buildings can cause city centers to be over 6 °C warmer than nearby rural areas (Peng et al. 2012). However, urban areas themselves are also highly heterogeneous, and intra-urban temperature differences can be just as significant as urban-rural differences (Buyantuyev and Wu 2010). This intra-urban heterogeneity can lead to heterogeneity in mosquito populations and disease transmission risk that is difficult to predict, given temperature's strong, but non-linear, effects on multiple functional traits.

Mosquito population dynamics are also affected by the biotic context of the urban ecosystem, especially species interactions such as competition. In the larval habitat, mosquitoes compete with conspecifics and other mosquito species. In fact, the fine-scale distribution of two invasive mosquito species, Ae. aegypti and Aedes albopictus, in cities and residential areas of the southeastern United States is partially determined by their interspecific competition (Lounibos and Juliano 2018). Aedes species develop in man-made or natural containers where limited resources can lead to high competitive pressure, but competition has been seen in other mosquito genera as well (*Culex*: Reiskind and Wilson 2008, *Anopheles*: Paaijmans et al. 2009). Studies have also assessed competition across-genera in other container breeding species, especially between *Culex quinquefasciatus* and *Aed. albopictus* (Bowden 2016; Saunders 2019). In addition to the direct effects of competition on larval survival and development, competition during the larval stage can result in carry-over effects on adult phenotypes (reviewed in Evans, Newberry, and Murdock 2020. These carry-over effects can influence adult body size, a proxy for fecundity, (Armistead et al. 2008; Muturi et al. 2011b; Chandrasegaran et al. 2018; Ezeakacha and Yee 2019; Moore and Fisher 1969), adult mortality (Reiskind and Lounibos 2009; Alto et al. 2012), and vector competence (Alto et al. 2005; Alto et al. 2008; Bevins 2008). Further, the magnitude and direction of the effect of competition on mosquito life-history traits can be dependent on abiotic factors, such as temperature Muturi et al. 2011a; Muturi, Blackshear, and Montgomery 2012 or resource type and quality (Reiskind, Zarrabi, and Lounibos 2012; Murrell and Juliano 2008).

A combination of biotic and abiotic factors cited above can lead to changes in mosquito community composition across an urban gradient (Hunt, Galatowitsch, and McIntosh 2017). In general, mosquito communities are less species rich and contain a higher percentage of anthropophilic mosquitoes in areas with higher anthropogenic disturbance as measured by biophysical metrics (e.g. higher impervious surface, human population density, lower NDVI, etc.) than less disturbed areas (Gardner, Lampman, and Muturi 2014; Johnson, Gómez, and Pinedo-Vasquez 2008; Norris 2004; Loaiza et al. 2017). This can be due to shifts in host community composition or habitat types. Host community composition changes across an urban gradient, becoming more homogenous and dominated by humans in more urbanized areas (Faraji et al. 2014; Muñoz et al. 2011). The availability of non-human hosts, such as birds, rats, or livestock, can also alter mosquito biting behavior and lead to changes in mosquito community composition based on species' host preferences (Goodman et al. 2018; Burkett-Cadena et al. 2013; Lafferty et al. 2018). The types of habitat may also shift from more permanent water bodies to a higher proportion of containers (Wilke et al. 2019), providing more habitat for artificial container-ovipositing species, which are often important vectors of disease (Yee et al. 2012). These resulting changes to mosquito community composition can create a mosquito community consisting of competent vectors disease, leading to higher risk of disease in urbanized areas.

Mosquito dynamics can also be influenced by the socio-political context of a city, often through indirectly affecting the biophysical landscape. Across an urban landscape, mosquito habitat may shift in both type and quantity (Wilke et al. 2019). For example, several studies have found higher numbers of non-functional water containers in low socio-economic neighborhoods than in high socio-economic neighborhoods resulting in higher abundances of pest mosquitoes in low socio-economic neighborhoods (Dowling et al. 2013; Kumar et al. 2014; Little et al. 2017; LaDeau et al. 2013). Similarly, the shift from natural habitats to artificial habitats across a rural-urban gradient can result in a decrease in mosquito species diversity across this same gradient (Zahouli et al. 2017; Honnen and Monaghan 2017; Valdez 2017). For example, building construction sites, particularly at the early phases of construction, contain artificial habitats that are preferred by mosquito vectors of human diseases, such as Ae. aegypti and Culex quinquefasciatus, and have higher abundances of these mosquitoes than nearby areas (Wilke et al. 2018). Host community composition can also be related to socio-economic factors. Lower socio-economic neighborhoods may have higher densities of rodent pests, such as rats, due to high population densities, older infrastructure, and inadequate public sanitation services (Feng and Himsworth 2014), leading to different host feeding behaviors across neighborhoods (Goodman et al. 2018). Livestock keeping patterns may also differ across a city, and can impact mosquito host biting behaviors (Lindahl et al. 2012). Urban microclimate is entangled with spatial patterns of race and socio-economic status (Mitchell and Chakraborty 2018; Pearsall 2017), partly due to racist and colonial histories of disinvestment (Wilson 2020). Local politics and tax revenues can determine the type and extent of vector control efforts undertaken by the state (Tedesco, Ruiz, and McLafferty) 2010) and cultural norms regarding individual vs. state responsibilities for management hazard risks can limit or facilitate public vector control efforts (vonHedemann et al. 2017; Shaw, Robbins, and III 2010). The abiotic and biotic drivers of mosquito populations and communities are themselves dependent on the socio-political context of the city, and their spatial patterns cannot be understood in a vacuum.

Interdisciplinary research and mosquito-borne disease

Clearly, changes to the biophysical environment within which mosquito populations exist cannot be separated from the socio-political context of the city. Yet, only around 3% of the work on dengue and chikungunya, two *Aedes*-borne diseases, involves a social science approach (Reidpath, Allotey, and Pokhrel 2011). Of those that do include social sciences, most studies are socio-epidemiological, identifying determinants of health, but rarely engaging with critical social theory (Allotey, Reidpath, and Pokhrel 2010). As a result, "our understanding and management of neglected tropical diseases (NTDs) is inevitably reduced to a strategy that relies on a repetitive, reductionist, flat-world science to overcome an acknowledged complex system" (Reidpath, Allotey, and Pokhrel 2011). We need social science approaches to mosquito-borne diseases and other NTDs to consider inequalities and vulnerabilities in the broader context of social justice and power, especially in urban environments, or risk reproducing these same inequalities. For mosquito-borne diseases, whose emergence and dynamics are closely tied to the ecological environment, there is also a need for interdisciplinary or biosocial approaches that can identify feedbacks and connections between the disciplinary silos (Barry 2014; Biehl and Petryna 2013).

Given the clear entanglement of humans and mosquitoes in determining disease dynamics, why is there such a paucity of interdisciplinary research? Many mosquito-borne diseases, with malaria a notable exception, are classified as neglected tropical diseases, a group of infectious diseases that primarily affect low and middle income countries (LMICs) in the tropics or sub-tropics. A relatively new term, NTDs gained traction as part of the Millenium Development Goals strategies for "Quick Wins" introduced in 2004 (Parker and Allen 2014), based on the premise that eliminating NTDs can reduce poverty in LMICs (Bonds et al. 2010; Molyneux, Hotez, and Fenwick 2005). This was followed by large-scale investment in public-private initiatives by private corporations and large international non-governmental organizations, led primarily by the Gates Foundation, including its Grand Challenges in Global Health initiative, a granting program for scientists working on technological solutions to global health problems (Allen and Parker 2012; Birn 2005). The ontologies of disease are created through its study, treatment, and prevention, and knowledge production thereby contributes to our conceptual understanding of what constitutes the disease (Mol 1999). In this sense, knowledge production is not simply accumulating evidence or 'knowing', but also an "act of doing" (Chandler and Beisel 2017), defining what types of knowledge are valid and worthwhile and what types of action or intervention are pragmatic (Kelly and Lezaun 2013). The influx of funding via the Grand Challenges program, which focused on technological innovation and a "magic bullet" solution, therefore changed the global narrative surrounding the causes and solutions to NTDs and led to "a narrowly conceived understanding of health as the product of technical interventions divorced from economic, social, and political contexts" (Birn 2005). This approach to vector-borne diseases, amongst other NTDS, is not new to the 21st century. Fred Soper's infamous yellow fever and malaria eradication campaigns in the Panama Canal, Brazil, and Egypt drew on the same narrative of colonial states' technological and military provess to control the natural, "savage" environments of the colonies, a narrative that was in turn used to reinforce state power (Mitchell 2002; Nading 2013). By placing mosquito-borne diseases squarely in the realm of physical and environmental sciences, colonial powers leveraged public health interventions to bolster their own techno-political institutions and legitimacy (Mitchell 2002). Therefore, the present lack of interdisciplinary approaches to mosquito-borne diseases is not simply coincidental, but a legacy of the history of colonial, or 'tropical' medicine and the current landscape of funders and researchers that reproduces North-South colonial power dynamics in NTD research (Green 2019).

Hence, the call for interdisciplinary work in the study of mosquito-borne diseases addresses not only the need for an approach that can adequately describe the complexities and feedbacks of a socio-ecological system, but is also an explicit rejection of the notion of "neutral" science (Harding 1995). The studies included in this dissertation were conducted with an awareness of this legacy of NTD research and the historical and current primacy of the medical and biological sciences in infectious disease research in general (Leach and Scoones 2013). As such, it relies on an integrative approach that stresses epistemological pluralism and embraces non-commensurability between epistemological perspectives to provide "openings for further research and/or action that no single perspective could yield in isolation" (Hirsch and Brosius 2013). This is achieved through the consideration of multiple epistemologies, especially with regards to how values are measured and aggregated, whose voices are included in the process, and the political power dynamics surrounding knowledge production and the issue at hand. Each chapter relies on a different perspective or approach to understanding spatial heterogeneity in mosquito-borne disease in urban areas. Given my primary discipline of ecology, the majority of chapters are based in a natural science approach. Because of this, I explicitly challenge the application of a unidisciplinary, quantitative, positivist approach to mosquito-borne disease in other chapters by drawing on feminist political ecology, which attempts to create a "boundary zone between positivist and critical paradigms" (Rocheleau 1995). Each epistemology is a lens through which to approach the research question, and the combination of all of these lenses offers a more comprehensive, though still partial, understanding of mosquito-borne disease in urban areas.

Overview of Chapters

In this dissertation, I use an integrative framework to investigate the drivers of spatial patterns in mosquito-borne diseases in urban areas across two urban field sites, Athens, Georgia, USA and Sarjapur, Bengaluru, India. Athens is a relatively small urban center, with a total population of approximately 127,000 across an area of 306 sq. km. While the city center is highly built up, with impervious surface values nearing 100% in places, the periphery of the city consists primarily of residential and agricultural land, and the overall average impervious surface is only around 10% (Evans et al. 2019). In contrast, Bengaluru is one of the largest cities in India, with a population of 12.37 million over a 2,196 sq. km.

located in the southeast of the city, approximately 25 km from the city center, and had a population of 11,800 in 2011 (Census of India 2011). Both towns exhibit a heterogeneous pattern of urban development within a matrix of relatively low impervious surface. Sarjapur, in particular, is in the midst of rapid urbanization due to its location on the periphery of the growing city of Bengaluru and the recent approval of two development projects within its bounds. The patterns of urbanization in each site provide a natural study site for exploring how the different hypothesized drivers of mosquito-borne disease change across an urban gradient and what the potential consequences are for mosquito dynamics. Each chapter of this dissertation examines a potential relationship between one aspect of urbanization and one aspect of mosquito-borne disease, following proposed causal pathways grounded in different research fields or epistemologies (Fig.).

Chapters 2 and 3 focus on the dynamics of the *Aedes albopictus* mosquito in Athens, GA and population responses to changes in microclimate across an urban gradient. Ae. albopictus is an invasive mosquito found across the southeastern US that is a competent vector of several arboviruses, particularly chikungunya (Benedict et al. 2007). These two chapters are primarily focused on changes in microclimate due to urbanization, particularly the urban heat island effect. While there are many laboratory studies that investigate the effect of temperature on mosquito life history traits in the lab, few have validated these results in the field. In **Chapter 1, we test these hypothesized relationships using a field experiment to explore the impact of fine-scale shifts in microclimate and larval habitat on** *Ae. albopictus* **population abundance across an urban gradient**. In addition to the direct effects of temperature on mosquito life-history traits, adult mosquito phenology can be shaped indirectly by the environment at earlier life-stages, a phenomenon known as carry-over effects. In order to understand the full effect of changes in urban microclimate on disease transmission, we need to understand both the direct and indirect effects of temperature on mosquito life-history traits, such as vector competence. In Chapter 2, we expand on the previous chapter by investigating how the microclimate differences observed in Chapter 1 may carry-over from the larval to adult stage of *Ae. albopictus* to influence dengue-2 vector competence.

Chapters 3, 4, and 5 are concerned with the mosquito species and urban environments of Sarjapur, India. In Chapter 3, we continue to explore the ecological dynamics of mosquitoes in cities by focusing on temperature-dependent competition between two urban mosquito vectors of public health importance, Ae. aegypti and **Anopheles stephensi.** Ae. aegypti and An. stephensi are the primary vectors of urban dengue and malaria in India, respectively, and both species use artificial containers as larval habitat (Thomas et al. 2016). An. stephensi is currently expanding its range into northern and sub-saharan Africa, where it could facilitate the spread of malaria into urban areas (Sinka et al. 2020). Chapter 3 uses a community ecology approach to consider the combination of abiotic and biotic factors on mosquito communities through a study of temperature-dependent competition between these two species in the lab to better understand how these species interactions might determine each species' distribution in a city. Chapter 4 introduces the socio-political drivers of spatial patterns in mosquito populations via a qualitative analysis of water access and mosquito burdens across Sarjapur. In Sarjapur, municipal water access is unevenly distributed and households rely on a combination of private and public "water compensation practices" (Truelove 2011) to meet their water needs. Some of these practices involve water storage, which can create habitat for mosquitoes, thereby influencing the spatial distribution of mosquito populations. This study considers how the water access practices available to each household are dependent on individuals' situatedness within the local socio-political context, and therefore how these practices used to navigate the political process may indirectly influence mosquito-borne disease. Finally, Chapter

5 combines the epistemological lenses of the previous four chapters through an integrative analysis of mosquito dynamics in Sarjapur, utilizing methods and frameworks across both natural and social science disciplines to explore how the entanglement of humans and mosquitoes changes across an urban landscape.

Figures



Figure 1: Conceptual diagram of dissertation chapters. Two epistemological lenses (ecology and political ecology) explore questions related to the fields' conceptualizations of urbanization and how these changes may result in unequal burdens of mosquito-borne disease.

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Chapter 1

Microclimate and larval habitat predict adult *Aedes albopictus* abundance in urban areas

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Abstract

The Asian tiger mosquito, *Aedes albopictus*, transmits several arboviruses of public health importance, including chikungunya and dengue. Since its introduction to the United States in 1985, the species has invaded over forty states, including temperate areas not previously at risk of Aedes-transmitted arboviruses. Mathematical models incorporate climatic variables in predictions of site-specific Ae. albopictus abundances to identify human populations at risk of disease. However, these models rely on coarse resolutions of environmental data that may not accurately represent the climatic profile experienced by mosquitoes in the field, particularly in climatically-heterogeneous urban areas. In this study, we pair field surveys of larval and adult Ae. albopictus mosquitoes with site-specific microclimate data across a range of land use types to investigate the relationships between microclimate, density of larval habitat, and adult mosquito abundance and determine whether these relationships change across an urban gradient. We find no evidence for a difference in larval habitat density or adult abundance between rural, suburban, and urban land classes. Adult abundance increases with increasing larval habitat density, which itself is dependent on microclimate. Adult abundance is strongly explained by microclimate variables, demonstrating that theoretically derived, lab-parameterized relationships in ectotherm physiology apply to the field. Our results support the continued use of temperature-dependent models to predict Ae. albopictus abundance in urban areas.

Introduction

The Asian tiger mosquito, *Aedes albopictus*, is an invasive mosquito that became established in the United States following its introduction in 1985 (Moore 1999; Sprenger and Wuithiranyagool 1986). Ae. albopictus can transmit several pathogens of public health importance, including La Crosse (Bara, Parker, and Muturi 2016), dengue (Paupy et al. 2010; Ibanez-Bernal et al. 1997 and chikungunya viruses (Weaver and Forrester 2015). Unlike another vector of these diseases, Aedes aegypti, which originated in East Africa, Ae. albopictus originated from a temperate area of Asia and is able to survive in cooler climates than Ae. aegypti. Following initial establishment in Texas, Ae. albopictus has invaded over 40 states(Hahn et al. 2016), and models predict its range will expand as the climate warms (Ogden et al. 2014; Kraemer et al. 2019). At present, established populations of Ae. albopictus are found in the United States as far north as Connecticut and New York (Armstrong et al. 2017; Shragai and Harrington 2019), well outside the present range of Ae. aegypti. Ae. albopictus is implicated in transmission cycles of dengue and chikungunya in the Mediterranean region of Europe (Rezza et al. 2007; Vega-Rua et al. 2013), which suggests that temperate regions of the US may be similarly vulnerable.

Given the potential role of Ae. albopictus in disease transmission, it is important to understand what factors influence its abundance. Ae. albopictus is sensitive to variation in temperature due to temperature-dependent life history traits such as development rates, fecundity, and survival (Delatte et al. 2009; Alto and Juliano 2001; Farjana, Tuno, and Higa 2011). Climate or meteorological predictors are widely used in mechanistic models and statistical models (Mordecai et al. 2017; Kearney et al. 2009; Focks et al. 1993; Kraemer et al. 2015; Rochlin et al. 2013; Benedict et al. 2007). Models leverage these relationships to predict mosquito presence, population growth rates, and abundances based on temperature metrics derived from weather stations or remotely-sensed datasets. However, urban landscapes are composed of a variety of land classes (e.g. residential, developed, vegetated), which vary in their microclimates at fine spatial scales less than 1 x 1 km (Cator et al. 2013; Kumar et al. 2018; Scott et al. 2017). This difference in microclimate can alter mosquito population growth (Li et al. 2014; Murdock et al. 2017), leading to variation in population abundances that may be missed by models that rely on coarser spatial data.

Additionally, adult abundance may be determined by the abundance of larval habitat. Ae. albopictus is fairly non-discriminate in its habitat use and larvae are found in both natural and artificial containers (Shragai and Harrington 2019; Bartlett-Healy et al. 2012; Medeiros-Sousa et al. 2015). Several studies have found that adult abundance is positively related to the availability of larval habitats (McClure, Lawrence, and Kilpatrick 2018; Bodner, LaDeau, and Leisnham 2019). This relationship is also the basis for larval source reduction techniques widely used in vector control (Fonseca et al. 2013). Urban microclimates can co-vary with mosquito larval habitat density, which may differ in quality and quantity across urban land-use (Li et al. 2014; McClure, Lawrence, and Kilpatrick 2018). Thus, when studied independently, the relative roles of microclimate and larval habitat may be confounded.

Here, we combine field surveys of larval habitat and adult mosquito abundances with microclimate data to investigate how microclimate and the availability of larval habitat contribute to changes in adult *Ae. albopictus* abundance across an urban landscape. We aim to answer the following questions:

- Does the density of larval habitat positive for *Ae. albopictus* change across urban land classes?
- Does the abundance of *Ae. albopictus* adults change across urban land classes?
- What is the relationship between microclimate and adult abundance?
- What is the relationship between larval habitat and adult abundance?

By investigating these relationships, our results inform if and how predictive models should include microclimate variables and data on larval habitat from the field in their predictions of adult *Ae. albopictus* abundance. Further, these results can help determine whether variation in land class alters the spatial distribution of *Ae. albopictus*, and if omitting this fine-scale variation may lead to bias in models.

Methods

The study was conducted between June 2016 and December 2017 in Athens-Clarke County, GA, USA. Athens-Clarke County is an urbanized area in a matrix of rural forested and agricultural land, representing a wide range of land classes. Following previous work (Evans et al. 2018), we used an impervious surface map (NLCD) to select three replicate 30 x 30 m sites each of low (0-5%), intermediate (6 - 40%), and high (41- 100%) impervious surface (Fig. 1.1). Percent impervious surface, an accurate predictor of land surface temperature (Yuan and Bauer 2007), was chosen to ensure the sites exhibited the full range of microclimates present in the city.

Aquatic Immature Surveys

At each site, we conducted surveys of the aquatic immature stages (larvae, pupae) bi-weekly from June - December 2016 and April - December 2017 to measure the density of positive larval habitats (e.g. number of larval habitats positive for *Ae. albopictus* larvae per 100m radius site). Each site was sampled within one day, and the full sampling period of surveys took place over several days, with a sampling period referring to the week in which surveys were conducted. Study areas were defined as a 100m radius surrounding the center of the focal 30 x 30m site. Each study area was inspected for the presence of standing water (i.e. puddles, ponds, artificial containers). Each body of water was assessed for the presence of immature mosquitoes visually and using dipping methods. If immature mosquitoes were present, samples were collected from that habitat. Because adult mosquitoes were sampled concurrently with larval habitat sampling, destructive sampling could bias the adult catch rate. For this reason, we collected measures of presence or absence of *Ae. albopictus* per habitat by sampling a subset of the immature mosquitoes per habitat (ranging from 5 - 27 individuals per habitat). Immature mosquitoes were kept separated by habitat and returned to the lab, where they were placed in 50 - 100 *mL* deionized water in 8 oz. glass jars (Ball) and provided fish food (Hikari Cichlid Gold Mini Pellet) *ad libitum* to ensure high emergence rates. Larvae and pupae were reared to adulthood in an incubator (Percival Scientific) at 27 \pm 0.5 °C, 80 \pm 5 % relative humidity, and a 12:12 h light:dark photocycle. Once mosquitoes emerged, they were immediately frozen at -20 °C, separated by sex, and identified to species following Darsie and Ward (2005). A habitat was determined 'positive' for *Ae. albopictus* during a sampling period if a male or female *Ae. albopictus* mosquito was identified as emerging from the habitat.

Adult Trapping

At each site, we trapped adults either bi-weekly (during the season of highest mosquito activity, June - Nov 2016 and June - Nov 2017) or monthly (Dec 2016 - May 2017 and Dec 2017). During the period of highest mosquito activity, adult trapping was conducted within one week of immature surveys. One BG Sentinel-2 (Biogents, Germany) mosquito trap was deployed in the center of each 30 x 30m site for two consecutive trap days per sampling period. Mosquito traps were baited with a BG-Lure cartridge (Biogents, Germany) and an octenol (1-Octen-3-ol) lure inside the trap. Trapping was not conducted during precipitation events, and traps were placed under the cover of vegetation to increase catch rates. Because *Ae. albopictus* is a day biting mosquito, the traps were run (with a battery powered fan) from the hours of 06:00h to 22:00h. After each trap day, catch bags were collected and replaced with

a new catch bag to reduce destruction of samples. Collected adults were taken back to the laboratory, frozen in a -20 °C freezer, and separated by sex and identified to species following Darsie and Ward (2005). Abundances for both trap days were combined to calculate the total abundance for that sampling period. The date of that sampling period is defined as the day on which the second catch bag was collected.

Microclimate Variables

Within each 30 x 30m site, we evenly distributed six data loggers (Monarch Instruments, Amherst, NH, USA: Radio Frequency Identification (RFID) Temperature Track-It Logger) to measure microclimate (e.g. site-specific climatic variables). Data loggers were placed in full shade under vegetation, approximately 0.9 m above the ground. The loggers recorded instantaneous temperature and relative humidity at ten-minute intervals. From the tenminute data, we calculated daily minimum, mean, and maximum values for both temperature and relative humidity for each logger. These values were then averaged across all six loggers for each site. Intra-site variability amongst loggers was low, with an average of 0.402 °C and 3.239 % relative humidity variability within a site.

Data Analyses

To determine if the density of positive Ae. albopictus larval habitat differed across land class, we used a generalized linear mixed model (GLMM) to test for the effect of land class on the density of positive larval habitats, including site as a random effect. The model included the week number of the study period as a basis-spline (B-spline) function to account for seasonal differences in mosquito catch rates. The B-spline function allows a curve to be fit using maximum likelihood without pre-specifying a function (de Boor 2001). A similar model was used to explore the effect of land class on Ae. albopictus adult abundance, again including site as a random effect and the week number of the study period as a B-spline function. Both models used a negative binomial distribution in which the variance increases quadratically with the mean (Eqn. 1.1):

$$Var(Y) = \mu + (\phi * \mu^2)$$
 (1.1)

where μ is the mean and ϕ is the dispersion parameter of the distribution (Hardin and Hilbe 2012). Models used a logarithmic link function. The statistical significance of land class' effect was assessed by comparing fitted models to a null model that did not include land class as a predictor variable using a likelihood ratio test.

We used univariate GLMM's to investigate the effect of the microclimate variables on the density of positive larval habitat and adult abundance. We chose to use univariate analyses because of high correlation (r > 0.75) between variables of a similar measurement, such as between minimum and maximum temperature. Further, a multivariate regression found no evidence of interactions between temperature and relative humidity for either the density of positive larval habitat or the adult abundance (Table 1.3). Temperature and relative humidity are interdependent, and our field-based study design is unable to control for this collinearity as could be done in a laboratory setting. Microclimate variables were fit using a B-spline function to allow for non-linear relationships and site was included as a random effect. All models were fit with the quadratic variance form of the negative binomial distribution described above and a logarithmic link function. We averaged each microclimate variable over the seven days prior to surveying to account for the fact that captured mosquitoes likely developed and emerged within that time period. We explored using two different lag widths, seven and fourteen days, in the models. Resulting models did not differ significantly, and so a lag of 7 days was used. This agrees with prior work in the same system that found

mosquito development rates to range from 7 - 10 days during periods of high mosquito activity (Murdock et al. 2017). This resulted in the following variables: mean weekly temperature and relative humidity, minimum weekly temperature and relative humidity, and maximum weekly temperature. Maximum weekly relative humidity was excluded from the analysis because 226 out of 234 trap periods had a maximum value of 100% relative humidity. We included the day-of mean relative humidity value in models of adult abundance to control for mosquito activity on that trap day. We assessed the statistical significance of each microclimate variable by comparing fitted models to a null model that did not include the variable as a predictor variable using a likelihood ratio test.

We also tested for the effect of the density of positive *Ae. albopictus* larval habitat (the number of larval habitats that had *Ae. albopictus* larvae present per site) on adult abundance within a site and sampling period. A GLMM was fit including the density of positive habitats as a predictor variable and site as a random effect. We fit the model with the same negative binomial distribution and logarithmic link function as described above.

All GLMMs were fit using the glmmTMB package in R version 3.5.2 (Brooks et al. 2017; Team 2018). Scaled residuals of the models were inspected for overdispersion and uniformity using the DHARMa package (Hartig 2019). Code and data to reproduce analyses are deposited on the figshare repository (https://figshare.com/s/8ea9037a5f39bd4a4961).

Results

A total of 1107 adult female *Ae. albopictus* mosquitoes were sampled from May 2016 -December 2017, encompassing 468 trap nights over two seasons of mosquito activity. This resulted in 26 adult sampling events for each of the nine sites, or 78 sampling events per land class. We sampled each site for larval habitat a total of 21 times and found 217 habitats positive for Ae. albopictus across all nine sites. While 92.57% of adult mosquitoes sampled were Ae. albopictus, the second and third most common species were Culex quinquefasciatus (5.45%) and Aedes triseriatus (0.92%). Similarly, Cx. quinquefasciatus and Ae. triseriatus were found in 61 and 36 larval habitats, respectively.

Land Class and Season

The density of larval habitats positive for Ae. albopictus was highly seasonal, peaking in June - August of both years (Fig. 1.2). The best fitting B-spline used a three-degree polynomial, and the effect of sampling week was significant ($\chi^2 = 37.023$, df = 3, p-value < 0.001). While suburban sites tended to have a higher density of positive larval habitat than rural and urban sites, this difference was not significant. A null model without land class as a predictor variable was not significantly different from the full model ($\chi^2 = 4.34$, df = 2, p-value = 0.110) and predictive performance was similar ($R_{NULL}^2 = 0.503$, $R_{FULL}^2 = 0.483$).

We found evidence of very strong seasonality in adult Ae. albopictus density across all sites, with densities peaking in July and August of both years (Fig. 1.3). There was a significant effect of the sample week on adult density ($\chi^2 = 112.050$, df = 4, p-value < 0.001) and the best fitting B-spline had a four-degree polynomial. There was no evidence for a difference in adult Ae. albopictus density across land class. The null model without land class as a predictor variable was not significantly different from the full model ($\chi^2 = 0.602$, df = 2, p-value = 0.740) and performed similarly ($R_{NULL}^2 = 0.813$, $R_{FULL}^2 = 0.813$).

Microclimate and Larval Habitat Density

Univariate analyses revealed a significant, non-linear relationship between all microclimate variables and the density of positive *Ae. albopictus* habitat (Table 1.1, Fig. 1.4). The density of positive larval habitat increased with increasing minimum, mean, and maximum

temperatures (Fig. 1.4). Larval habitat increased with increasing minimum relative humidity until approximately 60% relative humidity, after which increasing relative humidity was associated with fewer larval habitats (Fig. 1.4). The relationship between mean relative humidity and the density of larval habitats was similarly unimodal, although its optimum neared 100% relative humidity. Importantly, the functional forms of these relationships differ from those between the microclimate variables and adult abundance. This difference suggests that the effects of microclimate on oviposition behavior and habitat availability differs from the effect of microclimate on mosquito emergence and adult longevity.

Microclimate and Adult Abundance

Univariate analyses revealed that all five microclimate variables significantly influenced adult abundances (Table 1.2). The relationships between microclimate variables and adult abundance were non-linear for all variables (Fig. 1.5). Mean and minimum relative humidity had a 3rd-order B-spline fit that increased exponentially as relative humidity approached 100% (Fig. 1.5). All three temperature variables also had a third-order B-spline fit, evidence of a non-linear relationship. Minimum daily temperature was similar to relative humidity in that it was an increasing function across the range measured in this experiment (-3.75 to 23.10 °C). The functional relationships between mean and maximum temperature and adult abundance were unimodal, decreasing after an optimal temperature threshold was reached (Fig. 1.5).

Larval Habitat Density and Adult Abundance

We detected a significant positive relationship between larval habitat density and adult abundance at a site ($\chi^2 = 17.788$, df = 1, p < 0.0001), although the effect size was highly dependent on site. Site-level random effects ranged from -0.975 to 1.280, compared to a regression coefficient of 0.364, suggesting that unmeasured covariates at the site level are also contributing substantially to adult abundances. This is further supported by the relatively low model fit ($R^2 = 0.39$) compared to the univariate models of microclimate variables described above.

Discussion

Spatial predictions of mosquito abundances often rely on temperature-dependent mechanistic models derived from mosquitoes' thermal performance curves (Mordecai et al. 2017; Kearney et al. 2009; Focks et al. 1993). However, availability of larval habitat can also be a strong determinant of adult mosquito abundances, and few models include these in their predictions (but see Focks et al. 1993). We found that while both climate and larval habitat influenced adult mosquito abundance, climate was a stronger predictor of adult abundance and the functional relationship between microclimate and adult abundance matches predictions based on theories of ectotherm physiology (Huey and Stevenson 1979). Further, neither adult abundance nor the density of *Ae. albopictus* positive larval habitat varied by urban land class, suggesting that, at least for smaller, residential cities, this variation is not significant, and models do not need to differentiate across land class in urban areas.

While we failed to detect a difference in adult abundance across land class, other studies have found mosquito abundances to differ across an urban gradient. Multiple studies that have defined urban gradients according to variation in vegetation density (Little et al. 2017; Reiskind et al. 2017), impervious surface (Johnson, Gómez, and Pinedo-Vasquez 2008), or land cover classifications (Gleiser and Zalazar 2010; Chaves et al. 2011; Zahouli et al. 2017; Cox et al. 2007) have found mosquito abundances to vary across these gradients. Li et al. (2014) focused specifically on *Ae. albopictus* and found adult abundance to increase with increasing urbanization, driven by an increase in larval habitat density (Li et al. 2014). Our study, however, found no evidence for a difference in positive larval habitat density across land classes, which may explain why we failed to detect a difference in adult abundance. A semi-field experiment conducted at the same study sites as this experiment estimated lower *Ae. albopictus* per-capita growth rates on urban sites compared to rural and suburban sites, driven by lower larval survival rates and smaller wing lengths of emerged adults (a predictor of fecundity) on urban sites (Murdock et al. 2017). Taken together, these findings suggest that per capita growth rates may not scale-up to site level population abundances. Other factors, such as the quantity and quality of larval habitat or the availability of hosts for blood feeding (Burkett-Cadena et al. 2013), may further mediate the relationship between container-level growth rates and site level abundances.

Temperature and relative humidity are likely the key variables driving seasonal trends in mosquito density, as they were important predictors of both the density of larval habitats positive for *Ae. albopictus* larvae and adult *Ae. albopictus* abundance. While many studies have observed seasonality in larval habitat abundance (Mukhtar et al. 2018; Leisnham, LaDeau, and Juliano 2014), few have directly paired these data with climate variables. The density of larval habitat had an exponentially increasing relationship with temperature, and, indeed, larval habitat was most abundant during the summer sampling periods. Hotter temperatures can increase mosquito biting rates and shorten gonotrophic cycles (Delatte et al. 2009), potentially leading to higher oviposition rates and a higher density of larval habitats. Relative humidity, in comparison, had a unimodal relationship with larval habitat, with the number of larval habitats decreasing at high minimum and mean relative humidity. Very few studies have investigated the effects of relative humidity on larval mosquito dynamics. However, Murdock et al. (2017) found that increases in relative humidity reduced larval survival through a suggested decrease in the surface tension of aquatic environments (Murdock et al. 2017). Another explanation is that high relative humidity is associated with strong rainfall events (Mitovski et al. 2010), which can lower the density of positive larval habitat through flushing events and oviposition avoidance (Dieng et al. 2012). Interestingly, these functional relationships (Fig. 1.4) differed qualitatively from those between climate and adult abundance (Fig. 1.5), suggesting the effects of temperature and relative humidity on mosquito populations may differ across life stages (ovipositing and hatching vs. emergence and adult survival).

Temperature and relative humidity were also key predictors of adult abundance. The nonlinear functions used in the temperature models match the unimodal functional form between ectotherm growth and temperature expected from physiological theory and empirical work in mosquito systems (Mordecai et al. 2017; Huey and Stevenson 1979). Ae. albopictus abundance was zero at mean temperatures below 10 $^{\circ}$ C, and increased to a peak temperature around 25 °C. This agrees with other studies in urban areas that found the minimum threshold for adult activity to be 10 $^{\circ}$ C and laboratory predictions of the optimum temperature of 25 $^{\circ}$ C (Roiz et al. 2010; Brady et al. 2013). In the case of the daily maximum temperature, temperatures during our study period exceeded the optimal temperature for Ae. albopictus, and adult abundance decreased at high temperatures, creating a hump-shaped curve. These field findings match general expectations of thermal performance curves derived from laboratory experiments, suggesting that empirically-derived thermal performance curves are applicable to mosquito populations in field settings. Adult abundance also increased with increasing levels of relative humidity. Another study observed adult Ae. albopictus mortality rates to decrease with increasing humidity in the field (Hylton 1969). This relationship between adult mortality and humidity may drive the positive relationship between relative humidity and adult abundance in our study. We found a positive, though weak, relationship between the density of positive larval habitat and adult mosquito densities. This is in agreement with

other studies that have found larval habitat to be predictive of adult densities (Li et al. 2014; Bodner, LaDeau, and Leisnham 2019). In addition to providing more space and resources for immature mosquitoes, high densities of larval habitat can also reduce the time spent searching for oviposition sites, shortening gonotrophic cycles and increasing population growth rates (Gu et al. 2006). The overall performance of the model including larval habitat was lower than one based solely on microclimate. This implies that, while adult abundance and larval habitat are correlated, microclimate alone may more accurately predict mosquito abundances.

By spanning two years, we replicated seasonality, but only across a limited number of sites. While we classified sites into urban land classes based on determinants of microclimate, namely impervious surface, unmeasured site-level characteristics were an important driver of *Ae. albopictus* abundance. For example, one urban site produced more than two-fold the number mosquitoes of any other urban site. This site received daily irrigation throughout the summer months, perhaps contributing to high *Ae. albopictus* abundances, as has been found in *Culex spp.* (Reisen et al. 1990). The types of artificial containers can differ across socio-economic levels in urban areas (Little et al. 2017). The type of larval habitat in our study varied widely across sites, from natural bodies such as ponds and treeholes to artificial containers such as flower pots and tires, but there was no pattern across land class (Table 1.4). Suburban and urban sites in particular had wide variation in habitat types, and the inclusion of social variables such as parcel value or income in our classification could lead to higher uniformity in land classifications.

We found that adult abundance was well predicted by microclimate variables and that the functional relationship between temperature and adult abundance matched that proposed by theory and empirical studies. This study contributes to a small number of studies exploring predictors of *Ae. albopictus* abundance in cities (Li et al. 2014; Little et al. 2017). Unlike past studies, we found no evidence for an effect of urban land class on *Ae. albopictus* abundances,

suggesting that city-scale predictive models may not need to explicitly incorporate differences across land classes. However, Athens, GA is a small city, with an average impervious surface of 10% and a population of 127,064, and these results may not apply to larger cities with wider variation in land class, which can differ in temperature by over 5 °C (Peng et al. 2012). Future work could expand field studies to additional cities to test the generalizability of these findings and identify contexts (e.g. tropical vs. temperate cities, small vs. large cities) in which these results differ. By pairing mosquito surveys with the collection of microclimate data, our findings support the continued use of temperature-dependent mechanistic models in the spatial prediction of mosquito abundances and mosquito-borne disease risk.

Tables

Table 1.1: Results of likelihood ratio tests comparing null model to univariate GLMMs containing microclimate variables to predict the density of *Ae. albopictus*-positive larval habitat. All microclimate variables were strong predictors of larval habitat density. GLMM was calculated across 9 sites (random effect), and within-site n = 21. We calculated conditional R^2 following Schielzeth and Nakagawa (2013).

Variable	df	c2	p-value	Conditional R2
Min. Temperature	3	93.516	< 0.0001	0.764
Mean Temperature	3	92.189	< 0.0001	0.830
Max. Temperature	3	61.480	< 0.0001	0.855
Min. Relative Humidity	3	52.522	< 0.0001	0.695
Mean Relative Humidity	3	24.776	< 0.0001	0.506

Table 1.2: Results of likelihood ratio tests comparing null model to univariate GLMMs containing microclimate variables to predict adult female abundance. All microclimate variables were strong predictors of adult abundance. GLMM was calculated across 9 sites (random effect), and within-site n = 26. We calculated conditional R^2 following Schielzeth and Nakagawa (2013).

Variable	$\mathbf{d}\mathbf{f}$	chi^2	p-value	Conditional R^2
Min. Temperature	3	104.27	< 0.001	0.835
Mean Temperature	3	110.94	< 0.0001	0.847
Max. Temperature	3	96.50	< 0.0001	0.910
Min. Relative Humidity	3	49.79	< 0.0001	0.608
Mean Relative Humidity	3	16.257	0.001	0.530

Table 1.3: Results of likelihood ratio tests comparing models with interactions to main effect GLMMs containing microclimate variables to predict the density of Ae. albopictus-positive larval habitat or adult Ae. albopictus abundance. There was no evidence for an interaction between temperature and relative humidity for either model, as demonstrated by the χ^2 value and comparison of AIC. GLMM was calculated across 9 sites (random effect).

Model	Variables	$\mathbf{d}\mathbf{f}$	chi^2	p-value	δ AIC
Larval Habitat Density	Mean Temp. * Mean RH	9	16.550	0.056	1.45
Adult Abundance	Mean Temp. * Mean RH	3	6.368	0.703	11.47

Table 1.4: Distribution of container types across land classes (positive/total). Most container types were found across all land classes, with the exception of rockpools.

	Artificial Container	Ground Pool	Pond	Rockpool	Treehole
Rural	46/201	4/12	1/6	0/0	0/5
Suburban	111/378	0/5	0/20	1/2	3/32
Urban	28/129	0/22	1/35	0/0	17/38

Figures



Figure 1.1: Map of sites in Athens, GA. Symbols represent land classes (square: rural, circle: suburban, and triangle: urban). Color shading represents the amount of impervious surface within the 210-m focal area of each pixel, as illustrated on the color bar on the bottom. Athens-Clarke County is outlined in black, and its location within the state is shown in the inset map of Georgia.



Figure 1.2: Positive larval habitat density across land class and time. The lines represent the fitted model averaged across all sites. Raw data are represented by the points and randomly jittered to improve visibility.



Figure 1.3: Adult female *Aedes albopictus* abundance across time. The lines represent the fitted model averaged across all sites. Raw data are represented by the points and randomly jittered to improve visibility.



Figure 1.4: Functional relationship between microclimate variables and the density of the positive *Aedes albopictus* habitat for a representative site of each land class. Functional relationships were the same across all land classes, and the larval habitat density did not differ across land class. The daily minimum, mean, and maximum temperatures are on the left side (A–C), and the daily minimum and mean relative humidity are on the right side (D and E). The lines represent fitted regression lines, and raw data are represented by the circles. Because the maximum relative humidity did not vary, no regression line was fitted.



Figure 1.5: Functional relationship between microclimate variables and adult female abundance for a representative site of each land class. Functional relationships were the same across all land classes, and the female adult abundance did not differ across land class. The daily minimum, mean, and maximum temperatures are the on the left side (A–C), and the daily minimum and mean relative humidity are on the right side (D and E). The lines represent fitted regression lines, and raw data are represented by the circles. Because maximum relative humidity did not vary, no regression line was fitted. The suburban and urban fitted curves for minimum relative humidity are visually indistinguishable, and so, the suburban curve has been shifted downward for visibility.

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Chapter 2

Carry-over effects of urban larval environments on the transmission potential of dengue-2 virus

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Abstract

Mosquitoes are strongly influenced by environmental temperatures, both directly and indirectly via carry-over effects, a phenomenon by which adult phenotypes are shaped indirectly by the environmental conditions experienced in previous life stages. In landscapes with spatially varying microclimates, such as a city, the effects of environmental temperature can therefore lead to spatial patterns in disease dynamics. To explore the contribution of carry-over effects on the transmission of dengue-2 virus (DENV-2), we conducted a semi-field experiment comparing the demographic and transmission rates of *Aedes albopictus* reared on different urban land classes in the summer and fall season. We parameterized a model of vectorial capacity using field- and literature-derived measurements to estimate the bias introduced into predictions of vectorial capacity not accounting for carry-over effects. The larval environment of different land classes and seasons significantly impacted mosquito life history traits. Larval development and survival rates were higher in the summer than the fall, with no difference across land class. The effect of land class on adult body size differed across season, with suburban mosquitoes having the smallest wing length in the summer and the largest wing length in the fall, when compared to other land classes. Infection and dissemination rates were higher in the fall and on suburban and rural land classes compared to urban. Infectiousness did not differ across land class or season. We estimate that not accounting for carry-over effects can underestimate disease transmission potential in suburban and urban sites in the summer by up to 25%. Our findings demonstrate the potential of the larval environment to differentially impact stages of DENV-2 infection in Ae. albopictus mosquitoes via carry-over effects. Failure to account for carry-over effects of the larval environment in mechanistic models can lead to biased estimates of disease transmission potential at fine-scales in urban environments.

Introduction

Climate plays an important role in the transmission of mosquito-borne pathogens, determining the geographic range of disease vectors and shaping transmission dynamics (Reiter 2001; Parham et al. 2015). Heterogeneity in environmental conditions can directly shape individuallevel variation in traits relevant to mosquito population dynamics (Delatte et al. 2009) and pathogen transmission (Murdock et al. 2012). In addition to these direct effects, mosquito phenotypes can be shaped indirectly by the environmental conditions experienced in previous life history stages, a phenomenon known as carry-over effects (Harrison et al. 2011). Carryover effects have been documented in a wide-range of species with complex life cycles, such as amphibians (Vonesh 2005), migratory birds (Norris and Taylor 2006), and damselflies (De Block and Stoks 2005). Similarly, the mosquito life cycle is characterized by ontogenetic niche shifts, with a larval aquatic stage and an adult terrestrial stage. Following these studies, we reason that the thermal environment a mosquito experiences during its larval stage is likely to have lasting impacts on adult traits, and, ultimately, on transmission potential.

Although it has been previously demonstrated that larval environmental temperature can alter individual mosquito traits important for transmission (Alto and Bettinardi 2013; Buckner, Alto, and Lounibos 2016), the net effect of temperature-mediated carry-over effects on overall transmission potential is ambiguous. Current models of mosquito-borne disease typically only incorporate direct effects of temperature, despite evidence that carry-over effects can have large impacts on adult phenotypes (Muturi et al. 2011b; Muturi et al. 2011a; Price et al. 2015). Additionally, laboratory studies designed to estimate temperature-mediated carry-over effects are often conducted across a wider range of temperatures than mosquitoes typically experience in the field (Cator et al. 2013). The studies are not easily "scaled-up" to explain transmission across a landscape when incorporated into temperature-dependent models of mosquito-borne disease (Reiner et al. 2013). Urban landscapes, in particular, are composed of a variety of microclimates, which can differentially impact mosquito life-history traits leading to heterogeneity in vector population dynamics across the landscape (Murdock et al. 2017). However, it is unknown if variation in microclimate across an urban area also has implications for carry-over effects of the larval environment on adult phenotypes.

We hypothesize that relevant environmental variation across an urban landscape during the larval stage will have lasting impacts on adult traits that are important for mosquito population dynamics and pathogen transmission. Further, we predict that failure to account for carry-over effects will result in a biased estimate of vectorial capacity, the rate at which future infections arise from one infectious mosquito. To estimate the effects of the larval environment in a spatially heterogeneous, urban environment, we conducted a semi-field experiment exploring population and dengue-2 virus (DENV-2) transmission relevant lifehistory traits from *Aedes albopictus* mosquitoes reared in three urban land classes across the summer and fall. We used a mixture of field-derived and temperature-dependent parameters to construct a model of vectorial capacity. Our modeled vectorial capacity was then compared to a calculation using the experimental grand mean for parameters affected by carry-over effects in order to estimate the bias introduced by not including these indirect effects.

Methods

We conducted a semi-field experiment across an urban gradient in Athens, GA, USA in the summer and fall of 2016. To explore the effects of microclimate variation across an urban landscape, we used an impervious surface map (National Land Cover Database 2011 (Xian et al. 2011)) to select three replicate sites (30 m x 30 m) each of low (0-5%), intermediate (6-40%), and high (41-100%) impervious surface. Percent impervious surface is an accurate

predictor of land surface temperature, particularly for urban landscapes (Yuan and Bauer 2007), and allowed us to ensure our sites exhibited the full range of urban microclimates. To select our sites, we calculated the percent impervious surface of each 30 m x 30 m pixel using a moving focal window of 210 m x 210 m, as the surrounding impervious surface can affect the microclimate in the pixel of interest. We then classified each pixel based on the mean impervious surface within its focal window, with 0 - 5 % representing low, 6 - 40 % representing intermediate, and 41 - 100 % representing high. Because impervious surface is an effective classifier of urban land classes (Lu and Weng 2006), we identified the sites as rural, suburban, and urban with low, intermediate, and high impervious surface scores, respectively. Final site selection was constrained by access and permissions, however, the final distribution of sites was chosen to ensure all sites were at least 3 km from others of the same land class, and were interspersed across the study area (Fig. 2.1).

Within each site, we evenly distributed four plastic trays (Sterilite, 13.625" x 8.25" x 4.875"), each containing 100 first instar *Ae. albopictus* larvae and 1L of leaf infusion. *Ae. albopictus* were from a laboratory colony obtained from the Centers for Disease Control (Atlanta, GA, USA) originating from Keyport, NJ, USA in 1995 (strain ATM-NJ95) (Marcombe et al. 2014) and maintained following standardized protocols. Leaf infusion was prepared as described in Murdock et al. (2017). Briefly, 80 g live oak (Quercus virginiana) leaves and 3 g of 1:1 yeast: albumin mixture were infused in deionized water. Trays were screened with a fine mesh, placed in a wire cage to deter wildlife, covered with clear plastic vinyl to keep rainwater from entering, and placed in full shade. We added deionized water to trays after two weeks to maintain a total water volume at 1L. We placed data loggers (Monarch Instruments: Radio Frequency Identification (RFID) Temperature Track-It Logger) in vegetation next to each tray, approximately 0.9 m above the ground. Data loggers recorded instantaneous temperature and relative humidity at ten minute intervals throughout the study period. Data loggers were also

placed in the trays to measure the larval, aquatic temperature, however three and 17 loggers (of 36) failed due to water damage in the summer and fall, respectively. Of loggers that did not fail during the experiment, water temperatures were highly correlated with ambient temperatures ($\rho = 0.929$); thus, only ambient temperatures are used as an approximation of larval environmental temperature. Sites were visited daily to collect emerging adults until all larvae had emerged or died (Summer Replicate: Aug. 1 to Sept. 3, 2016, Fall Replicate: Sept. 26 to Nov. 8, 2016). We quantified the total number of adults emerging per day, and recorded the sex and wing length of each emerged adult. Adult females were collected to use in vector competence assays.

Dengue virus in vitro culturing and mosquito infections

DENV-2 stock was obtained from the World Reference Center for Emerging Viruses and Arboviruses at the University of Texas Medical Branch (PRS 225 488, originally isolated from human serum in Thailand in 1974 Vazeille-Falcoz et al. 1999). We propagated virus by inoculating Vero (African green monkey kidney epithelial) cells with a low MOI infection. Virus-containing supernatant was harvested when the cells exhibited more than 80 % cytopathic effect. Supernatant was cleared of cell debris by centrifugation (1000xg, 1 minute), aliquoted into cryo-vials, and stored at -80 °C. We quantified viral titers of virus stock using TCID-50 assays, calculated by the Spearman-Karber method (Shao et al. 2016; Willard et al. 2017). When mixed 1:1 with the red blood cell mixture, the final concentration of virus in the blood meal was 3.540×10^6 TCID50/mL.

Adult mosquitoes were collected as they emerged from trays, aggregated by site, and stored in reach-in incubators at 27 ± 0.5 °C, 80 ± 5 % relative humidity, and a 12:12 hour light:dark cycle. To ensure infected mosquitoes were of a similar age, mosquitoes were pooled into cohorts of 4-6 days old in the summer and 4-9 days old in the fall (due to slower and more

asynchronous emergence rates). Mosquitoes were allowed to mate and fed *ad libitum* with a 10 % sucrose solution. Forty-eight hours prior to infection, the sucrose was replaced with deionized water, which was then removed 12-14 hours before infection to encourage feeding. Infectious blood meals were administered to mosquitoes through a water-jacketed membrane feeder and consisted of 47 % human red blood cells washed in DMEM (vol/vol), 1 % sucrose (weight/vol), 20 % FBS (vol/vol), 5 mM ATP, and 33 % DMEM medium combined with 1 mL of virus stock (Shan et al. 2016). Blood-fed female mosquitoes were then maintained as described above for the duration of the experiment.

For a mosquito to become infectious, arboviruses must pass through multiple tissues that impose significant barriers to infection, namely the midgut and salivary glands (Cheng et al. 2016). Therefore, we assessed mosquitoes for infection, dissemination, and infectiousness through salivation assays and tissue dissections 21 days post infection (Anderson, Richards, and Smartt 2010). First, mosquitoes were cold anesthetized and immobilized by removing their legs and wings. Wings were mounted on a glass slide to measure wing length from the distal end of the alula to the apex of the wing via a dissecting scope and micrometer. The proboscis of each female was then inserted into a sterile pipette tip containing 10-20 µL of FBS (with 3 mM ATP and red food coloring) and allowed to salivate on a plate kept at 27 °C for 15 minutes, after which the salivation media was expelled into 500 µL of DMEM and stored at -80 °C. After salivation, we removed the head of each individual and stored the body and head separately at -80 °C.

To determine variation in the proportion of mosquitoes that become infected (bodies positive for virus), disseminated (heads positive for virus), and infectious (saliva positive for virus), we used cytopathic effect (CPE) assays to test for the presence of virus in each collected tissue (Willard et al. 2017). Individual bodies and heads were homogenized in 500 μ L of DMEM and centrifuged at 2,500 rcf for 5 minutes. 200 μ L of homogenate was added to

Vero cells in a solution of DMEM (1 % pen-strep, 5 % FBS by volume) in a 24-well plate and kept at 37 °C and 5 % CO2. Salivation media was thawed and plated on Vero cells as above. After 5 days, Vero cells were assessed for presence of DENV-2 via CPE assays. Samples were identified as positive for virus if CPE was present in the well.

All infection work was conducted in an arthropod containment level 2 (ACL-2) facility at the University of Georgia in the College of Veterinary Medicine. The physical space as well as experimental protocols have been reviewed and approved by the University of Georgia Office of Biosafety (2015-0038). Briefly, all DENV-2 exposed mosquitoes were counted initially and throughout the experiment, housed in secondary containment cages, and handled in a glove box and on ice when they were removed from secondary containment for forced salivations. All virus assays were also conducted in a biosafety cabinet in our biosafety level II (BSL-2) facility. Finally, we used designated and approved secondary containment to transport virus or infected tissues between our ACL-2 and BSL-2.

Intrinsic growth rates (r') and vectorial capacity (VC)

We calculated the per capita population growth rate per tray following Livdahl and Sugihara (1984) (Eq. 2.1):

$$r' = \frac{ln(\frac{1}{N_0}\sum_x A_x f(\bar{w_x}))}{D + \frac{\sum_x x A_x f(\bar{w_x})}{\sum_x A_x f(\bar{w_x})}}$$
(2.1)

Following Livdahl and Willey (1991), we assume N_0 to represent the initial number of females before accounting for mortality during the larval stage. This enables the mortality rate to be included via the summed $\frac{A_x}{N_0}$ parameter. Setting N_0 equal to the number of emerged mosquitoes would imply a 100% larval survival rate, which was not the case in our study. Unfortunately, we cannot identify the sex of first-instar larvae, and must assume a ratio within the initial cohort. While we do record the proportion of emerged mosquitoes, this represents those that have survived the larval environment until emergence, and, given our findings regarding the effects of the larval microclimate on larval survival, may not be representative of the initial cohort. In our study, males emerged 1–3 days earlier than females in the summer, and up to a week earlier than females in the autumn. This additional time in the larval environment could have exposed female mosquitoes to stressful temperatures and lower resource concentrations than the male mosquitoes that emerged earlier, resulting in lower emergence rates. Eggs used in the experiment were drawn from a laboratory colony which is known to have approximately a 50:50 male:female sex ratio. Therefore, we used this value (50% of the larvae, 50) in our calculations. The other parameters are defined as follows: A_x is the number of mosquitoes emerging on day x, D is the time to reproduction following emergence (assumed to be 14 days [28]), $f(\bar{w}_x)$ is fecundity as a function of mean wing size on day x (w_x ; Equation 2.2). This relationship is assumed to be linear and calculated via Lounibos et al. (2002) (Eqn. 2.2):

$$f(\bar{w}_x) = -121.240 + (78.02 \times \bar{w}_x) \tag{2.2}$$

While it is possible to reason how changes in each parameter will result in carry-over effects that individually affect disease transmission, determining the overall net effect and magnitude of the change is less straightforward. Therefore, we calculated the vectorial capacity (VC; Eqn. 2.3) for each site and season using a modified temperature-dependent dengue calculation defined in Mordecai et al. (2017)to create a quantitative estimate of the influence of carry-over effects on disease transmission. Using the experimental mean for field-derived parameters affected by carry-over effects (fecundity and vector competence),

we calculated an additional site-level VC to serve as an estimate of this value when not accounting for site-specific carry-over effects.

$$VC(T) = \frac{a(T)^2 b(T) c(T) e^{-\mu(T)/EIR(T)} EFD(T) p_{EA}(T) MDR(T)}{\mu(T)^2}$$
(2.3)

Here, mosquito traits are a function of temperature (T), as described in Table 2.1. Site-level VC was calculated using a combination of traits empirically measured in this study and traits estimated from thermal response models as described in Mordecai et al. (2017). The bite rate (a(T)), adult mosquito mortality rate $(\mu(T))$, and extrinsic incubation rate (EIR(T))were calculated for mosquitoes at a constant 27 °C using temperature-dependent functions from Mordecai et al. (2017), to match the adult environment used in the experiment. Vector competence (b(T)c(T)) was calculated as the proportion of infectious mosquitoes per site as determined by our DENV-2 infection assays. Conventionally, vector competence is the product of the proportion of mosquitoes that become infected after biting an infected human and the proportion of bites by infectious mosquitoes that infect humans. Our estimate, the proportion of infectious mosquitoes as measured by CPE assays, is the same as the product of the proportion of mosquitoes that become infected following an infectious blood meal and the proportion of infected mosquitoes that have DENV-2 virus particles in their saliva. With this formulation we are assuming that all infectious bites result in human infection, as we are not directly measuring dengue infection outcomes in humans (i.e. effects of human immunity on DENV infection). The number of eggs produced per female per day (EFD(T)) was calculated by estimating fecundity from average female wing length following Eqn. 2.2, and then dividing this by the expected lifespan of mosquitoes $(\frac{1}{\mu})$. The egg-to-adult survival probability $(p_{EA}(T))$ was defined as empirically measured egg-to-adult survival probability (the average proportion of adult female mosquitoes emerging per site). The mosquito immature development rate (MDR(T)) was calculated as the inverse of the mean time to emergence for female mosquitoes per site, resulting in a daily rate of development. To estimate bias introduced by not including carry-over effects, we compared our site-level calculated VC to one calculated using the experimental grand mean for site-level EFD and bc. All other parameters were the same across the two models.

Statistical Analysis

We used linear mixed models (LMMs) to explore if microclimate (i.e. mean, minimum, maximum, and daily ranges of temperature and relative humidity), larval development rate (1/days to emergence), female body size, and per capita growth rate differed across land class and season. Egg-to-adult survival (the proportion of adult females emerging per tray) and metrics of vector competence (i.e. infection, dissemination, and infectiousness) were fit using generalized linear mixed models (GLMMs) with binomial distributions and logit links. In all models, fixed effects included land class, season, and their interaction, with site as a random effect. The effect of body size on infection dynamics was also explored at the level of the individual mosquito, fitting a binomial GLMM including wing size as a fixed effect and site as a random effect. Vectorial capacity was calculated at the site-level, and so did not require site to be included as a random effect. We therefore used a regression model to estimate the effect of land class, season, and their interaction on site-level vectorial capacity.

To confirm the relationship between the categorical variables of land use and season and temperature, we fit additional models containing mean temperature as a covariate to the residuals of the original models including season and land use as fixed effects. This test explored if there was additional variation in the response variable due to temperature that was not explained by land class and season. To explore if the effect of temperature differed across season, we fit individual models to the above response variables including mean temperature as averaged across each season (e.g. summer or autumn) as a covariate, using the same distributions and link functions. For egg-to-adult survival, larval development, body size, and the per capita growth rate, mean temperature was calculated over each individual season (e.g. summer and autumn) at the tray level, and site was included as a random effect. Because mosquitoes were pooled by site for infection assays, temperature was aggregated to the site level and no random effects were included for analyses of infection metrics and VC.

All analyses were conducted with respect to the female subset of the population, as they are the subpopulation responsible for disease transmission. In the case of data logger failure (n = 3), imputed means from the site were used to replace microclimate data. In the case of trays failing due to wildlife tampering (two urban and one suburban in the autumn replicate), collected mosquitoes were used for infection assays, but trays were excluded from demographic analyses. For all mixed-models, significance was assessed through Wald Chi-square tests $(\alpha = 0.05)$ and examination of 95% confidence intervals. Pearson residuals and Q-Q plots were visually inspected for normality. All mixed models were fit using the 1me4 (Bates et al. 2015) package in R v. 3.5.0 (Team 2018). Code to run analyses and create figures is deposited on figshare (doi:10.6084/m9.figshare.5558128).

Results

Effects of land class and season on microclimate

We found that microclimate profiles differed significantly across both season and land class (Fig. 2.2, Table 2.2). In general, temperatures were warmer in the summer and on urban sites, replicating what was found in a prior study in this system (Murdock et al. 2017). We did observe a significant interaction between season and land use on the mean daily minimum temperature and diurnal temperature range, with no effect of land use on these response

variables in the summer. Urban sites in the autumn were characterized by significantly higher daily average minimum temperature and smaller diurnal temperature range relative to rural sites (Table 2.2). Mean relative humidity was higher in the summer than the autumn: (mean (95% CI), summer: 87.93% (86.33–89.54%); autumn: 73.32% (71.72–74.92%). In the summer, minimum and mean relative humidity was significantly lower on urban sites compared to rural and suburban sites (Table 2.2). A similar trend was seen in the autumn, with urban sites having lower mean relative humidity compared to other land classes, but no difference in minimum relative humidity (Table 2.2).

Direct and carry-over effects of land class and season on population growth

Of the 3600 first-instar larvae placed in each season, a total of 2595 and 1128 mosquitoes emerged in the summer and autumn, respectively. The total female egg-to-adult survival per tray was significantly higher in summer than autumn (Table 2, mean (binomial asymptotic 95% CI), summer: 0.670 (0.598–0.735); autumn: 0.297 (0.235–0.366)), but did not differ across land class (Fig. 2.3a, Table 2). The mean rate of larval development per tray was significantly different between summer and autumn (Fig. 2.3b, Table 2), with daily mean \pm SE development rates of 0.074 \pm 0.002 and 0.0387 \pm 0.002, respectively. There were no significant differences in larval survival or development rates across land class. We did not observe a significant carry-over effect of land class or season on mosquito wing size, however there was a significant interaction between the two (Table 2). We found a significant difference in wing size across season for mosquitoes on rural sites only, with larger bodied mosquitoes in the summer (mean \pm SD 2.451 \pm 0.211 mm), than the autumn (2.300 \pm 0.202 mm). While urban mosquitoes tended to be larger in the autumn, and suburban mosquitoes tended to be larger in the summer, these effects were not significant. After incorporating the number of adult females emerging per day, the day of emergence, and their body size into the per capita growth rate equation (Eqn. 2.1), we found that the estimated per capita growth rate was higher in the summer season than the autumn season (Fig. 2.3c, Table 2, mean \pm SE, summer: 0.135 \pm 0.005; autumn: 0.068 \pm 0.006) with no difference across land class. The effect of temperature within a season was only significant for egg-to-adult survival, and differed in direction across season (mean $\beta \pm SE$, summer: -0.328 \pm 0.148; autumn: 0.368 \pm 0.135, Table 2.5). This mirrors a trend for the effect of land class on egg-to-adult survival to differ across season (Table 2). When controlling for land class and season, temperature explained no additional variation for any response variable (Table 2.6).

Carry-over effects of land class and season on vector competence

A total of 319 female mosquitoes were assessed for infection status, 20 per site in the summer and varying numbers per site in the autumn due to lower emergence rates (sample sizes reported in Table 2.4). Carry-over effects of the larval environment on infection status were limited to infection and dissemination rates. We found that land class and season did significantly impact the probability of a mosquito becoming infected and disseminating dengue infection (Table 2). Both metrics were higher in the autumn compared to the summer replicate, with urban sites having the lowest infection and dissemination rates across both seasons (Fig. 2.4a, b). While there was a trend for a higher proportion of mosquitoes becoming infectious in the summer (Fig. 2.4c), this was not significant ($\chi^2 = 3.63$, P = 0.057). The probability of becoming infectious did not differ across land class, nor season (Fig. 2.4c, Table 2), despite the higher probability of mosquito infection and dissemination in the autumn, and on suburban and rural sites. Similarly, there was no effect of temperature on any infection metric within a season (Table 2.5), and temperature did not explain any additional variation after controlling for land class and seasons (Table 2.6). This suggests that the ability of virus to escape the midgut and invade the salivary glands differs in adults reared in the summer vs the autumn and across land class, with a higher proportion of dengue infected mosquitoes becoming infectious in the summer and on urban sites (Table 2.4, (χ^2 = 13.65, P < 0.001). We also found the probability of infection to decline with increasing body size ($\chi^2 = 4.776$, P = 0.0289), although there was no evidence for a relationship between body size and the probability of dissemination or infectiousness.

Integrating direct and carry-over effects into estimates of transmission potential

We found VC to be higher in the summer (mean \pm SE: 5.847 \pm 0.768) than the autumn (0.252 \pm 1.097) (Fig. 2.5, Table 2). In the summer season, there was a trend for VC to increase with increasing urbanization (Fig. 2.5). This trend was not significant, however, given the small sample size (n = 9) and the disproportional impact of having no infectious mosquitoes at one site, resulting in a value of VC = 0 for one sample. There was no effect of temperature on VC within a season (Table 2.5), and temperature did not explain any additional variation after controlling for land class and season. When comparing VC calculations using field-based or grand mean estimates of EFD and bc, we found that the effect of land class and season were not significantly different (land class: $\chi^2 = 0.381$, P = 0.826), season: $\chi^2 = 1.408$, P = 0.235), suggesting that the omission of carry-over effects in calculations did not lead to biased estimates of relative VC in different seasons or land classes. However, the use of the grand mean did lead to an underestimate of VC on some suburban and urban sites in the summer, with a two-fold decrease in predicted VC (Fig. 2.5, 2.6). The calculated VC for rural sites in the summer and across all land classes in the autumn more closely resembled the grand mean calculated VC.

Discussion

Mathematical models of mosquito-borne disease rarely include mosquito larval stages (Reiner et al. 2013), and of those that do, few include the influence of carry-over effects on important mosquito life-history traits (but see Roux et al. 2015). This is likely because there are relatively few empirical studies parameterizing carry-over effects in mosquito-pathogen systems (Parham et al. 2015), and most are laboratory studies conducted across a wider range of temperatures than those seen in the field. Here, we demonstrate that fine-scale differences in larval microclimate across land class and season generate carry-over effects on adult fecundity and vector competence for DENV-2. When integrated into a model of vectorial capacity, we find that vectorial capacity differs across season, but not land class. Further, failure to account for site-specific carry-over effects across urban land classes results in biased estimates of DENV-2 transmission potential, underestimating potential disease transmission in urban areas.

The subtle heterogeneity in microclimate we observed across season resulted in significantly different predicted population growth rates through its effects on demographic traits. Daily mean temperatures (25.43 °C) across all sites in the summer were closer to the predicted thermal optimum of *Ae. albopictus* (24–25 °C) (Mordecai et al. 2017) than in the autumn (17.69 °C), leading to higher egg-to-adult survival rates. We also observed more rapid larval development rates in the summer relative to the autumn. This is likely due to the strong positive relationship observed between development rates and mean larval temperature, as the metabolic rate of mosquitoes will increase with warming temperatures (Delatte et al. 2009). Temperature explained no additional variation in any response variable after accounting for land class and season, suggesting that our coarser characterizations of land class and season contain the temperature variation necessary to predict changes in demographic and infection rates. Additionally, we only found an effect of temperature within a season for egg-to-adult

survival (Table 2.5). While we did not find a significant influence on many traits, our trends do agree with a previous study in this system that found lower egg-to-adult survival on urban sites (Murdock et al. 2017). The variation in mean temperature across land class in our study was very small (< 1 °C), and we expect these relationships would be magnified in mega-cities that can have urban heat island effects of up to 6 °C (Peng et al. 2012).

Surprisingly, we found no main effect of land class or season on female mosquito body size, despite the difference in temperatures across season. Following allometric temperaturesize relationships of ectotherms, warmer larval temperatures should lead to smaller-bodied mosquitoes (Angilleta, Steury, and Sears 2004). However, contrary to predictions generated from the allometric temperature-size relationship, we observed mosquitoes on rural sites to be larger in the summer despite the fact that all land classes were cooler in the autumn relative to the summer. Our results contrast with many laboratory studies that have found a negative relationship between rearing temperature and mosquito body size (Ae. albopictus (Reiskind and Zarrabi 2012), Culex tarsalis (Dodson, Kramer, and Rasgon 2012), Anopheles gambiae (Koella and Lyimo 1996)). However, these studies all used a constant temperature treatment, while mosquitoes in our field-based study experienced fluctuating temperatures. Among studies using fluctuating temperatures, there is mixed evidence for a relationship between rearing temperature and mosquito body size (Murdock et al. 2017; Mohammed and Chadee 2011). Larger temperature fluctuations at the more extreme temperatures (cool and warm) can lead to counterintuitive effects of temperature on organismal traits if these temperatures approach or cross the thermal maximum or minimum (at which trait performance is zero) and induce thermal stress (Carrington et al. 2013; Colinet et al. 2015). Rural sites in the autumn did experience a larger average diurnal range of temperatures than in the summer, suggesting this differential effect of temperature fluctuations at thermal extremes could be acting on body size. Our findings demonstrate that, while the use of fluctuating temperatures in studies of mosquito life-history traits is relatively new, these fluctuations can have significant impacts on mosquito ecology and should be integrated in laboratory-based studies of mosquito vectors to more closely approximate field conditions.

Our results agree with laboratory studies in other arboviral systems (chikungunya (Adelman et al. 2013), yellow fever (Adelman et al. 2013), and Rift Valley fever (Turell 1993)) that found cool larval environmental temperatures to enhance arbovirus infection relative to warmer larval environments. Studies in the Ae. albopictus-dengue virus system have also found that low larval temperatures enhance mosquito susceptibility to viral infection, although this is dependent on larval nutrition (Buckner, Alto, and Lounibos 2016) and the stage of the infection (i.e. midgut vs dissemination vs saliva) (Alto and Bettinardi 2013). While we found infection and dissemination of DENV-2 to decrease with increasing temperatures across season and land class, there was no effect on viral presence in the saliva, suggesting carry over effects due to microclimate variation may alter the overall efficiency of dengue infection. Thus, even though a smaller proportion of mosquitoes reared on urban sites and in the summer became infected and disseminated infection, these mosquitoes were more likely to become infectious, resulting in no net difference in overall vector competence across land class and season. Larval environmental temperature may differentially impact later stages of viral infection (i.e. salivary gland penetration) compared to earlier stages (i.e. midgut escape) through effects on mosquito physiology and immunity, as well as on important tissue barriers to infection (Murdock et al. 2012; Adelman et al. 2013; Franz et al. 2015; Houk, Obie, and Hardy 1979). Further, our study considered only DENV-2, and other arboviruses and mosquito-borne disease are likely influenced by the mosquito's larval environment differently.

Current models of vector-borne disease focus primarily on direct effects of environmental variables on mosquito densities and disease transmission and rarely include the effects of the larval stage, either directly or via carry-over effects (Reiner et al. 2013). While we found carry-over effects due to seasonal and urban environments to have a significant impact on DENV-2 infection and dissemination, we found no net effects on saliva positivity for the virus. Therefore, when incorporating parameters into calculations of vectorial capacity, we did not find a significant difference in predicted vectorial capacity due to land class. However, we did find VC to be higher in the summer relative to the autumn, driven by differences in demographic rates such as larval survival and development rates, rather than differences in adult vector competence. Unfortunately, given the logistical limitations imposed by a field experiment setting, we were unable to measure additional life-history traits important for disease transmission in conjunction with vector competence. Laboratory studies have found that factors such as adult longevity (Christiansen-Jucht et al. 2014), biting rate (Moller-Jacobs, Murdock, and Thomas 2014), and pathogen extrinsic incubation period (Shapiro et al. 2016; Bara et al. 2015) are also be impacted by carry-over effects. For example, warmer larval temperatures correspond with decreased adult longevity in mosquitoes (Christiansen-Jucht et al. 2014), and including this relationship could mediate the seasonal differences in VC found in our study, with decreased adult longevity in the summer corresponding to decreased VC. Less is known about traits specific to transmission such as biting rate and EIP, which have only been investigated in response to larval diet and competition (Moller-Jacobs, Murdock, and Thomas 2014; Shapiro et al. 2016; Bara et al. 2015). Carry-over effects of the larval environment can act on multiple adult phenotypes, often in conflicting ways, and the net effect of this on disease transmission has yet to be fully explored.

Our study was further limited by the difficulties in obtaining appropriate sample sizes. While semi-field experiments incorporate more realistic variation in environmental temperature than laboratory experiments, they require additional space and travel time in order to distribute replicates in a manner that meets assumptions of independence across sites. Given the size of our study area, nine was the maximum number of sites that it was possible to visit daily. Unexpectedly low emergence rates of mosquitoes in the autumn further reduced the sample size of mosquitoes that could be used in infection assays. Despite this limitation, we did find significant differences in mosquito demographic rates across season and in infection and dissemination rates across land class, suggesting that site-specific characteristics can directly and indirectly impact vector-borne disease dynamics. Yet, due to the low replication across sites, these results must be interpreted conservatively.

Carry-over effects are not simply limited to microclimate, and can result due to variation in larval nutrition (Moller-Jacobs, Murdock, and Thomas 2014), intra- and interspecific densities (Alto et al. 2005), and predation (Roux et al. 2015) in mosquito systems. Further, abiotic and biotic factors will likely interact to influence carry over effects (Buckner, Alto, and Lounibos 2016; Muturi, Blackshear, and Montgomery 2012), and this interaction could be scale-dependent (Leisnham, LaDeau, and Juliano 2014). For example, biotic processes are predicted to be more important at local geographical scales, while abiotic processes dominate at regional geographical scales in species distribution models (Cohen et al. 2016). Future exploration of the scale-dependent contribution of different environmental factors and their interactive influence on both direct and carry-over effects is needed to improve models predicting the distribution of mosquito vector species, mosquito population dynamics and disease transmission.

We found fine-scale variation in microclimate across season and urban land class to shape *Ae. albopictus* population dynamics and DENV-2 transmission potential through direct effects on larval survival and development rates, and indirectly through carry-over effects on vector competence and fecundity. Although sample sizes were limited, our study indicates the potential effects that site-specific environments can have on mosquito demographics and infection dynamics. DENV-2 infection and dissemination rates were higher in mosquitoes from rural and suburban land classes than urban ones, and were higher in the autumn compared to

the summer. However, there was no difference in overall infectiousness. Therefore, the seasonal differences in VC we observed were due to the direct effects of the larval environment on egg-to-adult survival and development rates, rather than carry-over effects. When comparing VC to a calculated VC that did not account for site-specific carry-over effects, we found that not accounting for carry-over effects results in an underestimate of predicted VC in suburban and urban sites in the summer, and an overestimate in the autumn. The interaction between the larval and adult environments, mediated by carry-over effects, could have complex consequences for adult phenotypes relevant to disease transmission for mosquitoes as well as other organisms. Given the devastating impact of disease in other species with complex life histories (e.g. chytridiomycosis in amphibians), carry-over effects in disease transmission are important, though understudied, mechanisms that must be better understood to control disease spread. Incorporating relationships between carry-over effects and organismal lifehistory traits into statistical and mechanistic models will lead to more accurate predictions on the distributions of species, population dynamics, and the transmission of pathogens and parasites. Mosquito-borne disease incidence is spatially heterogeneous in urban areas (Santos-Vega et al. 2016), and a better understanding of both the larval and adult environments, including their interaction, could improve the accuracy of fine-scale predictions of disease incidence across a city.

Tables

Table 2.1: Parameters used in the VC calculation. Parameters sourced from Mordecai et al. 2017 were mathematically estimated at a constant temperature of 27 °C, the temperature at which our adult mosquitoes were housed. Parameters that included carry-over effects are starred. Mean and range are shown for each parameter, except for those calculated at a constant adult temperature which did not change.

Parameter	Definition	Source	Mean (Range)
a(T)	Per-mosquito bite rate	Mordecai et al. 2017	0.294 (-)
$b(T)c(T)^*$	Vector competence	Present Study	0.107(0-0.353)
$\mu(T)$	Adult mosquito mortality rate	Mordecai et al. 2017	0.011(-)
EIR(T)	Extrinsic incubation rate (inverse of extrinsic incubation period)	Mordecai et al. 2017	0.196 (-)
$EFD(T)^*$	Number of eggs produced per female mosquito per day	Present Study	18.678(15.260-22.800)
$p_{EA}(T)$	Egg-to-adult survival probability	Present Study	0.485(0.090-0.775)
MDR(T)	Larval development rate	Present Study	$0.056 \ (0.027 - 0.087)$

Table 2.2: Mean microclimate values across season and land class. 95% confidence intervals are listed in parentheses. Superscripts represent differences as measured by pair-wise comparison using Tukey multiple comparison of means, adjusting for significance with the Holm-Bonferroni method.

	Summer			Fall			
	Rural	Suburban	Urban	Rural	Suburban	Urban	
Min. Temperature	$21.726 (20.926, 22.525)^{a}$	$21.997 (21.198, 22.797)^{a}$	$22.667 (21.867, 23.466)^{a}$	$11.031 \ (10.231, 11.83)^{\rm b}$	$12.231 \ (11.432, 13.031)^{\rm bc}$	$13.411 (12.611, 14.211)^{c}$	
Mean Temperature	27.577 (27.132,28.021) ^a	$27.381 (26.937, 27.826)^{a}$	$27.451 (27.007, 27.896)^{a}$	$19.45 (19.005, 19.894)^{b}$	$19.547 (19.103, 19.991)^{\rm b}$	$19.951 \ (19.507, 20.396)^{\rm b}$	
Max. Temperature	31.533 (30.763,32.302) ^a	$30.86 (30.091, 31.629)^{a}$	$31.399 (30.63, 32.168)^{a}$	$27.567 (26.798, 28.336)^{\rm b}$	$26.58 (25.811, 27.35)^{b}$	$26.846 (26.077, 27.615)^{\rm b}$	
Daily Temperature Range	$9.807 (8.507, 11.107)^{a}$	$8.863 (7.563, 10.163)^{a}$	$8.732 (7.432, 10.032)^{a}$	$16.536 (15.236, 17.836)^{\rm b}$	$14.349 (13.049, 15.649)^{bc}$	$13.435 (12.135, 14.735)^{c}$	
Min. Relative Humidity	$73.49 \ (69.39, 77.59)^{\rm ab}$	76.29 (72.19,80.39) ^a	$67.403 \ (63.303, 71.503)^{\rm b}$	$47.676 (43.576, 51.776)^{c}$	$48.835 (44.735, 52.935)^{c}$	$44.143 (40.043, 48.243)^{c}$	
Mean Relative Humidity	$89.006 \ (86.232, 91.779)^{\rm ab}$	$90.382 (87.609, 93.155)^{a}$	84.428 (81.655,87.201) ^b	$75.388 (72.614, 78.161)^{c}$	$75.567 (72.794, 78.34)^{c}$	$69.005 (66.232,71.778)^{d}$	
Max. Relative Humidity	31.533 (30.763,32.302) ^a	$30.86 (30.091, 31.629)^{a}$	$31.399 (30.63, 32.168)^{a}$	$27.567 (26.798, 28.336)^{\rm b}$	$26.58 (25.811, 27.35)^{b}$	$26.846 (26.077, 27.615)^{c}$	
Daily Humidity Range	$26.458 (22.065, 30.851)^{a}$	23.69 $(19.296, 28.083)^{a}$	$30.978 (26.585, 35.371)^{a}$	$51.686 \ (47.292, 56.079)^{\rm b}$	$50.094 (45.701, 54.487)^{\rm b}$	$47.628 (43.235,52.021)^{\rm b}$	

Table 2.3: GZLM model results of land class, season, and their interaction on demographic and infection rates. Significance was assessed via Wald Chi-square tests ($\alpha = 0.05$) and there was no evidence that data failed to meet assumptions of normality. Significant effects at the 0.05 level are indicated in boldface.

	Class			Season			Class*Season		
	df	χ^2	p-value	df	χ^2	p-value	df	χ^2	p-value
Survival	2	0.0361	0.982	1	61.129	< 0.001	2	5.891	0.0526
Development Rate	2	3.847	0.1461	1	597.51	$<\!0.001$	2	3.108	0.2114
Wing Length	2	0.835	0.6587	1	2.7937	0.0946	2	14.748	< 0.001
Per Capita Growth (r')	2	0.667	0.717	1	219.84	< 0.001	2	2.622	0.230
Infection	2	18.168	< 0.001	1	12.271	< 0.001	2	1.985	0.371
Dissemination	2	14.253	< 0.001	1	14.909	< 0.001	2	0.941	0.625
Infectiousness	2	1.105	0.575	1	3.63	0.057	2	0.302	0.860
Vectorial Capacity	2	0.161	0.922	1	5.721	< 0.0017	2	0.905	0.636

Table 2.4: Dengue infection rates. The rates of infection (mosquitoes with dengue positive bodies), dissemination (infected mosquitoes with dengue positive heads) and infectiousness (infected mosquitoes with dengue positive saliva) across season and land class. Raw numbers of positive samples are shown with denominator in parentheses.

Season	Land Class	No. infected (n)	No. disseminated (n)	No. infectious (n)
Summer				
	Rural	22 (56)	19(60)	6(60)
	Suburban	32(57)	26(57)	10(57)
	Urban	10(51)	10 (53)	7(53)
Fall				
	Rural	32 (50)	30(50)	3(47)
	Suburban	28(43)	25 (41)	3(43)
	Urban	26 (59)	22 (57)	4 (59)

Table 2.5: Effect of temperature within a season. Model results from GZLMs estimating the effect of temperature within a season. Binomial models were fit with a logit-link function. Except for those models predicting infection metrics and vector competence, site was included as a random effect.

		eta	$\mathbf{d}\mathbf{f}$	χ^2	F-value	p-value
Summer	Survival	-0.328	1	4.943	-	0.026
	Development	0.000	1	0.007	-	0.936
	Wing Length	0.060	1	2.343	-	0.126
	Growth	-0.006	1	0.774	-	0.379
	Body Inf	-0.348	1	0.240	-	0.624
	Head Inf	-0.346	1	0.223	-	0.637
	Sal Inf	-0.488	1	0.580	-	0.446
	VC	-5.484	1	-	2.275	0.175
Fall	Survival	0.368	1	7.441	-	0.006
	Development	0.002	1	2.554	-	0.110
	Wing Length	0.037	1	1.644	-	0.200
	Growth	0.011	1	1.717	-	0.190
	Body Inf	-0.211	1	0.378	-	0.539
	Head Inf	-0.346	1	1.032	-	0.310
	Sal Inf	-0.932	1	1.276	-	0.259
	VC	0.295	1	-	2.173	0.184

Table 2.6: Additional variation in residuals explained by temperature. Model results from fitting temperature to residuals of original models (land class x season) for each response variable. In all models, temperature did not explain any additional variation, as evidenced by low mean sum of squares and F-statistics.

	df	Mean Sq	F value
Survival	1	1.948	0.302
Development	1	0.000	0.324
Wing Length	1	0.002	0.055
Growth	1	0.000	0.000
Body Inf	1	0.795	0.617
Head Inf	1	0.156	0.124
Sal Inf	1	0.079	0.132
VC	1	0.031	0.006

Figures



Figure 2.1: Map of study sites in Athens, GA. Inset illustrates location of Athens-Clarke County (black outline) in the state of Georgia. Symbols represent land classes (square: rural, circle:suburban, triangle: urban). Colors represent the amount of impervious surface within the 210m focal area of each pixel, as illustrated on the color bar on the bottom.



Figure 2.2: Temperature and relative humidity across season and land class. The solid line represents the mean temperature and relative humidity across trays in each land class. The dotted lines represent the mean minimum and maximum temperature and relative humidity across trays in each land class.



Figure 2.3: Demographic rates of mosquitoes across season and land class. Female a) larval development rate, b) egg-to-adult survival, and c) per capita population growth rate across the summer (circle) and fall (diamond) trials and rural, suburban, and urban land classes. Points represent site-level means (e.g. the mean of all four trays within a site for each season) with standard error bars. Some standard error bars are not visible because they are small enough to be obscured by the point.



Figure 2.4: Infection rates of mosquitoes across season and land class. Rates of a) infection, b) dissemination, and c) infectiousness of dengue in female mosquitoes at 21 days post infection across the summer (dark fill) and fall (light \S) trials and rural, suburban, and urban land classes. Mean site-level values are plotted with error bars representing standard error (n = 3).



Figure 2.5: The effect of larval temperature on predicted vectorial capacity. The calculated vectorial capacity by site across individual mean temperature prior to infection assays for field based (circle, dotted box) and grand mean (diamond, solid box) calculations. Boxplots represent mean \pm s.d. per calculation type and block.



Figure 2.6: Bias in VC due to not accounting for site level carry-over effects across land class and season.

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Chapter 3

Assessing temperature-dependent competition between two invasive mosquito species

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Abstract

Invasive mosquitoes are expanding their ranges into new geographic areas and interacting with resident mosquito species. Understanding how novel interactions can affect mosquito population dynamics is necessary to predict transmission risk at invasion fronts. Mosquito life-history traits are extremely sensitive to temperature and this can lead to temperature-dependent competition between competing invasive mosquito species. We explored temperature-dependent competition between Aedes aegypti and Anopheles stephensi, two invasive mosquito species whose distributions overlap in India, the Middle East, and North Africa. We followed mosquito cohorts raised at different intraspecific and interspecific densities across five temperatures (16 °C - 32 °C) to measure traits relevant for population growth and to estimate species' per capita growth rates. We then used these growth rates to derive each species competitive ability at each temperature. We find strong evidence for asymmetric competition at all temperatures, with Ae. aegypti emerging as the dominant competitor. This was primarily due to differences in larval survival and development times across all temperatures that resulted in a higher estimated intrinsic growth rate and competitive tolerance estimate for Ae. aegypti compared to An. stephensi. The spread of An. stephensi into the African continent could lead to urban transmission of malaria, an otherwise rural disease, increasing the human population at risk and complicating malaria elimination efforts. Competition has resulted in habitat segregation of other invasive mosquito species, and our results suggest that it may play a role in determining the distribution of An. stephensi across its invasive range.

Introduction

Multiple mosquito species have invaded new regions in recent decades (e.g., Aedes albopictus in the US and Europe (Medlock et al. 2012), Culex coronator in the US (Wilke, Benelli, and Beier 2020), Aedes japonicus in Europe (Schaffner et al. 2009)). Invasive mosquito species often compete with native mosquito species for resources and have been implicated in the decline of native species in several instances (Kaufman and Fonseca 2014; Lounibos et al. 2016). However, some invasive mosquito species are able to coexist with the native species in a portion of their range due to differences in competitive outcomes dependent on the environmental context (Lounibos and Juliano 2018).

Context-dependent competition results when competition dynamics depend on the environmental context, particularly abiotic variables such as temperature (Chamberlain, Bronstein, and Rudgers 2014). For example, temperature-dependent competition has been observed in many systems and especially for temperature-sensitive organisms such as *Tribolium* beetles (Park 1954), *Daphnia spp.* (Fey and Cottingham 2011) and aphids (Grainger, Rego, and Gilbert 2018). Like most ectotherms, mosquito life history traits are highly dependent on temperature, and whether competition results in co-existence or exclusion may depend on temperature and species' individual thermal niches.

Environmentally-dependent competition has affected the invasion dynamics of two mosquito species in the Southeastern United States, *Aedes aegypti* and *Ae. albopictus. Ae. aegypti* was introduced to the Americas in the 1700s (Brady and Hay 2020), while *Ae. albopictus* was introduced more recently in the 1980s (Sprenger and Wuithiranyagool 1986). Since its introduction, *Ae. albopictus* has reduced the range of *Ae. aegypti* in the southeastern US through a combination of female satyrization and larval competition (Lounibos and Juliano 2018). However, larval competition is temperature-dependent, with *Ae. aegypti* able to persist at higher temperatures (Lounibos 2002). The environmental-dependence of species coexistence is further complicated by the higher desiccation tolerance of *Ae. aegypti* eggs compared to *Ae. albopictus* (Juliano et al. 2002). In this case, temperature-dependent competition between *Ae. aegypti* and *Ae. albopictus*, in addition to asymmetric reproductive interference, has contributed to habitat segregation and reduced population abundances of *Ae. aegypti* locally (Lounibos and Juliano 2018).

Similar to the invasion of Ae. albopictus in the southeastern US, the range of Anopheles stephensi is currently expanding from its previous distribution within the Indian sub-continent and the Arab peninsula to parts of Northeast Africa, where Ae. aegypti is endemic (Seyfarth et al. 2019; Surendran et al. 2019). Unlike other Anopheles species that only breed in natural water bodies, An. stephensi breeds in artificial containers in urban areas (Thomas et al. 2016), where it serves as a primary vector of malaria (Singh et al. 2017). In these habitats, An. stephensi is often found co-habiting with other container species, including Ae. aequpti (Mariappan et al. 2015). Whether these species interact has not been studied. Both species demonstrate sensitivity to temperature, but their specific life history traits differ in their responses to temperature (Mordecai et al. 2013; Mordecai et al. 2017), which may translate to temperature-dependent differences in competitive ability. Additionally, Ae. aequpti is endemic to the African continent and a primary vector for arboviruses such as yellow fever and dengue, while An. stephensi is a primary vector of urban malaria in its endemic range. Understanding how these species interact can aid in predicting how the local mosquito vector community, and therefore human disease risk, may be affected by the invasion of An. stephensi.

We tested for the existence and measured the strength of temperature-dependent competition between *Ae. aegypti* and *An. stephensi* across a range of temperatures (16 °C - 32 °C). At each temperature, we followed cohorts of mosquitoes reared at different intra- and interspecific densities and measured life history traits relevant to population dynamics. We calculated per capita growth rates from these trait measurements and fit competition models to these data. From these models, we then calculated competition coefficients to estimate the relative competitive ability of each species at each temperature.

Methods

Experimental

We used a response surface design across fifteen density treatments (Fig. 3.1, Table 3.1) and five temperature treatments (16 °C, 20 °C, 24 °C, 28 °C, 32 °C) to explore pairwise competition between *Ae. aegypti* and *An. stephensi*. Response surface designs vary the densities of competing species independently across a range of total densities, which allows for the fitting and parameterization of competition models (Inouye 2001). Densities were chosen so that the median total density corresponded to standard rearing conditions for these strains (200 larvae/1 L of water), allowing for species densities that were lower and higher than optimum. The range of temperatures represented the full range at which each species can persist when reared individually, including field-relevant temperatures. The strain of *Ae. aegypti* was an outbred field-derived population originating from Tapachula, Chiapas, Mexico, 2016. The F5 generation was used in this experiment. The strain of *An. stephensi* (Liston) was sourced from a long-standing colony housed at Pennsylvania State University that was originally obtained from the Walter Reed Army Institute of Research. This experimental design was replicated three times.

Larvae were hatched on experimental Day 0. On Day 1, 1st instar mosquito larvae were placed in quart-size mason jars with 250mL of reverse osmosis filtered water and 0.1g cichlid pellet food (Hikari Cichlid Cod Fish pellets). Rearing jars were placed in incubators (Percival Scientific), following the intended temperature treatments with 85% (\pm 5%) relative humidity (RH), and 12:12hr light:dark diurnal cycle. Temperature regimens were programmed to a mean given by the experimental treatment (16 °C, 20 °C, 24 °C, 28 °C, 32 °C \pm 0.5 °C) and daily periodic fluctuation of 9 °C, following the Parton-Logan equation (Parton and Logan 1981), which is characterized by a sine wave during the daytime and exponential curve at night. Rearing jars were inspected daily for emerged mosquitoes and the numbers of males and females emerging on each day recorded. Following emergence, adults were pooled by day of emergence, temperature, species, and density treatment. Adults were kept in a 16 oz paper cup in a walk-in incubator (Percival Scientific) at 27 °C (\pm 0.5 °C), 85% RH (\pm 5%), and 12:12hr light:dark cycle and offered a 10% sucrose solution *ad libitum*.

Mosquitoes that emerged up to and including the day of peak emergence were allowed to mate four to six days before being offered a blood meal. Forty-eight hours prior to blood feeding, the sucrose was removed and replaced with deionized water, which was then removed 24hr later. Blood meals were administered via a water-jacketed membrane feeder at 38 °C for 30 minutes. A maximum of 10 blood-fed females per treatment were sorted into individual oviposition containers and kept at 27 °C (\pm 0.5 °C), 85% (\pm 5%) RH, 12:12hr dark:light cycle. Oviposition containers consisted of a 50mL centrifuge tube with a damp cotton ball and filter paper at the bottom to collect eggs. Centrifuge tubes were covered with a fine mesh to keep mosquitoes inside and allow for air circulation. During this time, females had access to a 10% sucrose solution *ad libitum*. Females were monitored daily for oviposition events. The date of the oviposition event was noted and the number of eggs was counted the following day to allow for females who were monitored while ovipositing to finish laying eggs. After oviposition, the filter paper and cotton ball were removed and each female was monitored daily until death. Wing length was recorded for all female mosquitoes to estimate fecundity for those mosquitoes whose fecundity was not directly measured (Armbruster and Hutchinson 2002). All females' wings were mounted on a glass side to measure the wing length from the distal end of the alula to the apex of the wing using a dissecting scope and micrometer.

Life History Traits

We measured five traits relevant to population dynamics: larval survival, time to emergence, fecundity, adult longevity, and wing length (a standard proxy for fecundity (Armbruster and Hutchinson 2002)). Larval survival was modeled as a binomial random variable for the number of larvae surviving from the 1st-instar larval stage until adult emergence. Time to emergence was measured as the median time for larvae to develop from 1st instar to an adult per jar, in days. The median was used because the distribution of emergence times within a jar was right skewed. Fecundity was the number of eggs laid during the first oviposition event. Females that did not oviposit were assigned a fecundity of zero. Adult longevity was the number of days between adult emergence and death. Wing length was the distance from the distal end of the alula to the apex of the wing in mm. All traits were only measured for females, and the number of females per treatment at the start of the experiment was assumed to be 50% of the initial number of larvae within each jar.

We used generalized linear mixed models to test for the effect of temperature, *Ae. aegypti* density, *An. stephensi* density, and the interactions between temperature and species' densities on each life history trait. We included replicate as a random intercept in all analyses. The models for larval survival were fit using a binomial distribution and a logit link. Because of the frequent occurrence of jars with no *An. stephensi* surviving, we used a hurdle model, which allows the degree of zero-inflation to vary across observations dependent on other predictor variables (Brooks et al. 2017a). In our model, the structural zero-inflation term was dependent on both species' densities. The time to emergence was modeled as the day that

50% of the females emerged and was fit with a generalized Poisson distribution and log link for both species. The generalized Poisson distribution is a mixture of Poisson distributions that is similar to a negative binomial distribution, but is more appropriate for right-skewed data due to its long tail (Joe and Zhu 2005). Fecundity was modeled with a negative binomial distribution and log link, including a term for zero-inflation to account for some females that laid no eggs. Adult longevity was modeled with a generalized Poisson distribution and log link. Wing length was modeled with a gaussian distribution and identity link. Due to the low survival of An. stephensi larvae, sample size for this species was low, and models with interactions only converged when the response variable was the time to emergence or wing length. Therefore, the other three An. stephensi models included main effects only, as our data did not contain enough information to explain these interactions. All models were fit using the glmmTMB package (Brooks et al. 2017b) and we assessed the residuals for divergence from normality using the DHARMa package (Hartig 2019) in R v. 3.6.4 (Team 2018).

Calculating the Per Capita Growth Rate

We calculated the per capita growth rate for each treatment following Chmielewski et al. (2010), substituting our own empirically-measured traits. We define the per capita growth rate, r, as the change in the population-level abundance of female mosquitoes attributable to one female mosquito:

$$r = \frac{lnR_0}{\tau} \tag{3.1}$$

where R_0 is the change in population size (ΔN) in one generation and τ is the generation time, or mean time to maturity and reproduction. R_0 is the total population fecundity divided by the initial population size (N_0) :

$$R_0 = \frac{\sum_x A_x F_x}{N_0} \tag{3.2}$$

where F_x is the total lifetime reproduction of an individual emerging on day x and A_x is the number of individuals emerging on day x.

Lifetime fecundity, F_x , is calculated from measured values of gonotrophic cycle length in days (g), adult lifespan (l), and the number of eggs per gonotrophic cycle (f_x) :

$$F_x = f_x g^{-1} l \tag{3.3}$$

When f_X was not directly measured for an individual, it was approximated by a speciesspecific linear regression relating wing length (w_x , in mm) to fecundity from experimental data (*Ae. aegypti*: $f_x = -98.51 + 52.42w_x$, *An. stephensi*: $f_x = -51.57 + 36.75w_x$). Some females had no intact wings to measure, and these were assigned the mean fecundity value for that temperature and density treatment for that species in that replicate.

Following Livdahl and Sugihara (1984), τ was weighted by the overall contribution to population fecundity:

$$\tau = \frac{\sum_{x} (x+g)(A_x F_x)}{\sum_{x} A_x F_x} \tag{3.4}$$

where x is the day of emergence, g is the gonotrophic cycle length in days, and A_x and F_x are the number of females that emerged on day x and their predicted lifetime fecundity, respectively.

This results in a final equation for the per capita growth rate for each density x temperature treatment:

$$r' = \frac{ln(\frac{1}{N_0}\sum_x A_x w_x g^{-1}l)}{\frac{\sum_x (x+g)(A_x w_x g^{-1}l)}{\sum_x A_x w_x g^{-1}l}}$$
(3.5)

Assessing the temperature-dependence of competition

As there is no consensus model for competitive interactions between mosquito species, we fit five theoretical discrete-time competition models that differ primarily in the shape of the response of the per capita growth rate to increasing species densities for each temperature treatment and mosquito species. We selected the best fit model using AIC (Table 3.2). All models were within 2 AIC of each other, and we chose the model with the lowest AIC, which approximates a Lotka-Volterra competition model where growth rates decline linearly with increasing species densities:

$$e^{r_i} = \lambda_i - \alpha_{ii} N_i - \alpha_{ij} N_j \tag{3.6}$$

where r_i is the per capita growth rate of species i, λ_i is the intrinsic growth rate of species i, α_{ii} is the competition coefficient of intraspecific competition, α_{ij} is the competition coefficient of interspecific competition, and N_i and N_j are the starting population densities of species iand j. We parameterized this model separately for each temperature level and species to explore how λ , α_{ii} , and α_{ij} changed as a function of the larval environment, and therefore if competitive interactions are temperature-dependent. We estimated the three parameters by fitting a non-linear least squares regression in R v. 3.6.3 (Team 2018).

We used the fit parameters from these equations to estimate each species' competitive ability (K_i) at each temperature following Hart et al. (2018):

$$K = \frac{\lambda_i - 1}{\sqrt{\alpha_{ii}\alpha_{ij}}} \tag{3.7}$$

Briefly, this definition of competitive ability is derived from the concept of mutual invasibility, which states that each species must be able to invade while the other is at equilibrium in order for the species to coexist (Chesson 2000). Solving for the conditions that allow for mutual invasion results in a ratio representing the average fitness difference of the two species, from which we derive each species fitness, or competitive ability, K. Importantly, this metric incorporates growth in the absence of competition $(\lambda_i - 1)$ and the species ability to tolerate both intra- and inter-specific competition $(\sqrt{\alpha_{ii}\alpha_{ij}})$. Because K incorporates a species' growth rate and tolerance for competition, it allows for the possibility of a species with a low overall growth rate, but which is very robust to competition, to be the dominant long-term competitor. Thus, a species that is tolerant of competition, even it grows slowly, can persist and grow to high overall abundance, increasing the overall amount of competitive pressure and ultimately outcompeting less tolerant species regardless of their growth rates. By choosing to use these parameters, rather than direct measurements of fecundity, this definition of competitive ability incorporates differences across all life history stages to evaluate long-term competitive outcomes.

Results

Our factorial design included fifteen species density combinations across five temperature treatments (75 treatments total) replicated three times. In one replicate, one jar (8 Ae. *aegypti*: 24 An. stephensi at 24 °C) had only male Ae. aegypti emerge, and so this was dropped from all analyses, resulting in 179 jars across three replicates. After adult emergence, we followed a total of 1242 Ae. aegypti and 134 An. stephensi females to estimate fecundity and adult longevity.

Life History Traits

Both species' larval survival rates exhibited a unimodal response to temperature, with survival highest at intermediate temperatures (Fig. 3.2 A,D, Table 3.3, 3.4). This response was strongest for *Ae. aegypti* mosquitoes at high overall densities. In general, *Ae. aegypti* survival decreased with increasing intraspecific densities, although the shape of this relationship depended on temperature (Fig. 3.2B, Table 3.3). There was no evidence for an effect of interspecific densities on *Ae. aegypti* larval survival (Fig. 3.2 C, Table 3.3). *An. stephensi* survival was strongly negatively impacted by both interspecific and intraspecific densities and no *An. stephensi* survived above interspecific densities of 32 (Fig. 3.2 E,F, Table 3.4).

Both species emerged more quickly with increasing temperatures and neither species' time to emergence was impacted by interspecific or intraspecific densities (Fig. 3.3, Table 3.3, 3.4). However, the time to emergence was generally longer for *An. stephensi* larvae than *Ae. aegypti* larvae at all treatment combinations (Fig. 3.3).

There was no evidence for an effect of temperature on *Ae. aegypti* female fecundity (Fig. 3.4 A, Table 3.3). Higher intraspecific densities resulted in lower fecundity (Fig. 3.4 B, Table 3.3) regardless of temperature treatment, but interspecific density had no effect (Fig. 3.4 C, Table 3.3). We found no evidence for an effect of temperature, interspecific density, or intraspecific density on *An. stephensi* fecundity (Fig. 3.4 E,F, Table 3.4).

Ae. aegypti longevity was highest in females that were reared at intermediate temperatures (Fig. 3.5 A, Table 3.3). We failed to find evidence for an effect of intraspecific or interspecific densities on Ae. aegypti longevity (Fig. 3.5 B,C, Table 3.3). We found no evidence for a difference in An. stephensi longevity across any of the three treatments (Fig. 3.5 D,E,F, Table 3.4). Across all temperatures, Ae. aegypti females lived approximately twice as long as

An. stephensi females, with mean adult lifespans of $32.1 \pm 16.0 \ sd$ and $16.7 \pm 9.80 \ sd$ days, respectively.

Increasing temperatures led to shorter wing lengths for both species (Fig. 3.6 A,D, Table 3.3, 3.4). *Ae. aegypti* wing lengths also decreased with increasing intraspecific densities (Fig. 3.6 B, Table 3.3), but were unaffected by interspecific densities (Fig. 3.6 C, Table 3.3). Neither species' density was found to influence *An. stephensi* wing lengths (Fig. 3.6 E,F, Table 3.4).

Per Capita Rates of Change

Temperature significantly influenced both species' per capita rate of change. Ae. aegypti growth rates had a unimodal relationship with temperature (Fig. 3.7 A, Table 3.3) and An. stephensi growth rates increased with increasing temperatures (Fig. 3.7 D, Table 3.4). Ae. aegypti growth rates decreased with increasing Ae. aegypti densities (Fig. 3.7 B, Table 3.3), but we found no evidence for an effect of An. stephensi density on Ae. aegypti growth rates (Fig. 3.7 C, Table 3.3). We found no support for an effect of either species' densities on An. stephensi growth rates (Fig. 3.7 E,F, Table 3.4).

Temperature Dependence of Competition

The parameters from fitted competition models differed across temperature levels (Fig. 3.8). Both species' intrinsic growth rates (λ) were dependent on temperature (Fig. 2A). Ae. aegypti growth rates had a unimodal relationship with temperature, peaking at 28 °C. An. stephensi growth rates increased with temperature (Fig. 3.8). However, competition models did not converge for An. stephensi at 24 °C and 32 °C due to a low sample size, rendering the shape of An. stephensi's response to temperature less clear. Both species' intraspecific competition coefficients (α_{ii}) increased with temperature (Fig. 3.8 B). The effect of Ae. aegypti density on An. stephensi population growth rates increased with increasing temperatures, while the effect of An. stephensi did not differ from zero at any temperature. Inserting these parameters into the general equation for competitive ability (Eq. 3.7) illustrates that Ae. aegypti is the dominant competitor at all temperatures tested (Fig. 3.8 D).

Discussion

Mosquito vectors are rapidly expanding their ranges into new geographic areas and competing with resident mosquito species (e.g. Ae. albopictus in the US and Europe, Ae. koreicus in Italy (Marcantonio et al. 2016), Cx. coronator in Southeastern US (Wilke, Benelli, and Beier 2020)). Understanding how novel interactions may affect mosquito population dynamics is necessary for predicting disease risk at invasion fronts, such as that of An. stephensi (Seyfarth et al. 2019; Takken and Lindsay 2019). We found strong evidence for asymmetric competition between Ae. aegypti and An. stephensi across the full range of temperatures tested in this experiment, with Ae. aegypti consistently emerging as the dominant competitor. The intrinsic growth rate of An. stephensi was lower than that of Ae. aegypti at all temperatures, and An. stephensi was less tolerant of interspecific competition than Ae. aegypti. Given the global range of Ae. aegypti, this competitive interaction has the potential to influence the rate of spread of An. stephensi in its invasive range.

Life-history traits were influenced by both temperature and species densities. Ecothermic metabolic theory predicts that colder temperatures result in longer development times that translate into larger bodied female mosquitoes that have higher fecundity rates (Kingsolver and Huey 2008). This has often been the case in mosquito systems (Armbruster and Hutchinson 2002,but see Reiskind and Zarrabi 2012). In our study, colder temperatures resulted in longer development times and wing lengths for both species, but the effect of temperature on

fecundity was much weaker. The size-fecundity relationship in mosquitoes is typically weakest towards the thermal minima (Costanzo, Westby, and Medley 2018), with fecundity saturating with decreasing temperatures. In this study, measured fecundity at 16 °C and 20 °C was less than predicted by a linear size-fecundity relationship (Fig. 3.4 A), mirroring this breakdown of the relationship at cold extremes. Interestingly, we did not find evidence that species' densities influenced either species' time to emergence, in contrast with previous studies on larval competition and mosquito development times (Couret, Dotson, and Benedict 2014). However, *Ae. aegypti* wing length and fecundity did decrease with increasing conspecific densities. This is in agreement with other studies that found that limiting resources via competition leads to smaller bodied mosquitoes (Alto et al. 2005; Juliano et al. 2014). Rather than delaying emergence to develop into larger bodied mosquitoes given resource limitations, mosquitoes under higher competitive pressures in our study emerged at similar times, but with smaller bodies.

While we found that both species' intrinsic growth rates and competition coefficients were temperature-dependent, this difference did not affect the outcome of competition. The species' responses to conspecific competition were comparable, but the effect of $Ae. \ aegypti$ on $An. \ stephensi$ was much stronger than the effect of $An. \ stephensi$ on $Ae. \ aegypti$. In the field, both species breed in artificial containers, but $Ae. \ aegypti$ is more tolerant to overcrowding than $An. \ stephensi$ (Yadav et al. 2017). This agrees with our finding that larval $An. \ stephensi$ survival was low at high densities. $Ae. \ aegypti$'s tolerance of crowding may be a result of the close association of $Ae. \ aegypti$ with humans throughout its evolutionary history, leading to adaptations well-suited for human-modified landscapes (Brown et al. 2014). Adult $An. \ stephensi$ were generally larger and had a longer development period than $Ae. \ aegypti$ in our study. This concurs with allometric theory, which predicts a positive relationship between organism body size and development time for ectotherms (Gillooly et al. 2002).

This difference in larval development rates led to a longer generational period and lower intrinsic growth rate for *An. stephensi* compared to *Ae. aegypti*, contributing to differences in competitive ability.

Our laboratory experiment suggests that long term coexistence between the two species is unlikely; yet, the two species co-exist at the landscape-scale in the endemic range of An. stephensi and An. stephensi is currently expanding into the range of Ae. aegypti. Our study only considers interactions within one larval habitat and does not account for mechanisms that act at a larger-scale that could explain the co-existence patterns found in the field. One such mechanism is the classical competition-dispersal trade-off: metacommunity level coexistence is possible if the inferior competitor's superior dispersal ability allows it to colonize new patches where the competitive pressure is lower (Hastings 1980). Indeed, Ae. aegypti flight range is estimated to be 83.4 \pm 52.2m, compared to a longer dispersal distance of 144.5 \pm 53.0m for An. stephensi (Verdonschot and Besse-Lototskaya 2014). Thus, while the species may not coexist within a single larval habitat, the wider dispersal range of An. stephensi may allow for landscape-scale coexistence at the level of the metacommunity. Similarly, species-specific microhabitat preferences may reduce the frequency of habitat overlap, and thereby competition, during the larval stage. While An. stephensi and Ae. aequpti are found together in small artificial containers, An. stephensi also oviposit in larger water bodies, such as overhead water tanks, where Ae. aegypti is less common (Thomas et al. 2016). These water bodies may serve as refugia for An. stephensi from high competitive pressure by Ae. aegypti and allow for broad-scale coexistence. Species differences at non-competing life stages may also allow for coexistence in the field. For example, our models assumed an equal embryonic development period for both species between oviposition and hatching. No studies have directly measured An. stephensi embryonic development times, but a study in An. albitarsis estimate that it takes around 34 hrs for eggs to fully mature, noting development timings

similar to An. maculipennis (Monnerat et al. 2002). In comparison, Ae. aegypti eggs are fully developed around 90hrs and require a week for embryonation (Raminani and Cupp 1978). These species differences in egg maturation rates could lengthen our estimated generation times for Ae. aegypti, decreasing the species' intrinsic growth rates. Finally, interpopulation differences in competitive ability have been found in Ae. aegypti (Leisnham and Juliano 2010), and invasive An. stephensi populations may have an increased competitive ability compared to those in endemic areas (e.g. the Evolution of Increased Competitive Ability hypothesis (Strayer et al. 2006)). If the invader genotype of An. stephensi is able to coexist with, or even outcompete, Ae. aegypti, then the result of strong asymmetric competition we found with our specific populations may not apply to competition in the region of North Africa where An. stephensi is currently invading. Further research that includes a variety of field-derived genotypes in competition experiments could explore the importance of genotype x genotype interactions in this system.

While we found the difference in competitive ability between the two species to be strong across all temperatures, this could also be an artefact of our specific abiotic and biotic experimental conditions. Food type and availability alters the outcome of competition between other container mosquitoes (Juliano 2010; Murrell and Juliano 2008; Yee, Kaufman, and Juliano 2007), and could play a role in this system as well. Other abiotic factors, such as desiccation tolerance of eggs (Juliano et al. 2002) or climate factors during adult life stages, may also change the outcome of this competitive interaction. The presence of additional species, such as predators (Juliano 2009), other competitors (Bowden 2016), or parasites (Westby et al. 2019), also have the potential to alter this pair-wise interaction. Additionally, the two strains used in this experiment have different domestication histories due to constraints on strain availability. The *Ae. aegypti* strain was recently derived from Mexico, while the *An. stephensi* (Liston) strain was originally established from an Indian population several decades ago and since kept in laboratory conditions. A laboratory strain could exhibit a high tolerance for crowding (Kesavaraju, Afify, and Gaugler 2012), but may also have reduced overall fitness due to inbreeding (Koenraadt, Kormaksson, and Harrington 2010). Additionally, these strains are not sympatric in nature, having originated in Mexico and India, and this combination may not reflect the competitive interactions between *Ae. aegypti* and *An. stephensi* in North Africa. Therefore, the overall effects of strain differences on competition outcomes are difficult to predict, but may alter our predictions regarding long-term coexistence.

Generally, invasive mosquito species exhibit a higher competitive ability than native species, leading to a reduction in the native population abundance or range (Juliano and Lounibos 2005; Kaufman and Fonseca 2014). Although An. stephensi is spreading into North Africa (Surendran et al. 2019), it may not significantly reduce the population abundance of existing Ae. aegypti populations as has been seen in the Southeastern US, given its low competitive ability relative to Ae. aegypti. Further, if Ae. aegypti is limiting the spread of An. stephensi into urban areas in the Middle East and North Africa, vector control efforts targeting Ae. aequivation acquired consequences for An. stephensi dynamics. For example, vector control efforts that reduce Ae. aequpti abundances could lead to an increase in An. stephensi abundances via competitive release. This unexpected consequence was observed when Ae. albopictus invaded urban centers in Manila, Philippines following a reduction of its competitor Ae. aegypti due to targeted insecticide spraying (Gilotra, Rozeboom, and Bhattacharya 1967; Lounibos 2007). Larval source reduction campaigns, however, could limit the abundance of both species by reducing their shared habitat. In areas with both mosquito vectors, vector control efforts should include a variety of approaches, rather than ones that target a single species, to avoid the competitive release of other mosquito vectors. We found evidence for strong asymmetric competition between Ae. aegypti and An. stephensi. This study is the first test of competition sbetween these two species and only considered one strain of each species across one environmental gradient (e.g. temperature). While more work is needed to assess the applicability of our results to the field, our study does suggest that competition is an important factor to consider in the context of the expanding range of An. stephensi. Temperature-based models of An. stephensi distribution predict high environmental suitability for the species in the Horn of Africa (Miazgowicz et al. 2020), but biotic interactions, such as competition, may alter this prediction. In addition to An. stephensi, many other mosquito species of public health importance have been the focus of temperature-based suitability models that rarely include biotic interactions (Golding, Nunn, and Purse 2015). For Ae. aegypti and Ae. albopictus, especially, biotic interactions are hypothesized to limit species ranges (Lounibos and Juliano 2018). Our study suggests that species interactions are also important for population dynamics of An. stephensi, and that these interactions should be empirically tested and, when appropriate, incorporated into our predictions of mosquito species ranges and invasion dynamics.

Tables

1able 3.1:	Species densities (per 250 mL) used in response surface design.
$An. \ stephensi$	$Ae. \ aegypti$
32	0
24	8
16	16
8	24
0	32
64	0
48	16
32	32
16	48
0	64
128	0
96	32
64	64
32	96
0	128

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Table 3.2: AIC values resulting from fitting five theoretical competition models to our estimates of per capita growth rates for Ae. aegypti. λ_i , α_{ii} , and α_{ij} are all temperature-dependent.

Model	$\mathbf{d}\mathbf{f}$	AIC
$e^{r_i} = \frac{\lambda_i}{1 + \alpha_{ii}N_i + \alpha_{ij}N_j}$	16	-314.3939
$e^{r_i} = \frac{\lambda_i}{(1 + \alpha_{ii}N_i + \alpha_{ij}N_j)^b}$	17	-313.234
$e^{r_i} = \lambda_i e^{-\alpha_{ii}N_i - \alpha_{ij}N_j}$	16	-314.8702
$e^{r_i} = \frac{\lambda_i}{1 + N_i^{\alpha_{ii}} + N_j^{\alpha_{ij}}}$	Unable to fit	Unable to fit
$e^{r_i} = \lambda_i - \alpha_{ii} \dot{N}_i - \alpha_{ij} N_j$	16	-315.1535

Table 3.3: Table of coefficients from models of *Ae. aegypti* life history traits and per capita rates of change. 95% confidence intervals are below in parentheses. For larval survival thru longevity, if CIs overlap 1, it suggests that the predictor variable did not have a significant effect on the life history trait. Similarly, if estimates of the coefficients for wingspan and the per capita rate of change overlap 0, it suggests that the predictor variable did not have a significant effect on the life history trait. Similarly did not have a significant effect on the life history trait. Significant effects are bolded.

Predictors	Larval Survival	Time to Emergence	Fecundity	Longevity	Wing Length	Rate of Change
A adag Dangity	0.67	1.01	0.89	1.03	-0.11	-0.06
Acues Delisity	(0.62 - 0.72)	(1.00 - 1.01)	(0.84 - 0.93)	(1.00 - 1.07)	(-0.120.10)	(-0.11 - 0.00)
Anopheles Density	0.99	1.00	1.01	1.01	-0.01	0.00
	(0.94 - 1.04)	(1.00-1.00)	(0.97 - 1.05)	(0.99 - 1.04)	(-0.02 - 0.00)	(-0.05 - 0.04)
bs(Temperature)1	12.45	0.36	1.17	3.16	0.06	0.87
	(0.95 - 163.39)	(0.31 - 0.43)	(0.37 - 3.68)	(1.45 - 6.88)	(-0.24 - 0.37)	(-0.19 - 1.93)
h - (TT)2	28.94	0.28	1.98	0.58	-0.26	1.11
bs(remperature)2	(2.49 - 336.02)	(0.23 - 0.33)	(0.84 - 4.71)	(0.31 - 1.07)	(-0.52 - 0.00)	(0.46 - 1.76)
bg(Tomponsture)?	4.17	0.30	0.62	1.21	-0.67	0.76
bs(Temperature)3	(1.50 - 11.59)	(0.28-0.33)	(0.37 - 1.04)	(0.84 - 1.74)	(-0.810.53)	(0.28 - 1.25)
$\mathbf{A} = \mathbf{A} = \mathbf{D} = \mathbf{a} \cdot \mathbf{b} = (\mathbf{T} = \mathbf{a} - \mathbf{a} + \mathbf{a})1$	0.83	1.02	0.96	0.95	-0.02	-0.03
Acces Density x bs(remperature)	(0.64 - 1.09)	(1.00-1.04)	(0.84 - 1.11)	(0.86 - 1.04)	(-0.05 - 0.02)	(-0.16 - 0.11)
Addas Dansity y hs(Tomporatura)?	0.83	1.01	0.96	1.08	0.00	-0.01
Acues Density x bs(Temperature)2	(.64 - 1.06)	(0.99 - 1.03)	(0.86 - 1.07)	(1.00 - 1.16)	(-0.03 - 0.03)	(-0.10 - 0.07)
Adda Dansity x hs (Tomporatura)?	0.84	1.00	1.01	0.97	0.02	-0.01
Actes Density x bs(Temperature)5	(0.75 - 0.94)	(0.99-1.01)	(0.95 - 1.08)	(0.94 - 1.01)	(0.01 - 0.04)	(-0.07 - 0.05)
Anopholos Donsity y bs/Tomporaturo)1	1.02	1.01	1.01	0.96	-0.01	-0.01
Anopheles Density x bs(1emperature)1	(0.86 - 1.20)	(0.99 - 1.02)	(0.92 - 1.11)	(0.90 - 1.03)	(-0.03 - 0.02)	(-0.11 - 0.10)
Anopholos Donsity y bs/Tomporaturo)?	1.04	1.00	0.93	1.04	0.01	0.01
Anopheles Density x bs(Temperature)2	(0.89 - 1.21)	(0.99 - 1.02)	(0.86 - 0.99)	(0.98 - 1.09)	(-0.01 - 0.03)	(-0.05 - 0.08
Anonholog Dongity y hg(Tomponoture)	1.08	1.00	0.99	0.99	0.00	0.00
Anopheles Density x bs(Temperature)	(1.01 - 1.16)	(1.00-1.01)	(0.95 - 1.04)	(0.96 - 1.02)	(-0.01 - 0.01)	(-0.05 - 0.05)
			0.28			
Zero-Inflation Intercept			(0.20)			
			(0.24 - 0.32)			
Observations	179	179	1242	1194	1088	174
Marginal / Conditional R2	$0.371 \ / \ 0.387$	$0.987 \ / \ 0.989$	$0.175 \ / \ 0.204$	$0.093 \ / \ 0.208$	$0.736 \ / \ 0.741$	$0.925 \ / \ 0.969$

Table 3.4: Table of coefficients from models of *An. stephensi* life history traits and per capita rates of change. 95% confidence intervals are below in parentheses. For larval survival thru longevity, if CIs overlap 1, it suggests that the predictor variable did not have a significant effect on the life history trait. Similarly, if estimates of the coefficients for wingspan and the per capita rate of change overlap 0, it suggests that the predictor variable did not have a significant effect on the life history trait. Similarly did not have a significant effect on the life history trait. Similarly did not have a significant effect on the life history trait. Similarly did not have a significant effect on the life history trait.

Predictors	Larval Survival	Time to Emergence	Fecundity	Longevity	Wing Length	Rate of Change
A - d - D it	0.82	0.99	0.94	0.99	0.03	0.00
Acues Density	(0.71 - 0.95)	(0.95 - 1.04)	(0.80 - 1.12)	(0.92 - 1.06)	(-0.07 - 0.13)	(0.00 - 0.01)
Anonholog Dongity	0.62	0.99	0.94	0.95	0.09	0.00
Anopheles Density	(0.53 - 0.72)	(0.95 - 1.03)	(0.70 - 1.25)	(0.88 - 1.02)	(-0.07 - 0.25)	(0.00 - 0.00)
	13.42	0.17	1.15	1.92	2.71	0.20
bs(Temperature)1	(2.50 - 72.09)	(0.04 - 0.71)	(0.52 - 2.51)	(0.83 - 4.47)	(0.46 - 4.96)	(0.11 - 0.28)
h - (0.79	0.55		1.08	-2.10	
bs(Temperature)2	(0.24 - 2.61)	(0.03 - 10.87)	-	(0.59 - 1.97)	(-4.65 - 0.44)	-
ha/Tarran anaturna)?	1.57	0.55		1.23	0.79	
bs(Temperature)5	(0.64 - 2.83)	(0.07 - 4.33)	-	(0.80 - 1.89)	(-1.17 - 2.76)	-
A - d D: t h-(T)1		1.19			-0.21	
Aedes Density x bs(Temperature)	-	(0.99 - 1.42)	-	-	(-0.46 - 0.04)	-
Andre Dongity y ha(Tomponature)?		0.91			0.06	
Aedes Density x bs(Temperature)2	-	(0.67 - 1.23)	-	-	(-0.18 - 0.31)	-
Andra Danaity y ha(Tampanatuna)?		0.95			-0.10	
Acces Density x bs(Temperature)5	-	(0.79 - 1.15)	-	-	(-0.27 - 0.07)	-
Anonholog Dongity y hg(Town onetype)1		1.14			-0.46	
Anopheles Density x bs(Temperature)	-	(0.93 - 1.40)	-	-	(-0.820.09)	-
Anonholog Dongity y hg(Town onetype)?		0.94			0.21	
Anopheles Density x bs(Temperature)2	-	(0.58 - 1.53)	-	-	(-0.20 - 0.63)	-
Anonholog Dongity y hg(Town onetype)?		0.90			-0.25	
Anopheles Density x bs(Temperature)5	-	(0.64 - 1.28)	-	-	(-0.59 - 0.09)	-
Zono Inflation Intercent	0.00		2.83			
Zero-innation intercept	(0.00 - 0.02)	-	(1.92 - 4.16)	-	-	-
Zero-Inflation	2.35					
Aedes Density	(1.70 - 3.26)	-	-	-	-	-
Zero-Inflation	2.14					
Anopheles Density	(1.57 - 2.92)	-	-	-	-	-
Observations	180	52	134	127	127	23
Marginal/ Conditional R2	$0.304 \ / \ 0.328$	0.896 / 0.909	0.547 / 0.641	0.046 / 0.09	0.547 / 0.641	$0.508 \ / \ 0.657$

Figures



Figure 3.1: Species densities (per 250 mL) used in response surface design. Species densities are also noted in Table 3.1



Figure 3.2: Effect of temperature (A,D), Ae. aegypti density (B,E) and An. stephensi density (C,F) on each species' larval survival. Top row (A-C) is Ae. aegypti and bottom row (D-F) is An. stephensi. The points represent raw data, with each replicate denoted by a different symbol, and solid lines represent model fits with 95 % CI. In panels A and D, three lines are shown for three unique species ratios, 16:16 (solid), 32:32 (dashed), 64:64 (dotted). In panels B,C and E,F, solid lines represent the model fit with the other species density held constant at 16.



Temperature (C) = 16 = 20 = 24 = 28 = 32

Figure 3.3: Effect of temperature (A,D), Ae. aegypti density (B,E) and An. stephensi density (C,F) on each species' time to emergence. Top row (A-C) is Ae. aegypti and bottom row (D-F) is An. stephensi. The points represent raw data, with each replicate denoted by a different symbol, and solid lines represent model fits with 95 % CI. In panels A and D, three lines are shown for three unique species ratios, 16:16 (solid), 32:32 (dashed), 64:64 (dotted). In panels B,C and E,F, solid lines represent the model fit with the other species density held constant at 16.



Figure 3.4: Effect of temperature (A,D), Ae. aegypti density (B,E) and An. stephensi density (C,F) on each species' fecundity. Top row (A-C) is Ae. aegypti and bottom row (D-F) is An. stephensi. The points represent raw data, with each replicate denoted by a different symbol, and solid lines represent model fits with 95 % CI. In panels A and D, three lines are shown for three unique species ratios, 16:16 (solid), 32:32 (dashed), 64:64 (dotted). In panels B,C and E,F, solid lines represent the model fit with the other species density held constant at 16.



Figure 3.5: Effect of temperature (A,D), Ae. aegypti density (B,E) and An. stephensi density (C,F) on each species' longevity. Top row (A-C) is Ae. aegypti and bottom row (D-F) is An. stephensi. The points represent raw data, with each replicate denoted by a different symbol, and solid lines represent model fits with 95 % CI. In panels A and D, three lines are shown for three unique species ratios, 16:16 (solid), 32:32 (dashed), 64:64 (dotted). In panels B,C and E,F, solid lines represent the model fit with the other species density held constant at 16.



Figure 3.6: Effect of temperature (A,D), Ae. aegypti density (B,E) and An. stephensi density (C,F) on each species' wing length. Top row (A-C) is Ae. aegypti and bottom row (D-F) is An. stephensi. The points represent raw data, with each replicate denoted by a different symbol, and solid lines represent model fits with 95 % CI. In panels A and D, three lines are shown for three unique species ratios, 16:16 (solid), 32:32 (dashed), 64:64 (dotted). In panels B,C and E,F, solid lines represent the model fit with the other species density held constant at 16.



Figure 3.7: Effect of temperature (A,D), Ae. aegypti density (B,E) and An. stephensi density (C,F) on each species' per capita rate of change. Top row (A-C) is Ae. aegypti and bottom row (D-F) is An. stephensi. The points represent raw data, with each replicate denoted by a different symbol, and solid lines represent model fits with 95 % CI. In panels A and D, three lines are shown for three unique species ratios, 16:16 (solid), 32:32 (dashed), 64:64 (dotted). In panels B,C and E,F, solid lines represent the model fit with the other species density held constant at 16.



Figure 3.8: Parameter estimates from the competition model for Ae. aegypti (filled) and An. stephensi (unfilled). Panels represent A) intrinsic growth rates λ_i , B) the intraspecific competition coefficient α_{ii} , C) the interspecific competition coefficient α_{ij} , and D) a comparison of species competitive abilities (on a natural-log scale). Sample sizes were too low at 24 °C and 32 °C to estimate parameters for An. stephensi.

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Chapter 4

Water and mosquitoes in the peri-urban: considering everyday mechanisms of access

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Abstract

Both water access and mosquito burdens are unequally distributed across cities, and are determined by a combination of processes at the state and household levels. We conducted a narrative analysis of semi-structured interviews to critically analyze how everyday practices and identity contribute to differences in access to water and vector control across households. Interviews revealed that households relied on multiple mechanisms of access (e.g. social, economic, and political capital) in order to benefit from household water provisions. Which mechanisms were available often depended on whether a household relied on municipal or private water sources, and successful water systems, whether private or public, relied on an individual household's capacity for water storage. Mosquito burdens, on the other hand, were experienced by everyone, and payment for frequent vector control services did not seem to provide access to a "mosquito-free" space. The same mechanisms of social capital that allowed community members to advocate for access to water with the municipality were unsuccessful in gaining access to waste and sanitation infrastructure that they requested to limit mosquito populations. Rather, the responsibility of mosquito control was placed on the individual household, a common theme in vector control narratives globally, effectively negating the public's claim to vector control as a duty of the municipality. By removing vector control from the responsibility of the state, this narrative shifts the responsibility for risk management to individuals, who do not always have control over the public spaces where mosquitoes thrive. In this rapidly urbanizing area, the micro-scale processes of water access and vector control are constrained by global narratives, creating tension between the state and individual and resulting in unequal access to environmental amenities.

Introduction

Often called the 'Silicon Valley of India', Bengaluru's population has grown at an average rate of over 4% annually, driven by an information technology (IT) boom beginning in the 1990s (Census of India 2011). This rapid growth has added stress to the city's formal water sources, primarily water sourced from the Kaveri river and groundwater extracted via borewells (Goldman and Narayan 2019). The municipal water supply of Bengaluru, provided by the Bangalore Water Supply and Sewerage Board, ranges from 3 - 92 liters per capita per day, well below the World Health Organization's minimum household guideline of 150 liters per capita per day (Mehta et al. 2013).

Accompanying the increasing water stress is a steady increase in the annual number of dengue cases across the state of Karnataka from 262 cases in 1997 to 2285 in 2010 (Chakravarti, Arora, and Luxemburger 2012). In 2019, there were over 10,000 cases in Karnataka, the majority in Bengaluru (Rao 2019). Dengue is a mosquito-borne disease that is closely tied to the availability of water. Mosquitoes lay their eggs in stagnant water, including drainage and storage containers, and an increase in available habitat for larvae can lead to an increase in mosquito abundance and disease risk (Wilson et al. 2020). Both of these burdens are not evenly distributed across the city, however, as there are clear spatial patterns in access to water (Balakrishnan 2016; Mehta et al. 2014) and dengue cases (Damodaran 2019). Given the potential for water and sanitation infrastructure to create and modify mosquito habitat, inequalities in water infrastructure may result in inequalities in mosquito burdens and disease within a city (Saravanan 2013).

Urban geographers and political ecologists have been attuned to the resultant inequalities caused by urban development for decades. Environmental resources, in particular, "may be enhanced in some places and for some people [by urbanization], lead[ing] to a deterioration of social and physical conditions and qualities elsewhere" (Swyngedouw and Heynen 2003). Water is well-studied in the framework of spatial patterns of urban inequality, as it is necessarily transformed from a common resource to a contained resource through the creation of water networks as part of the process of urbanization (Bakker 2003). The history of water infrastructure in many urban cities, particularly those that were built in colonial times, contains evidence of the uneven infrastructure development that created these inequalities that persist today (Kooy and Bakker 2008). The uneven supply of water is also continued and reproduced by current practices, such as the privatization of water that caters to those wealthy enough to pay (Bakker 2003) or the installation of infrastructure as a response to political influence, rather than development needs (Chaplin 2011). In all instances, inequalities in water access are often a manifestation of broader social inequalities engendered via institutional and structural mechanisms.

Due to these inequalities in water access, a variety of different "compensation practices" (Truelove 2011) are used by households to meet their water needs, such as paying for network expansion through residential associations (RAs) (Ranganathan 2014b), relying on public stand posts (Mukherjee, Chindarkar, and Grönwall 2015), or hiring private water tankers (Ranganathan 2014a). Given the life cycle of the mosquito, these water compensation practices may facilitate or limit mosquito-borne diseases via their impact on mosquito larval habitat, as the overall effects of these practices are complex and indirect. While some studies have found that piped water decreased risk of mosquito-borne disease (Hayden et al. 2010; Schmidt et al. 2011), others have found piped water to increase the risk of disease (Lippi et al. 2018), especially if service is intermittent, which may encourage more storage of water (Stewart-Ibarra et al. 2013). This complexity is exemplified in the broader discussion questioning the simplistic notion that dengue is a "disease of poverty" (Mulligan et al. 2015), and there is a lack of social and interdisciplinary work that addresses the connection between patterns in

power, water inequality, and mosquitoes. Patterns in mosquito-borne disease may be caused by the same structural inequalities driving patterns in access to water, rendering disease not simply a result of the proximate ecological processes, but of the underlying political and social processes contributing to inequality in water access.

This study leverages the established frameworks for studying water inequality in urban areas to critically analyze differences in household water practices and how they manifest as differences in mosquito burdens. Drawing on five months of field observations, in-depth interviews, and entomological surveys, we aim to determine how everyday practices and identity contribute to differences in water access and mosquito dynamics across households.

Theoretical Framework

We draw on feminist and urban political ecologies to consider how social inequalities determine everyday water compensation practices and ultimately manifest in inequalities in disease burdens. Political ecology approaches urbanization by recognizing that the construction of nature in cities (e.g. the transformation of environmental resources into amenities) is tied to socio-political processes and hierarchies of power (Swyngedouw, Kaika, and Castro 2002; Robbins 2004; Gandy 2008). By drawing on political ecology, we challenge the notion that patterns in the environment, such as mosquito abundances, are the result of natural ecological processes, but are, rather, the result of political and social processes inherent to the production of an urban landscape. This can specifically be considered a feminist political ecology framework, which "investigates how social relations of class, gender, and race inform the process of urbanization and come to codify unjust urban geographies - producing healthy environments for some, while others live close to hazards" (Lawhon, Ernstson, and Silver 2014).

By also grounding our analysis in feminist theory, we emphasize the explicit role of power in determining differences in everyday practice: who can access which practices and how power dynamics are reproduced or disrupted by everyday practices are key focuses of our analysis (Truelove 2011). Although the field began in response to the absence of gender in political ecology, feminist political ecology has since been re-envisioned to be "more about a feminist perspective and an ongoing exploration and construction of a network of learners than a fixed approach to a single focus on women and/or gender" (Rocheleau 2015). A feminist approach also includes a rejection of dualistic narratives such as that of the urban core vs. periphery, rich vs. poor, and households connected vs. not-connected to piped water. Dualistic narratives are premised on a, usually gendered, system that legitimizes the domination of one group at the expense of the other, marginalized group (Plumwood 1994). These narratives further serve the capitalist system itself by limiting the avenues for change available to those marginalized by the system (Gibson-Graham 1996). This is partly because dualistic narratives are an oversimplification that obscures the microsphere of everyday practice, which determines the fine-scale spatial patterns of water inequality seen within a city (Anand 2011). Everyday practices are the multiple choices made by individuals as they navigate their lives, and they rarely fall into a binary categorization. The scale of everyday practice is the scale of experience and embodiment (Doshi 2016), the finest scale at which inequality can be observed, and focusing on the everyday allows for these inequalities to be directly analyzed and addressed. Therefore, our analysis focuses on everyday water compensation practices at the household level.

In our analysis of water compensation practices, we also draw on Ribot & Peluso's (2003) theory of access to examine how compensation practices result in access to water. Access is thereby defined not as "rights" or "ownership" over a resource, but "the ability to benefit from things" (Ribot and Peluso 2003). The focus on ability, rather than rights, "brings

attention to the wider range of social relationships that can constrain or enable people to benefit from resources without focusing on property relations alone" (Ribot and Peluso 2003). In short, this approach focuses on the differences in mechanisms available to people, rather than the resulting differences in access. In cities where publicly supplied water does not meet household needs, households may rely on a variety of mechanisms to access water, such as advocating for water access via civic organizations, drilling private borewells, or hiring private water tankers. In these examples, mechanisms are accessed by a combination of social networks, claims of citizenship, and monetary capital, all of which are themselves dependent upon a household's identity (e.g. class, gender, migrant status, religion, caste, ethnicity, etc.). How a household accesses water, therefore, is contingent on micro-scale power dynamics and a household's ability to wield power, or not, as a result of their identity. There are clear parallels between this approach and the feminist political ecology approach described above, and we will use the language of "mechanisms of access" to describe the everyday practices by which people navigate their own physical and socio-political positions in order to access water. Specifically, our work aims to address the following questions:

- Which mechanisms of access do households use to access water and how are these dependent on households' identities?
- Which mechanisms of access do households use to mitigate mosquito burdens and how are these dependent on households' identities?
- How do the mechanisms of access for these two health amenities differ and why?

Methods

Study Site

Sarjapur is a town located at the southeastern periphery of Bengaluru, approximately 25 km from the city center. Bengaluru is a city of approximately 12.2 million people that expanded from an area of 69 km^2 in 1949 to 741 km^2 in 2020, with outward growth into the rural and peri-urban periphery (Ramachandra et al. 2020; Verma, Chatterjee, and Mandal 2017). Sarjapur Road, in particular, is the site of several Special Economic Zones (SEZs). SEZs offer state and local tax and regulation benefits to developers of the zones and corporations housed within the zone, essentially "public subsidies that underwrite capital accumulation" to attract foreign investment (Roy 2009). The establishment of SEZs has been accompanied by the development of residential communities, large apartment complexes or colonies consisting of individual single-family homes, to house the employees of IT companies. As a result, Sarjapur is becoming a major residential center in the city (Moharkan 2017). Recently, two large (approximately 80 & 200 acres) SEZs (sponsored by Azim Premii Foundation and Infosys) within Sarjapur have been approved. In combination, these two developments will have over 34,000 employees when completed (Jyothi 2012), in a town whose population is presently 12,000 (Census of India 2011). This is not to imply that residents of Sarjapur will provide the primarily white-collar labor to these companies. Rather, the presence of the SEZs will increase migration to the area and the rate of residential development, particularly private communities. In fact, the 2031 Bengaluru Municipal Development plan rezones Sarjapur town from an agricultural area in the 2015 plan to an area with no agricultural zones in 2031 plan, consisting primarily of residential and industrial land (Bangalore Development Authority 2007; Bangalore Development Authority 2017).

Underlying this broad narrative of economic development and urbanization is a heterogeneous urbanization process. Like the rest of Bengaluru, Sarajapur consists of patches of villages within the urban matrix (Fig. 4.1), which complicates the classification of neighborhoods into rural or urban (Nagendra, Unnikrishnan, and Sen 2013). Rather, it is best thought of as a peri-urban area that blurs the rural-urban dichotomy at the scale of the city and the neighborhood, and should be considered an area not just "in transition" to urban, but with its own "sense of place" defined by its present biophysical, political, and cultural realities (Dymitrow and Stenseke 2016). We structured the spatial distribution of our entomological sampling and interview recruitment with an attention to these differences in the human and mosquito environments across space. Urbanization is characterized by the development of buildings and infrastructure, and fine-scale variation in urbanization can be approximated by the proportion of impervious surface (Lu and Weng 2006). Nagendra et al. (2013) used housing type as a "dimension of rurality in lifestyle" in an analysis of urbanization in Bengaluru, specifically the presence of one-story, sloped roof, traditional style houses within the city that were often built prior to the recent urbanization boom. Therefore, we chose twelve sites that incorporated a range of impervious surface and housing types and categorized them into three categories: village (village-style housing, moderate impervious surface), town (village-style housing, high impervious surface), and colony (Western-style housing, moderate impervious surface) (Fig. 4.1). The study region was divided into four blocks and we attempted to stratify site selection across these blocks and choose sites at least 1 km from sites of the same land class. However, given the layout of Sarjapur, sites in town were necessarily closer together than 1 km, while still representing distinct neighborhoods.

Data Collection and Analysis

During five months of field work, we explored the differences in water access and mosquito burdens across Sarjapur through a combination of observations, semi-structured interviews and key informant interviews. We conducted semi-structured, in-depth interviews with 21 households and three key informants (panchayat members or staff) between August -December 2019. Interviews focused on household characteristics, household water access practices, uncertainty in water provision, differences in water access across households, water storage practices, and perceptions of mosquito risk in relation to water and the environment. The goal of these interviews was to understand how household identities contribute to inequalities in water compensation practices across Sarjapur, and how water compensation practices relate to perceptions of mosquito risk. In addition to the in-depth interviews, interviewees participated in a mapping exercise where they identified the spatial location of water infrastructure and mosquitoes and discussed the relationships between the two. This mapping exercise encouraged participants to focus on the fine scale spatial distribution of water infrastructure and mosquito burdens within their neighborhood and led to discussions of spatial patterns of inequality.

Interviews were in-depth and semi-structured, following questions regarding the topics described above using an interview guide (Appendix 5.1). Participants were recruited for interviews via a convenience sample of households in proximity to our sites. Neighbors were approached, the goals of the project were explained, and contact information was provided if people consented to be interviewed. In several instances, we relied on existing social networks to identify potential participants and introduce us as researchers in a way that legitimized our presence in the community, a method similar to snowball sampling that can successfully recruit participants in hidden or hard-to-reach populations (Ellard-Gray et al. 2015). At some sites, community members were reluctant to participate unless a fellow community member could vouch for our legitimacy, given our position as outsiders. Therefore, a combination of spatial stratification across housing types (a form of purposive sampling), opportunistic sampling, and snowball sampling allowed us to recruit a group of participants that represented the full variation in experiences with water access (Stratford and Bradshaw 2016). All interviewees were adults over the age of eighteen and managed their household's water in some capacity. Prior to each interview, we obtained verbal consent from participants. Interviews were conducted in Kannada, Hindi, and English, depending on the preference of the participant, and many interviews were multilingual. Interviews ranged from 25 to 90 minutes in length, with the majority around forty-five minutes long. Interviews were audio-recorded and later translated and transcribed by the two interviewers. This study was approved by the University of Georgia's Institutional Review Board (PROJECT00000227).

In addition to qualitative data collection, we also sampled mosquito populations at each site. Following standard entomological procedures, we placed a CDC light trap baited with dry ice at each site for one 24 hour period each month to estimate the abundance of adult mosquitoes. These traps attract female blood-seeking mosquitoes, which can then be counted and identified to species. From these traps, we were able to estimate the relative abundance of mosquitoes at each of our sites, based on the number of mosquitoes caught during a 24-hour trapping period. For a more detailed analysis of this information, please see our parallel study (Chapter 5).

Two researchers (MVE and SB) conducted the fieldwork involved in this study. MVE (a white, American woman) and SB (an Indian man) were both outsiders to the community being interviewed, although SB had lived in the area for several years and was familiar with some of the participants. We were associated with a local university, Azim Premji University, which has at times had conflict with the local government over the development of its new

university campus in Sarjapur. However, some (6/21) interview participants were unaware of the presence of the university in the area, and this tension was never raised by other participants. Because we visited all field sites multiple times per week for the mosquito survey portion of this work, we interacted with participants on a more frequent basis than a one-time interview and took part in many informal conversations and observations. Given the positionality¹ of those conducting the fieldwork and the other researchers on this study (a combination of American and Indian scientists), we write from a "foreign pose for a foreign gaze" (Abimbola 2019), resulting in a study approached from an outsider's perspective and written for an outside audience. We aim to center and value the contributions and knowledge of local community members, however, we recognize that our standpoint and identities necessarily limit our ability to do so in a way that is justifiably decolonial (Harding 1987; Smith 2012).

Data Analysis

Transcribed interviews were analyzed in atlas.ti software, following a narrative approach. Unlike a realist approach, which assumes "interview responses index some external reality", a narrative approach "treats interview data as accessing various stories or narratives through which people describe their worlds" (Silverman 2003). A narrative approach embraces the 'messy' and 'fragmented' modes of reality and aims to understand how people "learn about, explain, and organize experience" (Wiles, Rosenberg, and Kearns 2005). This resulted in a contextualized thematic analysis about community members' experiences accessing water or interacting with mosquitoes. Because we use a framework grounded in feminist

¹We use the term "positionality" instead of position to stress how various axes of identities are based in explicit and implicit power structures that necessarily influenced the way we conducted this research. The term positionality is often used by feminist science and technology studies scholars in their consideration of how researchers' standpoints influence the production of knowledge, and we use it here in reference to those works.

theory, particular attention was paid to passages that described how individuals leveraged their identity (e.g. class, group membership, etc.) to access water for their household. These included instances where people described control or lack of control over how their household water was extracted, delivered, or stored and relationships of supposed or realized accountability with water providers. Sketch maps were manually georeferenced and sites of water access and mosquito burden were digitized into geolocated polygons using QGIS (Open Source Geospatial Foundation Project 2020). These maps were used in combination with interview transcripts to assess the spatial pattern and abundance of noted sites of water access and mosquito habitat. Mosquitoes were counted to estimate mosquito abundance for each month by site combination.

Key findings

There were several key findings from our study, which are discussed in detail below. Differences in household water access were primarily attributed to whether a household relied on public or private water sources and whether a household had a sump². Individual households leveraged a combination of identities and resources as mechanisms of access to meet their water needs via these systems. Contrary to our expectations, we found no evidence for a relationship between household water systems and mosquito abundances across our sites. Interestingly, the same mechanisms of access that households successfully leveraged to gain access to water were ineffective in gaining access to mosquito-free space. We argue that this is due to the global narratives surrounding water rights and public health being reproduced in the governance process of the local government.

 $^{^{2}}$ A sump is an underground tank that stores water (often at least 3000 L) and is common in individual houses, particularly those of middle and upper class families.

Overview of water systems in Sarjapur

The majority of households (17/21) were satisfied with their current water acquisition system, initially reporting "no problem". However, as is detailed below, this initial "no problem" response matured into more critical evaluations of the situation throughout the course of the interview, as the details of their everyday practices were interrogated. All households had an established system, or combination of multiple systems, that generally met their water needs, with the exception of irregular disruptions such as equipment breakages or borewell failure. However, the specifics of a system varied greatly across households, even when households were neighbors, due to limitations in households' abilities to deploy different mechanisms of access. Systems could generally be divided into three steps: extraction, delivery, and storage (Fig. 4.2). Depending on the system used, each step may have multiple sub-steps involved, and some households had access to multiple systems, providing greater capacity for adaption in times of water stress. We refer to the process by which households initiated and maintained these systems as "mechanisms of access", focusing not just on materiality of the infrastructure, but the forms of power that individuals call upon and leverage in their narratives to explain how they benefit from the resource (Ribot and Peluso 2003).

Water was initially sourced from ground water via private or public boreholes. Private boreholes were located on-site, and water was then piped directly to communal storage tanks, from where it was piped to individual homes or apartments. Public boreholes directed water to communal tanks owned by the panchayat and then delivered to households via underground pipes. Both private and public boreholes often ran dry in the summer months, and piped water was then supplemented by water delivered by water tankers. Private tanker costs were borne by individual households, but panchayat-provided tanker water was delivered free of charge. Storage took place at both communal and household levels. In the colonies we surveyed, all houses were constructed by the same developer and included both a sump and overhead tank (OHT) per house which allowed for individual capacity to cope with water stress. As one community member described:

"This is an individual house, so I'm sure I have enough in my tank. Water is there. At any time, if I open the tap, water will come."

Within the town and villages, there was much more heterogeneity. One house may rely on plastic drums and buckets for water storage, while the neighbor has a motorized sump-OHT system. Sumps are generally installed in "big houses", which are newly built and often multiple stories. These tend to be the households of wealthier families or recently immigrated middle-class families. As one community member noted, "People who put more money [into their house] have less problems [with water] than those who don't."

Public vs. private water provision in Sarjapur

The differences in water extraction and delivery across Sarjapur closely align with whether water provision is provided by the panchayat (public) or a third party (private). Panchayat water is provided free of cost to those who live in individual houses or smaller apartment buildings, while private water is provided by the development manager or residential association (RA) of a colony or via private water tankers hired by individuals. All residents of villages and residents of three of the four neighborhoods surveyed in town had access to a panchayat water tap. Private water was provided more regularly and was considered more reliable than panchayat water. Notably, the mechanisms of access used by households were different depending if they relied on public or private water.

Those who relied on municipal water provision by the panchayat used several identities to frame themselves as members of the larger abstract *public* to whom the local government is accountable. Some households mentioned that the politicians are accountable to them as part of the electorate:

"In the panchayat, there will be the person who won the election here, right? If I

tell them [piped water is not coming], they'll send tankers."

Another civic-minded identity was as a taxpayer, who should benefit from development projects such as water infrastructure because their taxes pay for them. Other studies of water in Indian cities have found close ties between urban citizenship and water access. In another community on the periphery of Bengaluru, for example, residents paid for municipal water infrastructure as a way to legitimize their citizenship and land tenure and create a pathway of accountability because "once you start paying taxes, you can start demanding things" (Ranganathan 2014b). Similarly, the lack of water provision to low-income, immigrant communities is a reproduction of the lack of citizenship and rights afforded to these communities by the state (Sultana 2020; Baviskar 2003).

Rather than formal displays of citizenship, the most common identity leveraged to exert accountability over the local panchayat with regards to water provision was a claim to membership of the local community, an abstract public that is not necessarily defined by formal actions of citizenship. Members of the panchayat are drawn from this local community, and participants expressed multiple forms of shared identity with the politicians who represent them. Many were neighbors with panchayat members and felt comfortable approaching them when water was not supplied:

"The panchayat chairman. She happens to be a lady too. She lives right here [motions to a neighboring house], she'll solve our problem."

"We have their [panchayat members] phone numbers. I know their house itself, so I have sometimes gone up to them and just told them [when there is a problem]." In spite of this shared identity, the relationship between an individual and the panchayat is not without power dynamics, and community members cited instances where the local government did or did not respond to their needs. For example, in multiple villages, neighbors lobbied together to persuade the panchayat to install a tap for each house, instead of the panchayat's original plan of one tap for every three houses, so that each house could have control over their own tap. They also cited instances where the panchayat responded very quickly to issues with the water supply, such as a broken motor or pipe, by trucking in water tanks to those in need. However, Sarjapur's location on the periphery of the city meant that community members also felt there was little oversight of the local government, implying that this accountability was tenuous:

"There [in the center of Bengaluru], MLAs (Member of the Legislative Assembly), MPs (Member of Parliament), the municipality. All of them look after the water. Ward members are there, they manage it correctly. There are a lot of officials over there. We have a lot of "low people" here in the village, "high people" there [city]...They keep doing this in the city, here, in the village, nobody asks. Because nobody asks, they don't do anything about it."

This community member's comment refers to the narrative of an urban-rural divide originating from India's city-focused development in the 1970s and 1980s, where the periphery of urban areas was considered marginal (Wang, Kundu, and Chen 2010). The narrative of the urbanrural dichotomy is one based in deprivation, with lower literacy rates, access to sanitation, and "backwardness" in rural areas compared to "developed" urban areas (Dymitrow, Biegańska, and Grzelak-Kostulska 2018). At the scale of the city, this narrative is often applied to the peri-urban periphery, in contrast to the urban core. In Bengaluru, like other large cities in India, many of the essential, yet underpaid, workers of the city (e.g. domestic workers, security guards, service workers) reside in the urban periphery and commute to work in the city center (Gidwani and Sivaramakrishnan 2003). As such, they witness the difference in infrastructure between the core and periphery on their daily commute, and this uneven development was brought up in interviews. As residents of the urban periphery, community members were aware of both the imagined and realized material differences across this gradient, and felt that their situatedness as a member of the urban periphery weakened their ability to hold their officials accountable.

As members of the urban periphery and low-income workers or agriculturalists, many residents of Sarjapur openly identified themselves as "low people", which influenced how they positioned themselves as citizens to access state resources. Unlike the urban elite, whose class, language, and wealthy privileges allow them access to their rights as citizens, the 'political society', that encompasses the majority of residents, particularly those who cannot access the state formally, rely on informal relationships with politicians (e.g. personal relationships) to access these rights (Chatterjee 2004). While residents of Sarjapur did employ conventional citizenship claims, these were combined with everyday practices of social negotiation and clientelism to access water. These informal processes of negotiating access to public resources through everyday practice provide a way for individuals who are otherwise excluded to engage in the local democratic process and hold the state accountable (Bénit-Gbaffou and Oldfield 2011).

In contrast, middle-class households in gated communities also performed identities of citizenship, such as paying taxes, but did not expect to access public resources via those mechanisms. One resident laughed-off the idea of the panchayat providing them with public services:

"Actually, we are paying house taxes, so it's the responsibility of the panchayat to supply water also for us...but we are not getting any facility from them. They will say, 'You are in a [colony], we can't. You do not come under our panchayat,.' But we are paying the tax [laughs]"

Participants in these communities lacked the shared identities or social ties needed to engage with the local government. They did not live next door to the panchayat chairperson or have a panchayat member's phone number saved in their mobile like the community members quoted above, and few (1/5) spoke the local language of Kannada. Rather, like their approach to water access, these households had opted-out of the political proletariat (Gopakumar 2009). Instead, they accessed water through economic capital and relations with the politically powerful housing developers who own the gated communities where they live. All of these communities had private borewells, which require that developers are granted a permit from the state government (Karnataka Ground Water Act 2011). Through their identity as home-owners and tenants of these private developments, these households were able to access private borewells which are inaccessible to lower-income households due to the costs and political leverage required to successfully acquire a permit and drill. Private borewells are privately maintained and can be rebored when dry, and generally offer a more reliable source of water than public borewells. For those who are able, paying for water via private boreholes allows one to choose to "disconnect" from the municipal water supply, which is supplied infrequently (Jaglin 2004).

Water storage creates inequalities at the household scale

WATERMAN: Most houses have sumps, only the poor households don't have one.

COMMUNITY MEMBER: Mine doesn't have one. WATERMAN: Mine doesn't either. COMMUNITY MEMBER: What's the use of being a waterman if you don't even have a sump?

The driving cause of inequality in water access was differences in water storage practices and capacities. Even in areas that received a regular water supply from the panchayat, those households with a limited water storage capacity received less water, and were more vulnerable to water shortages when municipal water failed, which happened multiple times a month during dry months. Piped water infrastructure has expanded in the past several years, and much of the town transitioned from relying on public water tanks interspersed throughout the neighborhood to individual water taps at each household. While this eases the burden for some households, it does not erase the inequality in water access between households because those houses with sumps are able to retain a larger share of water than houses without. In fact, some community members worried that, due to the limited flow of water, the installation of large sumps uphill of their pipe outlet actually decreased the amount of water flowing to their pipe:

"When water comes straight from the pipe, if there are sumps that are very deep, the water comes hard there. When that happens, then other houses don't get water. ... Water itself doesn't come for us. Water they have saved [stored], it is all at the cost of us getting water."

There are several reasons households without sumps surrounded by households with sumps may have less access to water than houses in more homogeneous low-income areas, where no one has a sump. As in other parts of Bengaluru (Post et al. 2018), in Sarjapur, a neighborhood of "sheet houses" (e.g. lower income households whose roofs are typically made of metal sheets and lack OHTs or sumps) receives water more frequently than nearby neighborhoods where the majority of households have sumps or OHTs. For example, one household living in a community of other similar 'sheet houses' on untenured land received water every alternate day, while a household with similar storage capacity, but located amongst multi-story single family homes, only received water once a week and found it very difficult to have enough water to last between water provision timings. One woman in this situation explained:

"It is quite difficult for me. Because it is left only once a week, it is quite difficult for me. If it was left at least twice a week, it would be better. So what we do, the four houses including my house, we form a group and ask for private tankers to come."

She joins with neighboring families in similar situations and orders a private water tanker when they need water. These private water tankers cost 300 - 450 Rs. for 5000 L of water, depending on the season, and costs are shared amongst the households. In contrast, those living in private layouts pay 225 Rs for 5000L of water, about 25% less. The unequal monetary cost of water has been seen in other cities across India and further limits the ability of lower-income households to leverage capital as a mechanism of access in their system of water access (Truelove 2011; Ranganathan 2014b; Juran and Lahiri-Dutt 2017).

In addition to higher water costs, living amongst large houses with sumps reduced the ability of the community to organize and advocate to the panchayat. For example, those with sumps were pleased with the switch from public stand post to piped municipal water. One man who had a sump mentioned the benefits of the new system:

"It was very difficult, then; everyone had to circle the tank and wait for their turn. It was very difficult when they kept those tanks [public stand posts] there. People fought. Now [my neighbor] here has put a tap right? She can also get water right to her house whenever she wants." For context, in this village, water was supplied by the panchayat twice a week, and the neighbor did not have a sump, but rather stored her water in multiple plastic containers, with an estimated storage capacity between around 800L. In contrast to those with sumps, households with limited storage capacity often preferred the old system of public stand posts. Another woman who did not have a sump-OHT system at her house described:

"That time [when we used standposts] was better. At least at that time we were getting water. But the only problem was we had to carry it back home. Anytime you wanted water, it was there. Unlike the taps that we have right outside."

These households recognize the current inequality created by the interaction of sump ownership and panchayat water provision frequency:

"We who have 'sheet' houses [houses with corrugated tin roofs that do not have OHT-sump systems] are the ones who normally face the brunt of the water problem."

And in some cases, this inequality was an obstacle to approaching the panchayat when there were problems with the water supply:

"One more problem is that "big-big" people, rich people, they have sumps. They get a lot of water, the water just goes into their sumps and they can store it. So for them, whether water is supplied everyday or not, it doesn't matter, they would have filled up their entire sump. People who don't have the necessary things, for them, it will be tough. For them, because they have these things, they can store water. However, for us middle-class people, we are not helped. Lifelong we won't have any help."

"The main problem is people are rich here. The people around, so they don't care."

Indeed, those with sumps reported no need to "approach anyone [the panchayat] because [they] have already forecast for the future." The reduced ability to organize can be a limiting factor in the political system, with one man noting that it is only "when a lot of people agitate, that's when they [the panchayat] do something about it." The inequality in sump ownership can impede a household's ability to use community action as a mechanism of access, which is particularly important for houses without sumps who are already more vulnerable to disruptions in water provisions.

On the other hand, heterogeneity among households could result in a community that is more resilient to water stress, if the water is redistributed among households. Community members remembered sharing their own water if they had a sump or relying on someone else in the village to get water in time of need:

"This place is like a community. We are together. Together. If this is one house, that's one house, that's one house, if there's some problem, we'll all come together. 'Oh, your house doesn't have water? Come, come to my house and take water from here.'...If there's any problem, we all stick together."

However, there are limits to a community's ability to support each other in times of water scarcity. A member of the same community, but living in a house with a sump-OHT system mentioned:

"We can help. Not at every time. We can give for one week, two week, or monthly. We can't give every day right, because we spent money on it so why should we give to others."

Although community members identified access to water as a universal right, discussions of who had a right to access water sometimes reproduced the larger global narrative surrounding the privatization of water at a local scale. Households with sump and OHT systems are able to benefit from their investment of capital or "spent money" and gain more stable access to water through a storage system that provides adaptive capacity during times of infrequent water provision. While all community members are able to use a mechanism of group membership to access water extraction and delivery, water storage remains accessible only via monetary capital.

Access to water is often framed as who is connected or not connected to public or municipal water sources, but the reality is much more complex (Jaglin 2004). Because the supply of municipal water is infrequent, those who can afford sumps have more regular access to water than those who rely on smaller water containers. The panchayat plans to expand the municipal pipelines as Sarjapur develops, replacing the permanent water tanks with a tap for each individual house. Simply expanding the pipes may reduce access to water for those households who cannot afford sumps, reproducing, rather than alleviating, current inequalities in water access.

Mosquito burdens were not related to water access

The primary goal of this study was to investigate the link between inequalities in access to water and inequalities in mosquito burdens. We hypothesized that differences in water compensation practices could lead to differences in mosquito abundances by providing habitat for larval mosquitoes to breed via water storage practices. As described above, we found water storage to differ greatly between households, from using several smaller plastic containers to automated systems of underground sumps and OHTs. However, every community member we interviewed, regardless of the water storage systems in place, expressed concern about the presence of mosquitoes near their home. This concern was common and transcended many of the identities (e.g. economic, community membership) that structured access to water. Further, those without sumps emptied and refilled their containers at least once a week, never allowing containers to sit long enough for mosquito larvae to develop. Community members recognized the widespread prevalence of mosquitoes, stating that "it's not just in [our neighborhood], every other place has mosquitoes". They did mention seasonal differences in mosquito burdens, but stressed that, during the monsoon season, mosquitoes are everywhere: "If it's [mosquitoes] there, it's everywhere. If it's not there, it's not there."

Our mosquito surveys found seasonal differences in abundance, but few predictable differences across sites (Table 4.1). At ten of the twelve sites, mosquito abundance was highest in September, corresponding to the middle of the monsoon season. The primary differences that we found in regards to water access, private vs. public water provision and the presence of a household sump-OHT system, were not associated with differences in mosquito abundances in our entomological sampling. We caught an average of 72.1 ± 55.6 mosquitoes in neighborhoods that relied on public water and an average of 130 ± 122 mosquitoes in neighborhoods that relied on private water. Similarly, neighborhoods where all households had access to an individual or communal sump had an average of 82.4 ± 83.1 and 59.5 ± 11.5 mosquitoes, respectively. High mosquito burdens were seen across socio-economic levels at village, town, and colony sites.

Mosquito-borne diseases in low and middle-income countries are often assumed to be "diseases of poverty", and public health narratives associate them with failing infrastructure, poor housing conditions, and "slum" neighborhoods (Mulligan et al. 2015). This is primarily due to the higher abundance of larval habitat, such as open drainage, solid waste, or uncovered water storage containers, that are associated with these neighborhoods. Modern vector control efforts often target these habitats at the level of the household, rather than considering structural inequalities perpetuated by state policies (Rodríguez-Díaz et al. 2017). By focusing on the household, rather than public sources of larval habitat, state-controlled vector control programs act as an agent of the state, often with a legal mandate to enter peoples' private homes (Lesser and Kitron 2016; Neely and Nading 2017). Our finding that mosquitoes were everywhere regardless of the water infrastructure suggests that this approach is not just a potentially problematic enaction of state power, but may also be ineffective at controlling mosquito populations in Sarjapur.

The drivers and responsibility of mosquito burdens

When asked about the primary drivers of mosquitoes in their neighborhood, participants did not mention containers of water, but did implicate vegetation (9/21), drainage (11/21), and garbage (13/21). In Sarjapur, drainage refers to covered and uncovered drains that line the roadside and direct wastewater and rainwater. For those living outside of a private colony or apartment building, both drainage infrastructure and waste management fall under the purview of the panchayat. Unlike peoples' expressions of accountability regarding water access, community members reported the panchayat did very little to control the mosquito problem, and then only "when people in those areas really demand it". Most reported the panchayat either fumigated or applied bleaching powder in drains several times a year. In contrast, private colonies fumigated twice weekly and additionally in response to residents' complaints.

Global health narratives often stress individual, rather than municipal, responsibility for vector control efforts (Kelly and Lezaun 2013; Robbins, Farnsworth, and Paul Jones 2008; vonHedemann et al. 2017), and this narrative was employed by one panchayat chairman:

"There's nothing really that can be done about mosquitoes. They're not under our control. We can clean one house, but another house might not be clean...Here and there, they keep throwing garbage. From the panchayat side, we have given them buckets to put their garbage in. We have our tractor, put it in that." In this narrative, the panchayat claims to fulfill their responsibility by providing solid waste pick-up and it is due to the "unclean behavior" of individuals that mosquitoes persist. This is not hidden from those who have been blamed, with one community member noting the irony of this responsibility given her lack of control over the frequency of water provision:

"All they do is tell us not to stock water and things like that, but what can we

do, we have to keep stock because they release water just once a week."

This quote illustrates that, given the structural inequalities of water access described above, community members do not always have the power to change their behavior. No community members identified their own individual practices as a cause of mosquitoes. Rather, community members attributed mosquitoes to the inadequate or non-existent drainage systems and lack of cleanliness in public spaces, specifically garbage and unmaintained vegetation, or "shabby gardens". These were the areas most often identified during the mapping exercise as sources of mosquitoes (Figure 4.3), and are on public, not private, land. The responsibility for that land, however, is complicated:

"Why is this happening, right? Because they [other community members] are not taking the responsibility. They are thinking in their home, they maintain a clean cleanliness, but outside they will throw whatever. They are not taking responsibility. The government will not take initiative."

Similar to the narrative used by the panchayat, this community member initially places the responsibility on other individuals who are using these public places to illegally dump their trash. However, they end by stating that it is ultimately the government that must take the initiative to keep the area clean. As residents of this town, they believe the government has a responsibility to provide what they view as basic municipal services: waste disposal and street and drainage cleaning. This was echoed by another community member who described

her experience requesting the panchayat clean an area near their house where people had been dumping trash:

"There's so much garbage that has been thrown here. Even if you want to clean, we won't be able to clean it. WHY DO PEOPLE JUST THROW THEIR GARBAGE OUT? I don't know about all that, but if we just call up the municipal office, only if we pay them some money will they come and clean it up. That is their duty, right, to clean it. Why should we do it? We can't give for anything and everything."

She clearly describes that this is the "duty" of the panchayat, and that they as individuals are not able to hold the panchayat accountable. In the past year, panchayat governments across Sarjapur have begun waste collection services, collecting trash at peoples' homes on a weekly basis and moving it to a communal dumping ground. Two of our sites were located in close proximity to these disposal areas, which were identified by participants as sources of standing water and mosquitoes. In explaining the situation, a community member explained that the tenancy statuses of the homes in that neighborhood were still being litigated in court. This, combined with the fact that it was the government themselves doing the dumping, meant that the residents felt they had little power to advocate for their right to remove the disposal site.

Global narratives of state responsibility for health

Notably, in the case of solid waste, the same mechanisms that community members relied on for gaining access to water (citizenship, shared identity, etc.) are not effective. Instead, community members must pay for these sanitation services, in spite of it being the "duty" of the panchayat. Community members provided examples of attempting to use mechanisms of access that relied on notions of citizenship or electorate duty and failing:

"I have told the panchayat three times to clean it [solid waste blocking the drainage], they have not done anything though...I have taken him to the exact spot where this accumulation is happening, but no action has been taken...Whether we write an arzi [formal petition] to the panchayat, or don't write, it doesn't make any difference."

This community member used both informal and formal appeals to the local government, leveraging his position as a constituent and member of the community to attempt to gain access to sanitation services, and thereby control of mosquito populations. In contrast, identical appeals, specifically an arzi, were cited as effective ways to request change in the water provision system from the panchayat, but are not effective for sanitation services. Because these mechanisms of access are context dependent, a household that has access to water may not have access to the services and provisions needed to control mosquito populations around their house.

Why would the same mechanisms of access not apply? While both water and mosquito control contribute to the health and well-being of an individual, mosquito control is emblematic of the New Public Health approach, in which disease risk is determined by individual behavior and the responsibility of prevention lies with the neoliberal 'self' (Petersen 2002). Governance systems drawing on New Public Health "responsibilize" citizens via policies premised on individual autonomy and responsibility, rather than policies that address structural determinants of health at a national scale (Viens 2019). In addition, modern mosquito-control programs arose out of tropical medicine programs led by colonizing nations, which used colonial narratives of "White purity" and "native filth" to justify coercive sanitation programs in the name of 'health' (Engel and Susilo 2014). Taken together, these frameworks imply there is an intrinsic 'characteristic' or behavior of a certain population that makes them more predisposed to unclean surroundings and the associated health risks, and disease is therefore not the responsibility of the state. In the context of vector control interventions, this leads to policies encouraging household-based larviciding and larval habitat control, rather than state-sanctioned public health programs. In Sarjapur, this population is those who live in sheet houses in the main town, Sarjapur's "urban poor". These neighborhoods generally lacked the cement drainage ditches that allow the unimpeded flow of water and, in one instance, was actually the site of the solid-waste dump for the local panchayat. From the viewpoint of New Public Health, it is a lack of personal accountability, not lack of state-provided support, that is resulting in an environment conducive to mosquito-borne disease in these neighborhoods.

In contrast, the global narrative surrounding water is one that highlights access to water as a human rights issue, a narrative that was repeated in community members' claims to water. While the definition of water as a basic human right has been criticized for its vagueness and inattention to power dynamics (Sultana and Loftus 2012), the publicizing of the water rights movement by large international organizations and the state's role in providing this service has increased awareness of these rights and, when adequate resources and legal protections exist, peoples' ability to advocate for their right to water (Mehta 2005). This framing also enables people to draw on their identity as protectorate of the state (e.g. resident or citizen) to claim this right, as was seen in Sarjapur. By identifying public areas with inadequate drainage or unmanaged vegetation and waste disposal, community members are attempting to create a similar narrative with regards to mosquitoes, that they have a right to a safe environment provisioned to them by the state. However, the panchayat employs a New Public Health narrative, which places the responsibility of health on the individual. This frustrates community members' calls for increased investment by the government in vector control and waste infrastructure.

Conclusion

Unlike a binary system of connected vs. not connected to public infrastructure, water access in Sarjapur was determined by individuals' abilities to wield certain mechanisms of access. Which mechanisms were available to whom was related to households' positions of class and identity. The panchayats of Sarjapur rely on the power of the rural, lower-class electorate, and so primarily served these communities through a system of clientelism. Indeed, those households that received water from the panchayat employed claims to citizenship and shared identity to frame themselves as members of the state protectorate, who have a right to publicly provided water. Wealthier, middle-class households were able to employ mechanisms of access based on their positions of relative wealth and political power to drill private boreholes and pay for access to water. Private borewells, which serve a much smaller population than public borewells, provided these households a more regular and reliable access to water than the public system.

Economic capital was also employed as a mechanism of access to build individual or community sump-OHT systems, which serve to mitigate risks inherent to the infrequent public water supply and any equipment failures (e.g. no power, broken pipe) of the private systems. Sumps provide access to a reliable water supply and households with sumps were more confident in their water system than those without. Households without sumps experienced difficulty in accessing water, particularly those who relied on public water, where the lack of a sump limited the ability of a household to weather infrequent water provisions. The only households who were not satisfied with their current system of accessing water were
those without sumps, who often relied on multiple systems to meet their water needs, at the expense of monetary cost and time.

In contrast to water access, mosquito burden was distributed throughout Sarjapur. No households were able to access a "mosquito-free" space and mosquito abundance was not associated with the primary differences in water access. Those households which held the panchayat accountable for water provision via claims to citizenship were unable to leverage that identity in their demands for waste removal or vector control. Unlike narratives of water access, which is viewed as a universal right and therefore the responsibility of the state, public health narratives place the responsibility for health on the individual. In this narrative, unhealthy environments are the result of the behaviors or characteristics of the people who live there, rather than the government policies or actions that create the environment. By employing this narrative, the local government makes it difficult for residents to hold the government accountable for managing sewerage and solid waste infrastructure as a form of vector borne disease prevention via their position as constituents. Without government support, there is little, if any, vector control activity in these neighborhoods.

In the midst of the periphery-facing urbanization of Bengaluru and the development of two large SEZs within its municipal limits, Sarjapur is rapidly changing. New industry and developments will bring more private colonies and apartment complexes, and some community members hope it will bring new infrastructure and decrease social inequalities. However, expansion of the piped infrastructure will continue to ignore those without sump-OHT systems, especially as higher pressure on existing boreholes results in less frequent water provisions. Simply viewing the effects of urbanization on water access and mosquito-borne disease as a binary process (e.g. connected vs. not connected) will reproduce existing power inequalities in the households' access to resources. Rather, analyses must take into account the ways that individual households navigate gaining access to these resources, and how local governance is framed by global narratives of neoliberal state responsibility.

Tables

							Mosquito Abundance		
Land Class	Building Type	Own Property	Private Water	Community Sump/OHT	Individual Sump/OHT	Water Frequency	Sept.	Oct.	Nov.
Colony	Tall Apt		Х	Х		24/7	92	36	17
Colony	Tall Apt	Х	Х	Х		24/7	4	78	71
Colony	Western House	Х	Х	Х	Х	24/7	674	180	13
Colony	Western House	Х	Х	Х	Х	24/7	500	52	46
Colony	Western House	Х	Х	Х	Х	24/7		55	40
Village	2-level Apt		Х	Х		Daily	20	2	10
Village	Multi-story house	Х			Х	Daily	20	2	10
Village	Traditional House	Х				3-4 days	227	157	183
Village	Traditional House	Х			X	3-4 days		101	100
Village	3-level Apt		Х	Х		24/7	- 79	53	NA
Village	Traditional House	Х			Х	3-4 days			
Village	Traditional House	Х				Daily	206	1	2
Village	Traditional House	Х				Daily			
Town	2-story Apt		Х	Х		24/7	1912	2	72
Town	Multi-story house	Х	Х		Х	24/7			
Town	Sheet House					2 days	122	3	0
Town	Sheet House					2 days			
Town	Sheet House	Х				5-7 days	81	59	55
Town	Traditional House					5-7 days			
Town	1-story Apt		Х	Х		24/7	- 55	79	55
Town	1-story Apt					3-4 days			

Table 4.1: Table of house and water system characteristics and mosquito abundance data from three months of trapping.

Figures



Figure 4.1: A) Map of Sarjapur town with twelve sites denoted with colored circles. B) Photographs of example landscapes for the three site categories depicting differences in impervious surface and housing types.



Figure 4.2: Water extraction, delivery, and storage steps involved in water access systems in Sarjapur.



Figure 4.3: Example of two sketch maps from one village site. Colored circles representing household water access (blue) and areas of mosquito habitat (red) have been added to increase visibility on digitized copies. All identifying information (road names, coordinates, etc.) has been removed.

Appendices

Appendix 5.1: Interview Guide

Basic Background and Demographic Questions

Questions following the Indian census:

- 1. Gender
- 2. Age
- 3. Occupation
- 4. Languages Spoken (highlight mother tongue)
- 5. Place of birth
- 6. Religion
- 7. Are you a member of a scheduled caste or scheduled tribe?
- 8. What is your highest level of education attained?
- 9. Questions regarding housing:
 - (a) Do you own your property? If not, who does and what is your relationship to them?
 - (b) When did you move to this house?

Household water use

1. How do you access and use household water? (Request to see the system if possible)

- 2. Who manages household water use in this house? List all that are involved and the tasks/responsibilities of each person.
 - (a) Which of these tasks is the easiest? Which is most difficult?
 - (b) Why was this person chosen to manage household water use?
- 3. Please detail how you were able to get access to water in this way. What were the steps involved?
 - (a) Were any steps difficult for you? Why
 - (b) Did you reach out to others for help with this step? What help did they provide?
 - (c) Do you feel like it is more difficult for you to obtain water than your neighbors? Than others in Bangalore?
 - (d) What is the cost of water? Both piped and RO treated.
 - (e) Do you feel like you had options at each of these steps?
- 4. If it involves boreholes:
 - (a) How did you get a permit to drill? Was this process more or less difficult than you expected and why?
 - (b) Is the borehole on your property/private?
 - (c) If borehole is on someone else's property, how do you have access to it (e.g. employer, payment, family member)? Do you provide something in exchange? Could they stop providing you access to the water if they wished?
- 5. If water is provided by the residential association of a condo building:
 - (a) What is the governing body for water in your RA? How were they elected/chosen?

- (b) Have you had any problems with water access? How were these dealt with? Do you have a way for recompense when there are problems with water?
- (c) Did the water situation play a part in your decision to move to this building? How did you learn about water access in different buildings?
- 6. If it involves a public standpipe or borehole:
 - (a) Who controls when this pipe is turned on and off?
 - (b) Who controls who has access to this pipe and how much water each household gets?
 - (c) Cost of bore/pipe water.
 - (d) How did this pipe get installed? How did it get chosen to be put in this place over others? Did you have a voice in this process?
 - (e) Have you ever had less access to this pipe than others? Why? How did you deal with this conflict?
- 7. If it involves water tankers:
 - (a) Do you have control over when tankers come and what the price is?
 - (b) How did you choose this water tanker provider over others?
- 8. When switching from one strategy to another, do you renegotiate terms? Are you confident in your ability to renegotiate? Why or why not?
- 9. Are you satisfied with your current strategy? Why or why not?
 - (a) Do you feel like you have control over household water? Who does have control over your water? What is their relation to you?

- (b) When something is wrong with your water (flow pressure, quality, cuts out), how do you fix this? Do you have confidence that things can be fixed when they arise?
- 10. What would be your ideal way to access water?
 - (a) What obstacles do you face in attaining this ideal strategy (e.g. cost, social network, geographic location, materials and knowledge)?
 - (b) Do you think you will be able to access water this way in the future?
 - (c) What needs to change so that you can access water in this way?

Experience with Mosquitoes

- 1. Does your current water strategy involve water storage? Why or why not? Where is it stored?
- 2. Do you worry that mosquitoes will breed in stored water?
- 3. Is there any government support to combat mosquitoes? Do you have control over mosquito populations?
- 4. What do you think about the relationship between water and mosquitoes?
- 5. What do you think is the cause of mosquitoes in your neighborhood?

Sketch Mapping Exercise

On this map of your neighborhood, please mark up places where you access water, and rank them from your most to least preferred.

- 1. Why is this your most preferred?
- 2. Do you think this is the most preferred for others? Who and why?

- 3. Why is this your least preferred?
- 4. Do you think this is the least preferred for others? Who and why?

On this map of your neighborhood, please mark areas where you experience high exposure to mosquitoes. Choose the area where the mosquito burden is highest.

- 1. What do you think is the cause of this?
- 2. How do you feel about this area existing in your neighborhood?
- 3. Do you prefer to avoid this area or spend less time there? Are you able to change your behavior to avoid this area?

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Chapter 5

An integrative approach to mosquito dynamics reveals differences in people's everyday experiences of mosquitoes

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Abstract

Urban environments are heterogeneous landscapes of social and environmental features, with important consequences for human-nature entanglements, such as that of mosquitoborne disease. Investigations into this intra-urban heterogeneity in mosquito dynamics find conflicting results, likely due to the complex socio-ecological interactions and the importance of place-based context. Integrative research, which synthesizes multiple perspectives and epistemologies, can help place ecological results into their social context to explore these placebased differences. Here, we develop an integrative approach to understanding spatial patterns of mosquito burdens in urban systems by combining entomological surveys, semi-structured interviews, and sketch maps. Although we found no evidence for a difference in mosquito abundance across an urban gradient, there were differences in individuals' everyday experiences with mosquitoes. These differences were mediated by how individuals moved through public space and their vulnerability to hazards in these spaces. This example of integrative research illustrates what can be gained from the inclusion of multiple epistemologies, particularly for research in socio-ecological systems.

Introduction

Urban environments are heterogeneous landscapes of social and environmental features, with important consequences for human-nature entanglements¹ and interactions. Mosquito-borne disease transmission, for example, occurs at the intersection of specific conditions of the abiotic

¹We use the word entanglement here to recognize that our study draws on the work of anthropologists and geographers Alex Nading, Uli Beisel, and Donna Haraway (among others) on species entanglements in disease emergence and biomedical research. It expands on our notion of ecological interactions by allowing the relationship between mosquitoes and humans to extend beyond finite instances of interactions, and recognizes that mosquitoes have shaped human history, politics, and evolution and that mosquitoes' lives are in turned shaped by these forces.

and biotic environment, mosquito vector, and human host. Human populations in urban areas are at particular risk for certain mosquito-borne diseases, particularly *Aedes*-borne viruses (Gubler 2011; Franklinos et al. 2019), due to high human population densities (Weaver and Reisen 2010; Rose et al. 2020), adaptation of mosquito species to urban and domestic habitat types (Brown et al. 2014), the abundance of larval habitat in anthropogenic landscapes (LaDeau et al. 2015), and microclimates conducive to mosquito and virus development (Murdock et al. 2017; Li et al. 2014). In fact, city-dwellers make up a substantial portion of the over 3.5 billion people at risk of vector-borne diseases (World Health Organization 2014). Within a city, however, mosquito-borne disease risk is uneven, a result of the underlying heterogeneity of the socio-ecological landscape (Romeo-Aznar et al. 2018; Alberti 2005).

Recently, there has been an effort to understand these spatial patterns of mosquito-borne diseases in a city, and the causes of these patterns, so that limited vector control resources can be allocated efficiently (Stone et al. 2019). The findings of these studies vary widely. Mosquito populations are more abundant in lower socio-economic neighborhoods (LaDeau et al. 2013; Mulligan et al. 2015) or higher socio-economic neighborhoods (Becker, Leisnham, and LaDeau 2014; Mulligan et al. 2015). More frequent provision of piped water can increase (Stewart-Ibarra et al. 2013; Lippi et al. 2018) or decrease mosquito population abundances (Hayden et al. 2010; Schmidt et al. 2011). The effect of climate is often non-linear and dependent on regional climate trends (Murdock et al. 2017; Li et al. 2014; Misslin et al. 2016). Clearly, many of these relationships depend on the specifics of the locale in question. Further, environmental factors (e.g. hydrology, microclimate, host distributions) are the result of and interact with the socio-political context of the city (Parham et al. 2015; Santos-Vega et al. 2016). For example, a study of water infrastructure and mosquito-borne disease in Ahmedabad, India found more malaria cases in areas with a low density of water infrastructure connections because illegal water connections led to high leakage and creation of habitat for

mosquito vectors, but that these connections also decreased water pressure for the whole network, influencing water storage patterns elsewhere in the city (Subramanian et al. 2014). Understanding mosquito-borne disease in cities therefore require a place-based, integrative approach that situates ecological findings in the social context needed to properly address the complexity of a socio-ecological system (Kinzig 2001; Mayer et al. 2006).

Here, we use the term "integrative" to refer to research premised on epistemological integration, with a particular focus on addressing the dichotomy between the hard/natural/quantitative and soft/social/qualitative sciences regarding what qualifies as knowledge and what are valid methods for producing knowledge (Adams 2007). In an effort to avoid the "theological hair-splitting" debates regarding the traits of inter-, multi-, trans-disciplinary etc. research (Rylance 2015), we rely on Repko's (2012) definition of integration: "a process by which ideas, data and information, methods, tools, concepts, and/or theories are synthesized, connected, or blended." Integrative research occurs within the current intellectual landscape characterized by a hierarchy of knowledge production in which the quantitative sciences sit at the top and are often regarded as the most "valid" or "objective" forms of knowledge production (MacMynowski 2007; Adams 2007). This is especially true in the field of urban ecology and ecology in general, whose foundations in systems science has resulted in the "epistemological sovereignty" of quantifiable concepts over qualitative description, in spite of the importance of natural history to the field (Miller et al. 2008; Travis 2020). Integrative research in urban systems should therefore be particularly attentive to disagreements between disciplines and focus on what can be learned from seemingly disparate, yet equally valid approaches, rather than using one to "validate" the other. Given the natural science legacy of urban ecology, it is also important to resist the tendency to simplify qualitative data into quantifiable concepts, which risks obscuring nuances needed to approach the problem of mosquito borne-disease equitably (Hicks et al. 2016).

The study of mosquito-borne diseases is particularly plagued by a lack of interdisciplinary and integrative research, limiting the types of research questions we can ask and therefore potential policy solutions. A review found that only 3% of the research on dengue and chikungunya, two *Aedes*-borne viruses, involves a social science approach (Reidpath, Allotey, and Pokhrel 2011) and the field rarely engages with critical social theory and prioritizes quantifiable metrics over qualitative analyses (Allotey, Reidpath, and Pokhrel 2010; King 2010). This is not meant to be a critique of one group or discipline, but recognition of an opportunity for the inclusion of a wider variety of disciplines in the study of mosquitoborne disease. The biophysical process of urbanization occurs within the socio-political context of the landscape, and resulting patterns in environmental amenities are structured by existing political processes and hierarchies of power (Swyngedouw and Heynen 2003; Heynen, Kaika, and Swyngedouw 2006). A critical social theory approach, which explicitly considers power dynamics, can help identify how spatial patterns in mosquito-borne disease risk are (re)produced by existing power inequalities. Integrative research is rarer still, but it is this type of work that is needed to question the dominant narratives regarding mosquito-borne diseases in cities, such as dengue as a disease of poverty (Mulligan et al. 2015), and create opportunities for novel policies and interventions (Bardosh 2014; Leach and Scoones 2013).

Our study demonstrates how an integrative approach expands on a purely ecological approach in the context of urbanization and mosquito-borne disease in a peri-urban area in southeast Bengaluru, Karnataka, India. This region has a recent history of rapid development and is the site of the city's outward-facing development into the previously rural periphery (Verma, Chatterjee, and Mandal 2017). In addition, Bengaluru has recently experienced outbreaks of dengue, an *Aedes*-borne virus associated with rapid urbanization (Balakrishnan et al. 2015). We demonstrate how the application of integrative research methods to urban ecological systems can be used to better understand people's everyday experience² with mosquitoes within the broader context of urbanization. Specifically, through this study, we address the following questions:

- How does the mosquito community's composition and abundance shift across an urban gradient?
- What are the consequences of these changes for human-mosquito interactions?
- What additional insights can be revealed through an integrative approach that may be missed by a single discipline?

The first question is based primarily in an ecological approach, focusing on metrics of community diversity and abundance. The second question attempts to understand what these findings mean in the context of people's interactions with mosquitoes by interpreting the results in the context of qualitative description of human-mosquito interactions. Finally, the third question reflects on what is learned by placing the results of the first two questions in the context of each other to better understand the partialness of each approach.

Methods

Integrative Framework

We base our work primarily in the principles of integrative research put forth by Hirsch and Brosius (2013), but which are shared with other formulations of integrative research (e.g. O'Rourke et al. 2019; Miller et al. 2008. We embrace epistemological pluralism (e.g. multiple

²In this study, the term "experience" includes not just people's perception of exposure to mosquitoes, but also people's experience of the interaction itself, including how and why they interact with mosquitoes and feelings of control surrounding these interactions. Following the narrative analysis approach, these descriptions are not meant to represent "facts" but rather to learn how people explain and organize their experiences.

ways of knowing and evaluating the validity of knowledge claims) through the incorporation of quantitative and qualitative data and methodologies into our examination of patterns in mosquito populations and mosquito-human interactions. Viewed through an ecological or entomological perspective, the relevant patterns are those in mosquito community diversity and abundance as they shift across an urban gradient. However, mosquito-borne disease transmission occurs at the intersection of mosquito vectors and human hosts, and so we also examine patterns in individuals' experiences with mosquitoes, questioning where, how, and why they may encounter high mosquito burdens. The construction of nature in cities (e.g. the transformation of environmental resources into amenities) is a direct consequence of existing socio-political processes and hierarchies of power, which often reproduce social inequalities in the resulting patterns in environmental amenities across a city (Robbins 2004; Lawhon, Ernstson, and Silver 2014; Gandy 2014). By focusing on power inequalities in our analysis, we aim to identify not just the patterns in mosquito populations, but the socio-political context that shapes these patterns.

In addition to an integrative approach, we ground this study in the work of feminist scholars and geographers, who recognize the power dynamics inherent to the production of knowledge and offer alternatives to conventional scientific methods through hybrid and critical approaches to the natural sciences (Kwan 2004; Harvey, Kwan, and Pavlovskaya 2005; Lave 2015). In practice, this meant that we did not to use quantitative data to validate qualitative results and did not view our own knowledge of the system as academic "experts" over that of the community members. This was especially important given the power inequality between researcher and researched and the colonial history of discounting local knowledge in the field of tropical medicine. We also embrace the concept of "staying with the trouble" (Haraway 2018) by deliberately pausing to consider tensions and incommensurabilities between perspectives in hopes of discovering new avenues of thought. Our methods include traditional ecological field methods of sampling mosquito communities and calculating metrics of abundance and species diversity. However, we also attempt to place these metrics into the surrounding socio-political context through the simultaneous and interdependent consideration of qualitative data, including interviews and sketch maps. Through this mixed-methods approach, we investigate how the mosquito-human interactions change across an urban gradient as a consequence of changes to ecological and social environments. The following methods section is purposefully written in a narrative way, intertwining the entomological and social methods used, rather than presenting them as separate methods in an effort to avoid presenting this work as a "view from nowhere" that implies our own neutrality in the process (Haraway 1988). This is especially important given the mixed-methods approach used here because community members' interactions with us as researchers of mosquitoes influenced our discussions with them during formal interviews. It also makes it easier to recognize our own positionality in the production of this study, particularly our positions as outsiders to the residents of Sarjapur, and recognize our knowledge as situated and partial (Haraway 1988).

Study Area and Site Selection

Sarjapur is a peri-urban town located on the southeastern periphery of Bengaluru, Karnataka, India. Although historically an agricultural area, Sarjapur is currently (as of Sept. 2020) the site of two planned Special Economic Zones, several hundred acre campuses of two of the largest information technology (IT) companies in the country. Currently under construction, these two developments are projected to employ over 34,000 people (Jyothi 2012), and have already spurred the development of new residential complexes in the area. Large tracts of land in the otherwise rural periphery of Sarjapur are being developed by housing developers to provide single-family homes in gated communities to the IT professionals immigrating to Sarjapur. These communities are planned and the public infrastructure (e.g. roads, pipes, vegetation) is managed by the housing developer. In the town of Sarjapur itself, high-density housing exists in the form of "sheet houses" (one-story homes with corrugated tin roofs) on the outskirts and multi-story apartment buildings in town (Fig. 5.1). It is in the context of this large-scale development that this study took place.

Within this region, we used a randomized site selection stratified across four land classes to select sixteen sites. Land classes were chosen to represent four characteristic land types of the region based on their percent of impervious surface and housing type, a qualitative measure of urbanization and an indicator of socio-economic status (Nagendra, Unnikrishnan, and Sen 2013). Impervious surface was measured via an unsupervised land class classification of Sentinel 2 data from January - March 2019 (described in detail in the Appendix 6.1) and approximated the amount of impervious surface in a 100m radius surrounding each site. This resulted in the following land classes: rural (low impervious surface, no housing), village (moderate impervious surface, traditional housing), town (high impervious surface, traditional housing), and colony (moderate impervious surface, Western-style housing) (Fig. 5.1). We divided Sarjapur into four blocks, corresponding to the East-West and North-South layout of the primary road system and associated development, and selected sites so that each block contained one site of each land class. Sites were at least 250 m from all other sites and over 1 km from sites of the same land class, except for town sites, which were clustered around the more highly developed center.

Data Collection

Two researchers, MVE and SB, visited each site at least weekly from August to December 2019 to collect entomological samples and conduct interviews. We visited each neighborhood regularly, and took part in many formal and informal conversations throughout these four months. This allowed us to establish a presence at the site, rather than a one-time extractive sampling regime reminiscent of "parachute research", when researchers "parachute in" to collect samples without meaningfully interacting with local community members or researchers (Lancet Global Health 2018). This familiarity with residents created a rapport that helped to recruit interview participants and conduct in-depth interviews. Weekly visits allowed us to directly observe changes to the landscape and mosquito community described in the interviews at a fine temporal scale. We conducted entomological sampling via CDC light traps and oviposition traps at the center of each site, with the permission from the resident or owner of that site. This person then served as our primary contact in the community for the interview portion of our study. As local experts, these community members also identified specific areas for trapping that were protected from disturbance and which they believed would successfully trap mosquitoes. Traps were placed in these identified areas, geolocated with a GPS device and were used as the center of each 100m site for subsequent analyses.

Oviposition traps consisted of a 1L plastic container filled with 750 mL nutrient-infused water. Nutrient infused water was prepared by mixing 20L water with 50g of ground cat food and allowing the mixture to sit for three days at room temperature. The oviposition container had two holes 1 cm from the top to allow for water to overflow and we suspended a plastic cover 10cm above the container to prevent rain and debris from entering the container. We installed two oviposition traps at approximately 1.5m height to protect from livestock and 5m apart at each site from August 26-28 2019, and then sampled weekly for larvae until November 11 2019, a total of 176 samples across the 16 sites. To sample, we filtered the container and we refilled the container with infused water to replace any water lost due to drying. While sampling, we often took the opportunity to discuss the mosquitoes found in that week's collection with residents and describe the different life-stages of mosquitoes using collected

samples in a clear container as an example. This provided context for our interviews with community members about mosquito habitat and its relation to water. As one community member mentioned, "I had heard of [mosquito larvae in water], but I had not seen it with my own eyes. But you both proved to us that mosquitoes can emerge from water." All larvae and pupae were brought to the lab at Azim Premji University, where they were reared to adults, frozen at -40C, and identified to species following (Das, Rajagopal, and Akiyama 1990; Christophers 1933; Tyagi, Munirathinam, and Venkatesh 2014). Weekly abundances were averaged across the two oviposition traps. In instances where one trap failed during a week (e.g. tipped over, knocked down, broken; 12/176 samples), we only included the working trap.

We also sampled monthly for adult mosquitoes using CDC light traps (John Hock Company and Arcturus Labs). We conducted this sampling once a month from September - November, trapping each site three times for a total of 48 trap nights. Traps were hung between 1.5 - 2 m from the ground in a covered area, to protect from rainfall. Lights were removed from the trap and traps were baited with approximately 1 kg of dry ice in an insulated plastic container hung directly next to the trap. Traps were placed in the morning and collected 24 hours later. Adult mosquitoes were frozen at -40C and identified to species following (Das, Rajagopal, and Akiyama 1990; Christophers 1933; Tyagi, Munirathinam, and Venkatesh 2014). As with oviposition sampling, we often shared the adult catches with residents to spark discussion of mosquito burdens. At the end of the sampling period, these results were shared with community members through the distribution of a multilingual brochure as a form of strategic communication.

Throughout the entomological sampling period, we also undertook semi-structured interviews with community members at each site, except for the rural sites which did not have houses nearby. Interviews focused on household water access and individuals' interactions with mosquitoes. The full methods for this are described in Chapter 5. Briefly, we recruited 21 community members through a combination of spatial stratification across housing types, opportunistic sampling, and snowball sampling (Stratford and Bradshaw 2016). Interviewees were adults over the age of eighteen who managed their household's water in some capacity. Verbal consent was obtained prior to each interview and each interview was audio recorded, translated from Kannada or Hindi, when necessary, and transcribed. Interviews consisted of a semi-structured interview and sketch mapping exercise, and generally lasted 45 minutes. The interview focused on one's experience with water access and perceptions of mosquito risk in relation to water and the environment. We asked participants to identify areas with high mosquito burden on satellite map imagery, referred to as sketch maps, and discuss the environmental causes of spatial patterns of mosquitoes. In some instances, community members accompanied us to these identified areas to discuss them in more detail.

Data Analysis

We conducted analyses of the entomological data, interview transcripts, and georeferenced sketch maps simultaneously, allowing for the synthesis of observations across these different forms of knowledge. In practice, this meant pairing results from analyses of the entomological data to the transcribed interviews and sketch maps. By interpreting these results together, we noted where they did and did not agree and why. We investigated the effect of land class and impervious surface on adult mosquito diversity, adult mosquito abundance, and oviposition trap abundances using regression in a Bayesian framework that accommodated random effects and non-normal distributions (McNeish 2016). We coded interview transcripts in Atlas.ti using a narrative approach to thematic analysis, which "treats interview data as accessing various stories or narratives through which people describe their worlds" (Silverman 2003). Our coding process paid particular attention to community members' interactions with mosquitoes and their agency and control over these interactions. Sketch maps were manually georeferenced and were analyzed alongside the interviews and entomological data using a process of grounded visualization (Knigge and Cope 2006). Results from the analysis of the entomological data and thematic analysis were interpreted in the context of finer scale spatial patterns denoted on the sketch maps and their placement in the larger spatial data depicting urbanization (e.g. maps of impervious surface and satellite imagery). Briefly, we iteratively visualized sketch maps and maps of impervious surface that were linked to interview transcriptions and entomological data. If, for example, a particular area of a site was mentioned in an interview as having a characteristic that is predictive of mosquito burdens, we could connect that to the map of the site and that area's location relative to the pattern of impervious surface at the site.

We calculated asymptotic estimates of Hill numbers from the adult mosquitoes sampled with CDC light traps for each site, aggregating across all three sampling months. Hill numbers are a set of diversity metrics that incorporate the number of species and their relative frequencies in a sample to estimate species diversity in units of "the equivalent number of equally abundant species that would be needed to give the same value of the diversity measured" (Gotelli and Chao 2013). Hill numbers are defined following Eq. 5.1:

$${}^{q}\mathbf{D} = \left(\sum_{i=1}^{S} p_{i}^{q}\right)^{1/(1-q)}$$
(5.1)

Where each species i in the total number of species S has relative abundance p_i and the parameter q, referred to as the order, controls the sensitivity of the measure to the community's evenness. For example, when q=0, ⁰D is equivalent to species richness, and the relative weight given to common species increases with increasing orders. For this study we calculated ⁰D, ¹D, and ²D, corresponding to species richness, the exponential form of Shannon entropy, and the inverse of the Simpson concentration (Chao, Chiu, and Jost 2014). Because the

number of individuals differed greatly across sites, we used the asymptotic estimate of Hill numbers to compare these diversity metrics across these sites by extrapolating each metric to a theoretically infinite sample size following Chao et al. (2014) using the iNEXT package (Hsieh, Ma, and Chao 2016) in R v. 3.6.3 (Team 2018). We tested for an effect of land class and impervious surface on these metrics using generalized linear models, with the response variable translated by subtracting 0.999 to better approximate a gamma distribution.

We used repeated-measures generalized linear mixed models to test for the effect of land class and impervious surface on adult mosquito abundance from the CDC light traps and abundance of *Aedes* mosquitoes from the oviposition traps. The abundance of the CDC light traps was the abundance of all mosquitoes caught in the trap for each site x month combination. The abundance measure from the oviposition traps represented the mean across the two traps at each site for each weekly sample, rounding up to the nearest integer.

All statistical models were implemented in Stan via the **brms** package (Bürkner 2017) in R v. 3.6.3 (Team 2018). We tested for potential spatial autocorrelation in our response variables using the Mantel test and found no evidence of spatial autocorrelation. We inspected the trace plots and effective sample size and performed posterior predictive checks of each model to ensure convergence. Model formulas, priors, and sampling settings are noted in Appendix 6.2. Model inference was implemented by calculating the Bayes factor (BF) for a full model compared to a null model. BFs are the ratio of the likelihood of the data given the null hypothesis to the likelihood of the data given the alternative hypothesis, in this case a hypothesized relationship between a covariate (e.g. land class or impervious surface) and the response variable (Makowski et al. 2019). This metric indicates the relative evidence for one model over another, given the data, with values above 1 corresponding to more evidence for the alternative hypothesis (e.g BF = 2 indicates the data are twice as likely to occur under the alternative hypothesis than the null hypothesis). We follow the language suggested by Jarosz and Wiley (2014) in our reporting of BFs, and purposefully choose not to provide thresholds or benchmarks for BFs in an effort to reject the arbitrary categorization of statistical measures (Wasserstein, Schirm, and Lazar 2019).

Results

Mosquito Diversity

In the words of one community member, "Mosquitoes, they're everywhere. There's nothing to avoid them." Sampling via CDC light traps caught 7,345 adult mosquitoes across 47 trap nights, consisting of 19 mosquito species (Table 5.1). The majority (95.8%) of mosquitoes were *Culex quinquefasciatus*, and three sites (one village, one town, and one rural site) only had *Cx. quinquefasciatus* in their traps. Rural sites tended to have a higher species richness than sites in other land classes, however the 95% CI overlapped for all land classes and there was little evidence in favor of an effect of land class (BF = 0.432, Fig. 5.2). Although all sites had high unevenness due to the dominance of *Cx. quinquefasciatus*, there was strong evidence for an effect of land class on higher order Hill Numbers (¹D BF = 15.71; ²D BF = 48.22; Fig. 5.2), with higher diversity at rural sites than other land classes. However, there was weak evidence for a relationship between impervious surface and all order of Hill numbers at the site level (⁰D BF = 1.12; ¹D BF = 2.27; ²D BF = 2.73; Fig. 5.2).

Community members' experiences of mosquito diversity tended to focus on *Aedes* mosquitoes, which are easily distinguished by their black and white markings and have been the focus of public education campaigns given their role in dengue and chikungunya transmission. However, people also distinguished between mosquito species based on their activity times, noting the difference between diurnal and crepuscular mosquitoes and how this influenced their interactions with mosquitoes. One community member described the timing of her interactions with mosquitoes, demonstrating in-depth knowledge of mosquito behaviors:

"The white-striped ones would be biting us around now [late afternoon]. It almost stops by the time the sun is down. The black ones bite in the night."

Some residents mentioned their habit of closing the doors and windows to their home in the early evening to keep mosquitoes from entering. Cx. quinquefasciatus is a crepuscular and nocturnal biter, and residents' descriptions of their interactions with mosquitoes align with the strong dominance of Cx. quinquefasciatus found in the entomological surveys. For people living with mosquitoes, diversity matters because it informs the measures that people can take to avoid mosquitoes. Given that all sites were so highly dominated by the "domesticated" Cx. quinquefasciatus, however, there was little perception of the difference in mosquito diversity as revealed by conventional ecological metrics.

Mosquito Abundance

We found no evidence for a difference in overall adult abundance or *Aedes* mosquito abundance, as measured by oviposition traps, across the urban gradient in Sarjapur. We found no evidence for differences in adult mosquito abundance across land class (BF = 0.434, Fig. 5.3) or impervious surface (BF = 0.954, Fig. 5.3). Three *Aedes* species were present in our sites, *Aedes aegypti* (54.1%), *Aedes albopictus* (43.1%) and *Aedes vittatus* (2.73%). We also caught one *Anopheles stephensi* individual in the oviposition traps. We found little evidence for an effect of land class (BF = 0.647, Fig. 5.4) or impervious surface (BF = 1.202, Fig. 5.4) on *Aedes* abundance in oviposition traps.

However, peoples' experiences with mosquitoes differed greatly across neighborhoods and did not always follow the differences in abundances that we saw from entomological sampling. One colony site had a relatively high abundance of mosquitoes compared to other sites, but the residents of this neighborhood did not express concern about the mosquito situation given their ability to request fogging by the development manager (Fig. 5.3). In contrast, a site in town had much lower abundances, but residents could not avoid areas with high mosquitoes, given the close proximity to their houses (Fig. 5.3).

In the sketch mapping exercise, community members identified areas with high mosquito burdens and described their interactions with mosquitoes in those areas. These areas included places with drainage (11/21), solid waste (13/21), or unmanaged vegetation (9/21). The size of these areas ranged from 1 - 4000 m^2 , but the median size was 72.3 m^2 . Many of these areas were close to community members' homes and unavoidable because residents conducted everyday tasks in these outdoor spaces. One woman identified a patch of vegetation next to her home with a high burden of mosquitoes that she could not avoid:

"Yes, I can't help it, I have to do my chores there. Yes, there are a lot of mosquitoes there. I have to wash the dishes there, clean my clothes also."

Further, some community members lived adjacent to open drains or waste disposal areas. One community member was dismayed by the proximity of his house to the sewage infrastructure because "the entire village's filth comes in front of [his] house". These narratives demonstrate that individuals differed in their ability to mitigate exposure to mosquitoes by changing their behavior or reducing mosquito abundances in public spaces through vector control.

However, these fine-scale differences were missed by our chosen metric of urbanization, percent of impervious surface. When we used grounded visualization to consider the sketch maps in the context of remotely sensed impervious surface data and satellite imagery, we found that the areas identified by residents as having high mosquito burdens were areas of lower impervious surface than the surrounding landscape in 7 out of 11 sites where residents marked mosquito habitat. This was particularly true for villages, where over 60% of identified areas had lower impervious surface than the surrounding landscape and tended to represent patches of vegetation within a matrix of built-up residential land.

Discussion

Changes to mosquito community composition and abundances across an urban gradient is one component of intra-urban heterogeneity in mosquito-borne disease burdens. However, it is also important to understand if these changes to the mosquito community translate to changes in peoples' experiences with mosquitoes, including both their perception of exposure and their stories of these encounters. Here, we use an integrative approach to address these questions in parallel, using a mixed methods methodology that includes both quantitative and qualitative analyses. We found that mosquito communities were more diverse in less urbanized, rural areas, but that the dominance of all communities by Cx. quinquefasciatus meant that there was little perception of this difference by the population. In contrast, we found no difference in mosquito abundance across an urban gradient, but qualitative analysis did reveal that peoples' experiences with mosquitoes was mediated by how they interacted with public spaces.

We found a difference in mosquito diversity across land classes, however this difference did not translate into differences in individuals' experiences with mosquitoes. The mosquito community in Sarjapur was more diverse in rural land classes than village, town, or colony land classes, which contained a nested subset of the full community. This homogenization of the mosquito community has been seen across other urbanization or development gradients (Câmara et al. 2020; Loaiza et al. 2017; Townroe and Callaghan 2014), and is hypothesized to be due to changes in host composition (Goodman et al. 2018), microclimate (Townroe and Callaghan 2014), and larval habitat types (Wilke et al. 2019). However, even rural areas
had high abundances of *Cx. quinquefasciatus*, which dominated the community at all land classes, and we found no evidence for a difference in total mosquito abundance across land class. Accordingly, community members perceived little difference in mosquito abundance across Sarjapur. Other studies of *Culex* species across urban gradients have found that the abundance of *Culex* species decreases with increasing urbanization (Rochlin et al. 2016; Field, Tokarz, and Smith 2019), however these effects may depend on the larger regional context (Bowden, Magori, and Drake 2011). Sarjapur is peri-urban, retaining characteristics of both agricultural and urbanized land classes, which may allow for similar abundances of *Culex* mosquitoes across the city.

In this study, mosquito abundance was similar across sites, but peoples' experiences of mosquito burdens differed across sites, primarily due to individuals' relationships with outdoor spaces. One difference was in an individual's ability to shift their behavior to avoid interacting with mosquitoes. For upper-class households living in colonies, outdoor space was primarily used for leisure or exercise, and individuals were able to change their schedule or avoid these areas when necessary. Other households, especially those without indoor plumbing, used outdoor space for everyday domestic tasks, and their ability to shift this schedule or access another public space for this purpose was limited. These examples illustrate how individuals' vulnerabilities differ in public spaces, drawing attention to the intersection between characteristics of the physical space and an individual's ability to avoid or mitigate hazards of that space, such as exposure to mosquito-borne disease (Watts and Bohle 1993). Viewing disease exposure within the context of vulnerability has proven a useful approach for placing spatial patterns in infectious diseases within their social, political, and economic contexts (McLafferty 2010). Similarly, we found that individuals' power to control a public space, via fogging or avoiding the space, helped reduce feelings of vulnerability to mosquito-borne disease exposure. Our findings regarding the everyday differences in exposure and vulnerability to mosquitoes suggest that vulnerability may be a useful lens through which to consider inequalities in mosquito-borne disease burdens as well (Chang et al. 2014).

One tension that arose through this study was the mismatch of spatial scale. Our study design focused on intra-urban heterogeneity at the scale of city, defining each site as an area of 100m radius. However, the sketch mapping exercise revealed that people conceptualized their experience with mosquitoes on a much finer spatial scale. Between-household variation in exposure to mosquito bites can be on a magnitude of 100x difference (Guelbéogo et al. 2018). and our findings suggest that high levels of spatial variation may characterize outdoor spaces as well. Further, it has been shown that landscape heterogeneity is predictive of mosquito diversity, in addition to the dominant land class (Chaves et al. 2011). Individuals also identified patches of vegetation within a matrix of higher impervious surface, which can act as refugia for mosquitoes (Hendy et al. 2020). Top-down vector-control campaigns necessarily conceptualize patterns in mosquito burdens at coarser-levels than community members are able to, given community members' in-depth local knowledge of the environment (Dickin, Wallace, and J. Elliott 2014; Nading 2014). Our discussions with community members illustrated their knowledge of mosquito dynamics in their own neighborhoods, a type of place-based knowledge that typifies a "bionomic" approach to vector control that relies on ecological relationships to identify the most productive larval habitats (Kelly and Lezaun 2013). As has been suggested elsewhere (Bempah et al. 2020; Dongus et al. 2007; Biehler et al. 2019), inclusion of local knowledge via participatory mapping and visualization activities is a promising opportunity for an alternative approach to vector control that includes place-based ecological knowledge.

Using an integrative approach allowed us to gain insight into differences that were not revealed by our entomological surveys. It shifted our conceptualization of risk from a quantity (e.g. the abundance of mosquitoes or the basic reproductive number) to one that incorporated peoples' lived experience with mosquitoes, highlighting a difference that was otherwise missed by our entomological analysis. The simultaneous collection of entomological and qualitative data also created opportunities for exploring the environment and everyday spaces with community members as they helped identify locations for sampling. Although these interactions occurred outside of the formal interview, we believe they enhanced our discussions with community members about the relationship between the environment and mosquitoes by providing tangible examples of these relationships, similar to other place-based interviewing methods (Holton and Riley 2014). However, an integrative approach does have additional costs associated with it, particularly in the time and expertise needed to enact multiple methodologies. While this does not require that an integrative approach must necessarily sacrifice depth for its epistemological breadth, it does suggest that providing structural and institutional support for facilitating research across disciplines, such as through collaborative, team-based science (Leahey 2016), could reduce these costs and encourage more integrative research.

We found that mosquito community diversity was higher in rural land classes than the other three land classes, but did not find evidence for a difference in mosquito abundance across the urban gradient of Sarjapur. However, semi-structured interviews revealed a difference in how individuals experienced mosquito burdens, particularly in their vulnerability to exposure. Individuals who used outdoor space for leisure activities were able to avoid areas during peak mosquito timings. Those who relied on outdoor space for domestic tasks had less flexibility and often could not avoid mosquitoes, placing themselves at higher exposure to bites. Using an integrative approach shed light on the relationship between ecological indices of diversity and abundance and peoples' everyday experience with mosquitoes, something that would not have been possible had we relied on a single discipline. We are not suggesting that all ecological studies should be integrative, but, rather, integrative research be considered for research of infectious diseases, especially in urban settings.

Tables

Species	Number	Percentage
Culex quinquefasciatus	7034	95.77
Culex gelidus	60	0.82
Aedes indicus	56	0.76
Aedes vittatus	50	0.68
Armigeres subalbatus	37	0.5
Culex vishnui	21	0.29
Culex tritaeniorhynchus	15	0.2
Aedes albopictus	14	0.19
Aedes aegypti	10	0.14
$Culex\ psuedovishnui$	10	0.14
Culex sitiens	10	0.14
$Culex\ bitaeniorhynchus$	9	0.12
Anopheles stephensi	7	0.1
Aedes spp. B	4	0.05
Anopheles subpictus	4	0.05
Aedes spp. A	1	0.01
Aedes thomsoni	1	0.01
$Culex\ mimeticus$	1	0.01
Mansonia uniformis	1	0.01

Table 5.1: List and count of species caught in CDC light traps over three month sampling period.

Figures



Figure 5.1: A) Map of sites in Sarjapur, Karnataka, India. Symbols represent land classes (square: rural, triangle: village, circle: colony, and diamond: town). Color shading represents the percent of impervious surface within each 30m pixel, as illustrated on the color bar on the bottom. B) A plot of each site's proportion of impervious surface in the surrounding 100m radius.



Figure 5.2: Top row: Effect of land class on asymptotic Hill numbers ⁰D, ¹D, and ²D. Gray bar represents the 95% credible interval (CI) and red triangle represents the median. Raw data are plotted in black circles. Bottom row: Effect of impervious surface on asymptotic hill numbers ⁰D, ¹D, and ²D. Line represents the median effect and shaded ribbon represents the 95% CI. Raw data are plotted in black circles.



Figure 5.3: A) Effect of land class on adult abundance in CDC light traps. Gray bar represents the 95% credible interval (CI) and red triangle represents the median. Raw data are plotted in black circles. B) Effect of impervious surface on adult abundance in CDC light traps. Line represents the median effect and shaded ribbon represents the 95% CI. Raw data are plotted in black circles. In both plots, points labeled with letters correspond to quotes from community members on the right hand side of the plot.



Figure 5.4: A) Effect of land class on abundance in oviposition traps. Gray bar represents the 95% credible interval (CI) and red triangle represents the median. Raw data are plotted in black circles. B) Effect of impervious surface on abundance in oviposition traps. Line represents the median effect and shaded ribbon the 95% CI. Raw data are plotted in black circles.

Appendices

Appendix 5.1 - Unsupervised classification of land classes

Impervious surface maps were created via unsupervised classification of Sentinel-2 satellite imagery in Google Earth Engine. Sentinel-2 imagery is collected globally on a 10-day frequency. We chose imagery between January - March 2019, when there is less cloud-cover, and filtered to only include individual images with less than 20% cloud cover. Because we wanted fine resolution imagery, we chose to include bands at the 10m resolution (red, blue, green, NIR). Each image was then classified into 15 land classes using the K-means Weka clustering algorithm (Frank et al. 2004). Resulting land classes were manually classified into impervious surface vs. not for each 10m x 10m pixel for each image collection date. Images were then averaged over the entire collection period, resulting in a 10m x 10m resolution image representing the uncertainty in classification. A pixel that was classified as impervious surface in at least half of the images was considered impervious surface with adequate certainty. This finalized image was then aggregated to the 30 x 30m resolution, resulting in a proportion of impervious surface in each 30m x 30m pixel.

Appendix 5.2 - Bayesian Model Specifications and Priors

Hill numbers

The regressions for estimating the effects of land class or impervious surface on asymptotic estimates of ⁰D used the following model formula and priors:

$$y \sim Gamma(\mu_i, shape)$$

 $log(\mu_i) = intercept + \beta_i * x$
 $intercept \sim Normal(0, 10)$

$$beta \sim Normal(0, 2)$$

 $shape \sim Gamma(0.01, 0.01)$

The regressions for estimating the effects of land class or impervious surface of asymptotic estimates of ^{1}D and ^{2}D used the same model formula but different priors, as the range of response variable was much smaller:

$$y \sim Gamma(\mu_i, shape)$$
$$log(\mu_i) = intercept + \beta_i * x$$
$$intercept \sim Normal(0, 2)$$
$$beta \sim Normal(0, 2)$$
$$shape \sim Gamma(0.01, 0.01)$$

All models were run on three chains, each with 500 iterations following a burn-in of 500 iterations, for a total of 1500 samples.

CDC Abundance

The two models of CDC abundance used the following model specification and priors:

$$y \sim NegBinom(\mu_i, shape)$$
$$log(\mu_i) = intercept_{[site]} + \beta_i * x$$
$$intercept_{[site]} \sim Normal(0, 10) + sigma_{[site]}$$
$$sigma_{[site]} \sim Student'st(3, 0, 10)$$
$$\beta_i \sim Normal(0, 1)$$
$$shape \sim Gamma(0.01, 0.01)$$

Where x was either the categorical variable of land class or the proportion of impervious surface at that site and y was the total abundance of mosquitoes for each sampling month. All models were run on three chains, each with 1000 iterations, following a burn-in of 1000 iterations, for a total of 3000 samples.

Oviposition Abundance

The two models of oviposition abundance used the following model specification and priors:

$$y \sim NegBinom(\mu_i, shape)$$
$$log(\mu_i) = intercept[site] + \beta_i * x$$
$$intercept_{[site]} \sim Normal(0, 10) + sigma_{[site]}$$
$$sigma_{[site]} \sim Student'st(3, 0, 10)$$
$$\beta_i \sim Normal(0, 1)$$
$$shape \sim Gamma(0.01, 0.01)$$

Where x was either the categorical variable of land class or the proportion of impervious surface at that site and y was the average abundance of mosquitoes per oviposition trap rounded to the nearest integer for each sampling week. All models were run on three chains, each with 1000 iterations, following a burn-in of 1000 iterations, for a total of 3000 samples.

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Conclusion

Summary of Findings

My main objective of this dissertation was to demonstrate how the entanglement of people, the environment, and mosquitoes in an urban landscape can contribute to spatial patterns in mosquito-borne diseases. The scope of this problem crosses multiple disciplines, methodologies, and ways of knowing, and I chose to address this through an integrative approach, recognizing that this is still partial and only incorporates a select few ways of approaching a "wicked problem". The dissertation chapters are presented in the near-chronological order of which they were conducted, moving from a purely positivist approach based in ecology to a mixedmethods approach that incorporates qualitative methods to a final experiment in integrative methods. The order of chapters is purposeful, as it parallels the development of my identity as a scientist and my conceptualization of research and knowledge during my doctoral work. The shift from an ecological approach to a feminist political ecology approach to an integrative approach represents the gradual disruption of disciplinary and mental boundaries within myself and my approach to disease ecology over the past several years. In this conclusion, I briefly review the objectives and findings of each chapter, attempt to put them in conversation with each other, and reflect on the process of integration.

In Chapter 2, I began to consider intra-urban heterogeneity by focusing on changes in microclimate and larval habitat at the scale of the 30 x 30 m pixel. This is a shift from prior ecology work, which often relied on climate data from weather stations or circulation models at a resolution of 5 km or coarser (e.g. Ogden et al. 2014; Kraemer et al. 2015) and therefore did not account for the high levels of ecological heterogeneity within a city. While I found that *Aedes albopictus* abundances differed across sites, this was only partly explained by the difference in the density of larval habitats and there was no evidence of a difference across rural, suburban, and urban land classes. The consideration of these two abiotic factors was not enough to explain site-level differences in mosquito abundance that were observed. However, I did find that microclimate variables explain adult abundance, providing support for the application of theoretically-derived, lab-parameterized thermal performance curves to the field.

I then investigated the effect of microclimate at the scale of the mosquito, estimating differences in mosquito life-history traits, particularly vector competence, across an urban gradient (Chapter 3). By zooming into the scale of the mosquito and including carry-over effects of the larval environment that traverse life stages, I purposefully countered the idea of a mosquito as a homogeneous vector of disease and attempted to include a more detailed consideration of the mosquito life cycle. Again, I found little evidence for differences in population dynamics across urban land classes. However, dengue-2 infections progressed differently in mosquitoes reared in urban areas than those in suburban or rural areas, with a smaller proportion of mosquitoes from urban areas becoming infected. This highlights the potential for transmission risk to shift across an urban landscape independently of mosquito

population dynamics because populations may have different susceptibilities based on the microclimate of their environment.

Chapter 3 revealed that the effects of urban microclimate on mosquito-borne disease can be indirect. I expanded on this in Chapter 4 by considering the interactive effects of temperature and competition on the co-existence of two urban mosquito species, *Aedes aegypti* and *Anopheles stephensi*. We found no evidence for temperature-dependent competition between *Ae. aegypti* and *An. stephensi* and *Ae. aegypti* emerged as the dominant competitor at all temperatures included in the study. This is the first study investigating competition between these two species and finds strong asymmetric competition between these species at the scale of the larval habitat. However, these species co-exist at the landscape scale and it is likely that processes at a coarser scale, such as dispersal, could allow for landscape-scale coexistence.

The first three chapters of my dissertation gradually incorporated additional complexity in their consideration of mosquito-borne disease in urban systems, examining processes across scales and in the context of other environmental factors. However, they did not include the social processes of this decidedly socio-ecological system. In Chapters 2 and 3, there were differences across sites that were not explained by our metric of urbanization, impervious surface. For example, land management practices varied widely, partly determined by individual aesthetic values of yards and whether the site was public or private property. Flower pots were common sites of mosquito habitat in our surveys (Chapter 2) and frequent irrigation can lead to high abundances of mosquitoes (Reisen et al. 1990), as was seen on one site that fell on university property. Site selection was stratified across impervious surface classifications, but not across relevant socio-economic variables (e.g. socio-economic level, parcel values, race). The density of larval habitat can change in relation to these variables (Becker, Leisnham, and LaDeau 2014; LaDeau et al. 2013) and our focus on primarily middle- and upper-class neighborhoods may have not incorporated adequate variation in larval habitat availability. In these chapters, we found no evidence for differences in *Ae. albopictus* abundances or growth rates across land class, but, by ignoring the spatial patterns in socio-demographic covariates, we may have missed other factors that contribute to spatial variation in mosquito dynamics in Athens, GA.

In these conventional ecological studies, we also did not attempt to identify the sociopolitical causes of differences in microclimate across Athens. For example, in the US, neighborhoods historically assigned a "D" on HOLC security ratings (e.g. "redlined") are presently 2.6 °C hotter on average than neighborhoods assigned an "A" (Hoffman, Shandas, and Pendleton 2020). The current distribution of impervious surface "hotspots" and associated extreme-heat areas in some cities is therefore a result of historical housing policies that disadvantaged Black households. Similarly, green space and tree cover, both of which can lower land surface temperatures, are often unequally distributed in cities, clustered in wealthier, Whiter neighborhoods (Heynen, Perkins, and Roy 2006). Following this reasoning, patterns in microclimate, and therefore mosquito dynamics, are closely tied to systemic social inequalities, such as the legacy of redlining and investment in public spaces. This was not something we addressed in our studies, but I believe presents a promising avenue as an example of spatial modeling of disease patterns that incorporates the social processes that created that landscape.

I began to include some of these social drivers of environmental inequalities in Chapters 5 and 6. I chose to ground these chapters in a political ecology approach because it is primarily concerned with the false binary often drawn between nature and society and has been widely applied to urban environments in a sub-field now known as urban political ecology Robbins 2004. Additionally, I continued to focus on a fine spatial-scale, as I did in Chapters 2 and 3 in the consideration of microclimate, by choosing to focus on everyday practice and household characteristics, rather than an analysis of socio-demographic variables at the level of the census or city. Feminist political ecology expands the lens of political ecology by "[providing] a more focused attention on construction of social difference and micropolitics within the scale and spaces of the everyday" (Truelove 2011). One of the goals of these chapters was to relate individuals' identities and "micropolitics" to patterns in mosquito-borne disease by applying a feminist political ecology approach to understand how social difference relates to landscape change relevant to mosquitoes and peoples' experiences with mosquitoes.

In Chapters 5 and 6, I investigated differences in mosquito population and community dynamics across an urban gradient, this time in Sarjapur, India. I again found no evidence for a difference in mosquito abundance across land classes. However, these studies also investigated differences in the social processes that create mosquito habitat and environmental conditions as well as differences in peoples' interactions with mosquitoes. I found there were differences in how households accessed water, but that these differences did not translate to differences in mosquito abundances via the hypothesized positive relationship between water storage and mosquito abundance. Rather, in exploring what mechanisms households used to access water, I found that a subset of the population relied on their economic capital and purchased private water or constructed underground sumps, while another subset of the population leveraged their position as citizens to claim a right to publicly-supplied water. While these mechanisms successfully resulted in water access, they were not successful in gaining access to a "mosquito-free" space, and mosquito abundance was similar across sites. However, Chapter 6 revealed that individuals' everyday experiences with mosquitoes did differ, and individuals with less control over their outdoor spaces were more vulnerable to mosquito exposure. These individuals were those without indoor plumbing or access to private vector control services, who were often left out of improvements to infrastructure that are associated with urbanization in Sarjapur. Although the measured abundance of mosquitoes in these neighborhoods was similar to others, community members' stories of experiencing mosquito burdens demonstrated their additional feelings of vulnerability.

I attempted to address the weaknesses I found in the first half of my dissertation in these final two chapters by including perspectives that I recognized had been missing. Chapter 5 attempted to place a potential cause of spatial patterns in mosquito population abundances, availability of larval habitat, into the socio-political context that could cause uneven patterns in larval habitat availability. Chapter 6 included an important actor in mosquito-borne disease that had been missing from my previous chapters: human hosts. As was expected, the inclusion of the human actor and the additional perspectives needed to address the sociopolitical processes revealed additional sites of difference and new potential causes of patterns in mosquito-borne disease. While two areas may have a similar degree of urbanization, how the population accesses urban infrastructure, such as piped water or sanitation services, is dependent on the population's ability to wield different mechanisms of access. For example, although households in private colonies and in the center of Sarjapur town both receive piped water to their homes, the ability to pay for piped water in private colonies provides access to more frequent, reliable water provision. Similarly, a more in-depth understanding of how people experience mosquitoes highlighted potential differences in exposure and vulnerability that a measure of mosquito abundance alone cannot address.

One common thread between all of the chapters is the issue of spatial scale. I began by arguing that the study of mosquito-borne diseases requires attention to processes that are happening at fine spatial scales of 30m or less. The results of this dissertation support this claim. We found the biotic and abiotic processes relevant to mosquito populations did vary at this spatial scale, and in some instances at even finer scales, with important consequences for how we conceptualize disease transmission across space. Similarly, access to public health amenities can have high variation between households within a neighborhood, particularly for cites undergoing rapid urbanization, such as those in tropical, low and middle income countries where mosquito-borne disease burdens are highest. This has important implications for how we approach spatial patterns in mosquito-borne disease in cities. Remotely-sensed environmental data, such as land surface temperature or land cover, is becoming widely available at fine-spatial scales with the launch of the Sentinel satellites that collect 10m imagery and relatively affordable private satellite imagery which is at a resolution of two to five meters and is available for the whole globe. In conjunction with socio-demographic and disease data, remotely-sensed data is already being used to predict disease risk at a much finer scale than was possible before. The use of this data has the potential to more accurately represent some of the fine-scale processes explored in this dissertation, particularly those related to microclimate, however it carries both metaphorical and physical characteristics of a "view from above". As this dissertation demonstrates, a place-based approach that incorporates local knowledge could be an appropriate complement to studies based in remote sensing. Integrative approaches that include both may be of most use to local vector control efforts because they are able to identify hotspots of mosquito-borne disease at multiple spatial scales.

Integrative Research: Challenges and Opportunities

In parallel to my formal graduate training and coursework, I have been fortunate to participate in multiple informal groups (often graduate-student led) that provided a place to discuss and explore the often hidden processes behind the production of science. Of particular interest to me is how the production of scientists influences the production of knowledge (Subramaniam 2014). I believe this interest is in line with the goal of the Integrative Conservation doctoral program's mission of creating "agile scientists" and found myself reflecting often on the acculturation aspect of my doctoral training (Reich and Reich 2006). While engaging with research and learning the methods outside of one's home discipline are certainly an important part of integrative training, there are also everyday practices of integrative research that seem less tangible, but nevertheless are necessary for a successful integrative approach. These are often referred to as "soft-skills" and allow one to develop the cultural competence needed to work across disciplinary cultures (Reich and Reich 2006).

One way to be attentive to the production of scientists and culturally competent in integrative research is through the practice of self-reflection, on one's privileged role as scientist, on one's preexisting assumptions and biases, and on one's disciplinary habits. This is similar to calls from feminist theory and feminist science and technology studies to question the "absence" of the scientist in our narratives of science and uses standpoint theory to not just recognize that all knowledge is partial, but understand in what ways it is partial and why (Haraway 1988). For me, the social relations in which I come to produce knowledge are based in my own scientific identity as a quantitative ecologist. My tendency is to value quantitative data over other forms of knowledge and I often found myself reducing qualitative data to quantitative summaries. Simplifying qualitative data to a quantitative summary is a useful technique for data reduction and clarifying patterns, but must not be done acontextually at the expense of the "thick description" provided by qualitative data (Sandelowski 2001). I am not rejecting quantitative measures, in fact all of my chapters rely on quantitative data to some respect, but by reflecting on my initial tendency to quantify and at times resisting it, I tried to ensure that the qualitative data continued to exist alongside the quantitative summary and avoid decontextualizing the numbers. An individual preference for disciplinary work is a noted barrier to interdisciplinary graduate work (Morse et al. 2007), and one that I struggled with. However, I found that locating myself as a scientist within the scientific process, and repeatedly reflecting on my own biases and assumptions was a useful bridge to interdisciplinary work.

My implementation of integrative research also stresses epistemological pluralism³, which has several challenges associated with it. Integrative research is often conducted as a team science with members from multiple disciplines (Wuchty, Jones, and Uzzi 2007). However, as a doctoral project, much of this work relied on epistemological pluralism at the individual level. This brought forth the challenge of engaging with and learning the concepts and vocabularies of each discipline, not to speak of combining them into one coherent dissertation. Creating a shared vocabulary is a common recommendation for interdisciplinary teams, but there are other disciplinary norms, particularly in the way we communicate and present our results, that can make communication across disciplinary boundaries difficult (Adams 2007; Reich and Reich 2006). For example, the format, style, and tone of manuscripts in a critical geography journal are not the same as those in an applied entomology journal, and communicating in a way that meets both audience's expectations can be a challenge. These tensions do present an opportunity for reflection on disciplinary norms, and provide some space for blurring the edges between disciplines as I attempt to do in Chapter 6, an example of integrative research manifest in the writing process. In this chapter, I combined qualitative and quantitative data in both the written and visualized results so that the reader could understand each in the context of the other. However, I acknowledge that this risks becoming a shallow "party trick", rather than a true hybridization of the data types if there is not true synthesis of the two data types in the analysis.

In spite of the challenges described above, I do still believe integrative research to be an appropriate approach for the study of mosquito-borne diseases, and infectious disease ecology in general. The skills gained from participating in integrative research continue to influence

³Epistemological pluralism is the practice of including multiple ways of knowing in scientific research, from the types of questions that are asked to the methodologies employed to the way results are communicated.

how I approach a new project or question, even if the project itself is not integrative. This is particularly true in my consideration of power dynamics in the production of knowledge: who is producing the knowledge and where are they positioned relative to the data and those who will be most impacted by the findings? Whether working *in silico*, *in vitro*, or *in vivo*, this remains a relevant question for scientists to pose about their own work to recognize the partialness of their own knowledge and methodologies. This question can also reveal how scientists can begin to collaborate with practitioners and others outside the academy. This is especially important for research in infectious disease ecology, where the inclusion of these stakeholders can lead to more actionable research.

Conclusions and Future Directions

Although the chapters of this dissertation span multiple field sites and species, there are some general conclusions that can be drawn. All chapters failed to find a difference in metrics of mosquito population growth and abundance across land classes, however I did find that microclimate, larval habitat density, and biotic interactions influenced mosquito abundances and growth rates and that these drivers are themselves heterogeneous across urban land classes. I also aimed to identify the socio-political drivers of the spatial patterns in some of these ecological characteristics, particularly larval habitat density. This did not result in identifying a clear potential causal pathway from social process to mosquito abundance. Rather, I found that the distribution of water access mechanisms and mosquito control were tied to a complex intersection of household identities that included economic and social positions. The explanations behind mosquito burdens rarely fell along a binary categorization of rich vs. poor, urban vs. rural, or private vs. public and were specific to the unique ecological and socio-political context of that city. This agrees with findings from studies of mosquitoes in urban areas (Nading 2011; Becker, Leisnham, and LaDeau 2014; Mulligan 2012) and adds to the call for more place-based infectious disease research that is attentive to the role of the local ecology and cultural context (Nash 2006).

This dissertation was integrative in that it bridged multiple disciplines and epistemologies, but did not bridge the academic-practitioner divide (Hirsch and Brosius 2013), particularly with regards to vector control agents and community health workers. While this dissertation discussed how global narratives are influencing local vector control and sanitation services with regards to public health, I did not explicitly study how local actors integrate scientific knowledge and narratives of international funding programs into their everyday practice. Understanding how vector control agencies use predictive maps of spatial mosquito burdens, or knowledge of what drives those burdens, could help scientists create maps that are more applicable to vector control agencies. Further, the role of a scientist should not end with the dissemination of research findings and collaborating with practitioners ensures that there is two-way communication between those producing and implementing knowledge. Indeed, true integrative work should blur the lines between production and application of knowledge by valuing and including knowledge that is produced outside of academic institutions. This is a thread that I hope to pursue in my future research as I continue to imagine alternatives to our current system of knowledge production and what benefits that entails for the study of infectious diseases.

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